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## Comparative Inflorescence Development of Two Cultivars of Forced Tuberous-rooted Dahlias<sup>1</sup>

J. E. Barrett<sup>2</sup> and A. A. De Hertogh<sup>3,4</sup>

Department of Horticulture, Michigan State University, East Lansing, MI 48824

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**Abstract.** Flower development of tuberous-rooted *Dahlia* 'Park Princess' and 'Miramar' was studied during 2 forcing seasons using scanning electron and light microscopy techniques. Each cultivar had a flat, rectangular (0.2 × 0.1 mm) vegetative meristem which domed and increased in diameter as the last leaf primordia developed. Subsequently, 8 outer involucre bract primordia were formed and the meristem became round with a diameter of approximately 0.35 mm. The first visible sign of floral initiation was the formation of inner involucre bract primordia. The floret primordium developed after the subtending bract primordium. The first unpinched plants of 'Park Princess' were reproductive 20 days after planting and 100% were reproductive after 30 days. 'Miramar' was reproductive 10 days later with a corresponding delay in anthesis. Unpinched 'Park Princess' and 'Miramar' were reproductive when the 4th and 6th leaf pairs had separated, respectively. When pinched, over 80% of the lateral branches of 'Park Princess' and 'Miramar' were reproductive after 12 days.

In past studies on the forcing of tuberous-rooted dahlias, considerable variation in the time to flower was observed both within and among cultivars (1, 2, 8). In order to determine the cause of this variation, the developmental sequence of the flowering process must be known. Krijthe (14) with line drawings followed flower initiation in 'L' Innocence' which occurred in the field when 7 pairs of foliage leaves had formed. This was 2-2.5 weeks after planting. With an early March planting date in a 15°-16°C greenhouse, initiation occurred after 5 leaf pairs had formed. In both studies flowering began 10 weeks after planting. Later, Konishi and Inaba (13) described and illustrated 7 stages in flowering development during a study on the effects of photoperiod on flower initiation and development. Philipson (18) detailed the development of individual bracts and floret primordia with medium longitudinal section photomicrographs of *D. gracilis* meristems.

There has been some confusion over the correct scientific name for cultivated dahlias. Many American authors have designated them as *D. pinnata* (5, 7, 12, 19), while others have used *D. variabilis* (3, 4, 6, 10, 17). *D. variabilis* is an incorrect designation, because it is a synonym for *D. pinnata* (21, 22). We

observed differences in the leaf morphology and the flower colors between cultivated dahlias and herbarium specimens of the wild species *D. pinnata*. Giannasi (11) and Sorensen (22) studied the morphological and genetic differences between the two and concluded that the cultivated dahlia should not be classed as *D. pinnata*. Modern dahlia cultivars have evolved from repeated crosses between wild species and cultivated forms (11, 15, 22). We agree with Sorensen (22) that it is best to utilize cultivar names for all dahlias that are not clearly selections from a wild species.

This study was undertaken to follow the process of flower initiation and development in the dahlia with the use of the scanning electron microscope (SEM) and to compare the development of 2 cultivars which reach anthesis at different times when forced as pot plants (1).

### Materials and Methods

**Cultural procedures.** In all experiments, 'Park Princess' and 'Miramar' were No. 2 size tuberous root clumps produced in The Netherlands. Clumps were shipped on Dec. 17, 1975 and Jan. 10, 1977, respectively, and received on Jan. 10, 1976 and Feb. 15, 1977, respectively. The clumps were held at 5° both during and after shipping.

Each clump was planted in 15 cm azalea pots with the crown just above the medium (equal parts of soil, peat, sand, and Perlite). Plants were grown under natural photoperiods (43°N latitude) with 17°C minimum night temperature. Ancymidol (0.5 mg/pot) was applied as a drench 14 days after planting using 100 ml of solution; Osmocote (14N-6.2P-11.6K) at 9 g/pot was surface applied 15-20 days after planting.

**Microscopic techniques.** Apices were prepared either fresh or in formalin, glacial acetic acid, ethanol, and water (10:5:45:40) (FAA) for examination with a binocular light microscope with a calibrated ocular eyepiece. For SEM viewing the apices were placed in FAA after removal of 1 or 2 pairs of unexpanded leaves. Large reproductive apices were first cut into

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<sup>2</sup>Present address: Ornamental Horticulture Department, University of Florida, Gainesville, FL 32611.

<sup>3</sup>Present address: Department of Horticultural Science, North Carolina State University, Raleigh, NC 27650.

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cubes of 5 mm or smaller and placed in FAA. The tissues were stored in FAA for a min of 24 hr before dehydration in a graded ethanol series (50%, 70%, 90%, 100%, 100%). After about 8 hr in 100% ethanol, the tissues were critical point dried using liquid CO<sub>2</sub> in a Denton DCP-1.

When required, the inner involucre bracts (IB) or chaff bracts (CB) were removed while the apices were in ethanol. When not required, the final isolation of the meristem was performed after critical point drying. The tissues were mounted on SEM stubs with Tube Coat (G. C. Electronics Co., Rockford, Ill.), sputter coated with gold, and viewed with an International Scientific Instrument Co. Super-Mini SEM using a 15 kv accelerating potential.

**1976 experiments.** 'Park Princess' and 'Miramar' were planted on Feb. 25 and 26, respectively. To determine plant size effects on the time of flower initiation, 22 days after planting 7-10 plants each of 'Park Princess' with either 2, 3, or 4 leaf pairs separated were randomly selected and the stage of meristem development was determined. The same was done 30 days after planting with 10-14 plants each of 'Miramar' with either 0, 1, 2, 3, 4, 5, or 6 leaf pairs separated. Expanding leaf pairs were considered separated when the edges of the blades were no longer in contact.

**1977 experiments.** 'Park Princess' and 'Miramar' were planted on Feb. 17, and no more than 3 shoots were allowed to develop from a single clump. Starting on the 10th day, 10 samples of each cultivar were taken at 5 day intervals. The days to flowering was determined for an additional 10 plants (5 replications of 2 pots each) of each cultivar.

Another group of 'Park Princess' and 'Miramar', planted Feb. 17, were pinched above the 3rd or 4th node 25 days after planting. The apex of the longest of the 2 laterals at the highest remaining node was collected from 10 plants of each cultivar at 3 day intervals after pinching.

## Results and Discussion

**Morphological development.** Prior to planting, the shoot consisted of the apical meristem and 5 to 8 pairs of bud scales and/or leaf primordia with associated axillary meristems. The apical meristem was flat and rectangular (0.1 × 0.05 mm). The bud scales and leaf primordia were arranged in a decussate phyllotaxy, and it was difficult to distinguish them. Krijthe (14) identified any structure with brown coloration on the abaxial side to be a bud scale and found 3-4 pairs.

The leaf primordia did not closely overlap the meristem (Fig. 1A & B) and the resulting open space above the meristem was filled with trichomes developing on the adaxial side of the leaf primordia (Fig. 1A). Thus, one function of trichomes in *Dahlia* may be protection of the meristem. After separation of 2 leaf pairs, the meristem measured 0.2 × 0.1 mm. As the transition from the vegetative to the reproductive stage began, the meristem became domed and enlarged rapidly. It then measured about 0.3 × 0.25 mm (Fig. 1D). The dome stage was also characterized by a breakdown of the decussate phyllotaxy (Fig. 1D). This phyllotactic rearrangement was particularly evident in 'Miramar' in which the last few leaf primordia can be formed individually rather than in pairs. Philipson (18) indicated that in *D. gracilis* the first few bracts are arranged in pairs and continue the decussate pattern found in the leaves. This was not observed in the cultivars in this study.

Normally, 'Miramar' and 'Park Princess' formed 8 outer involucre bracts (OB), but observations of other cultivars indicated that the number can vary from 5 to 8. Sherff (21) and Sorensen (22) stated that wild species form 4 to 7 OB but 5 is most common. At the end of the OB formation stage, the meristem was round with a diameter of about 0.35 mm (Fig. 1E).

In another study (1) it was shown that the last leaves formed prior to OB formation could be simple leaves. These are dis-

tinguishable from the OB primordia because leaf primordia are pointed at the apex, usually have trichomes, and have a broad base. The OB primordia are rounded at the apex, do not possess trichomes, and have narrow bases (Fig. 1F). Furthermore, lateral meristems (LM) were observed in the leaf axials (Fig. 1E).

The 2nd type of bract produced on the *Dahlia* inflorescence was the IB, and one subtended each ray floret (RF) (Fig. 1E and Fig. 2). At anthesis, the OB and IB can be easily distinguished (21, 22), but the primordia can not (13). Using the system of Konishi and Inaba (13), we designated the 9th bract primordium as the first IB. Normally, the first IB arises on the same side of the meristem as and distal to the first OB. Therefore, in a topographic view it was hidden by the enlarging OB (Fig. 1E).

Philipson (18) reported that in *D. gracilis* the first indication of the floret primordium was a narrow plate of cells formed by anticlinal cell divisions in both tunica layers when the subtending bract primordium was becoming visible. Therefore, we considered a meristem to be reproductive when the first IB primordium appeared.

A 3rd type of bract on the *Dahlia* inflorescence was the CB which subtended each disk floret (DF) (Fig. 2E). In the fully double flowered dahlias studied, there appeared to be no morphological differences between the IB and CB, and Sherff (21) and Sorensen (22) indicated a similarity in the single flowered wild species.

Initially, there were only a few IB primordia on the periphery of the meristematic mantle (Fig. 2A), but after further development many IB primordia were formed almost simultaneously (Fig. 2C). The meristematic mantle, which was measured between the innermost series of bract primordia, enlarged until it was about 0.5 mm in diameter and it remained that size until it decreased as the last CB and DF primordia were produced.

The IB and CB primordia elongated rapidly, became imbricated, and overlapped the more distal parts of the capitulum. The floret primordia elongated after being covered by the subtending bract (Fig. 2). Krijthe (14) reported that in 'L' Innocence', a mignon dahlia which produced only 1 row of RF, the DF were well formed with various organ primordia visible before it was covered by the subtending CB. Durso and De Hertogh (10) have shown that short days caused 'Park Princess' to produce flowers with few RF and many DF. In flowers with open eye centers, we observed a development of the CB and DF very similar to that described by Krijthe (14).

The first structure formed by both RF and DF was the corolla. In RF, corolla enlargement occurred on the abaxial and lateral sides of the apex without the formation of distinct corolla lobes (Fig. 2D). Sattler (20) has shown that in marigolds 5 distinct lobes are formed, but only the lateral 2 and the one on the abaxial side develop to form the ligule. In salsify (*Tragopogon pratensis* L.), 5 lobes are formed on the corolla, but the ligule is formed by enlargement of the portion of the corolla below the lobes (20).

In dahlias, the DF formed 5 corolla lobes with the abaxial one being the last to arise (Fig. 2E). Inception of the 5 anther primordia occurred rapidly after the corolla lobes were formed (Fig. 2E). Through enlargement of the abaxial and lateral lobes the corolla enclosed the apex (Fig. 2F). The gynoecium developed in the center of the androecium after the apex was covered by the corolla (Fig. 2F).

At anthesis of the first RF, 'Park Princess' had produced 150-300 RF and 50-100 DF, while 'Miramar' had 150-200 RF and 69-90 DF. In both cultivars some meristems were still forming DF at this time. Often, the inflorescence terminated by forming a single large floret with abnormally large number of corolla lobes, anthers, and gynoecia. The most distal florets often did not reach anthesis because they aborted or the entire

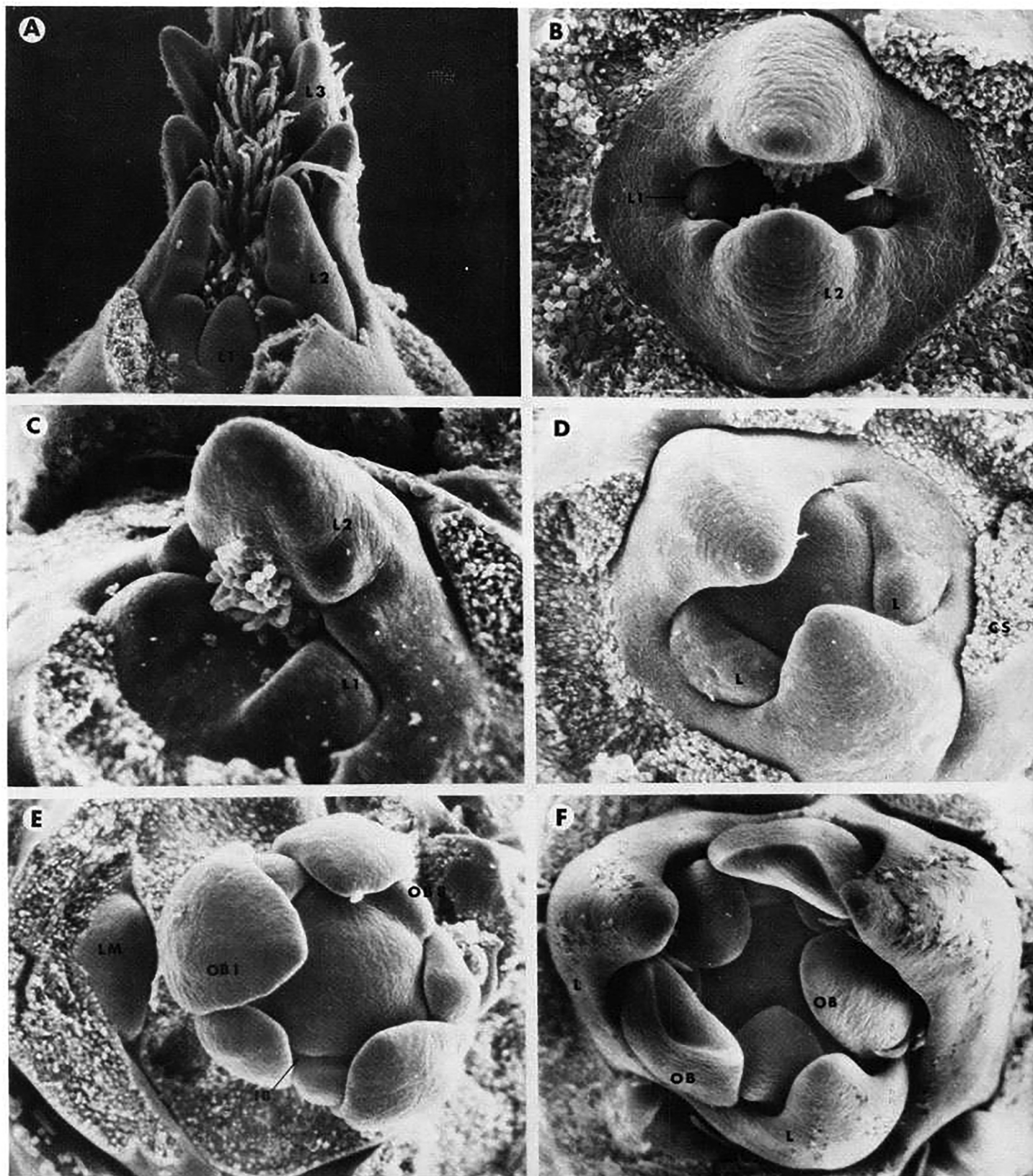


Fig. 1. Scanning electron micrographs of main shoot apices from *Dahlia* 'Miramar'. A. Vegetative apex, leaf (L) primordia at 3 nodes present (L1-L3), viewing adaxial side of L3 and abaxial side of L1, 0° tilt, × 58. Plant had 3 leaf pairs separated. B. Vegetative apex, topographic view, note decussate insertion of L1 and L2, 0° tilt, × 109. Plant had 2 leaf pairs separated. C. Vegetative apex, note trichome development on adaxial surface of L2, 50° tilt, × 123. Plant had 3 leaf pairs separated. D. Prefloral apex, meristem enlarged, domed, insertion of leaf primordia (L) not decussate, cut surface (CS) after removal of leaf primordium, 0° tilt, × 98. Plant had 5 leaf pairs separated. E. Reproductive apex, all leaf primordia removed, 8 outer involucrate bract primordia (OB) present, 4 inner involucrate bract primordia (IB) visible, 0° tilt, × 74. Plant had 6 leaf pairs separated. F. Reproductive apex, 3 leaf primordia present, some OB and IB obscured, 0° tilt, × 56. Plant had 6 leaf pairs separated.

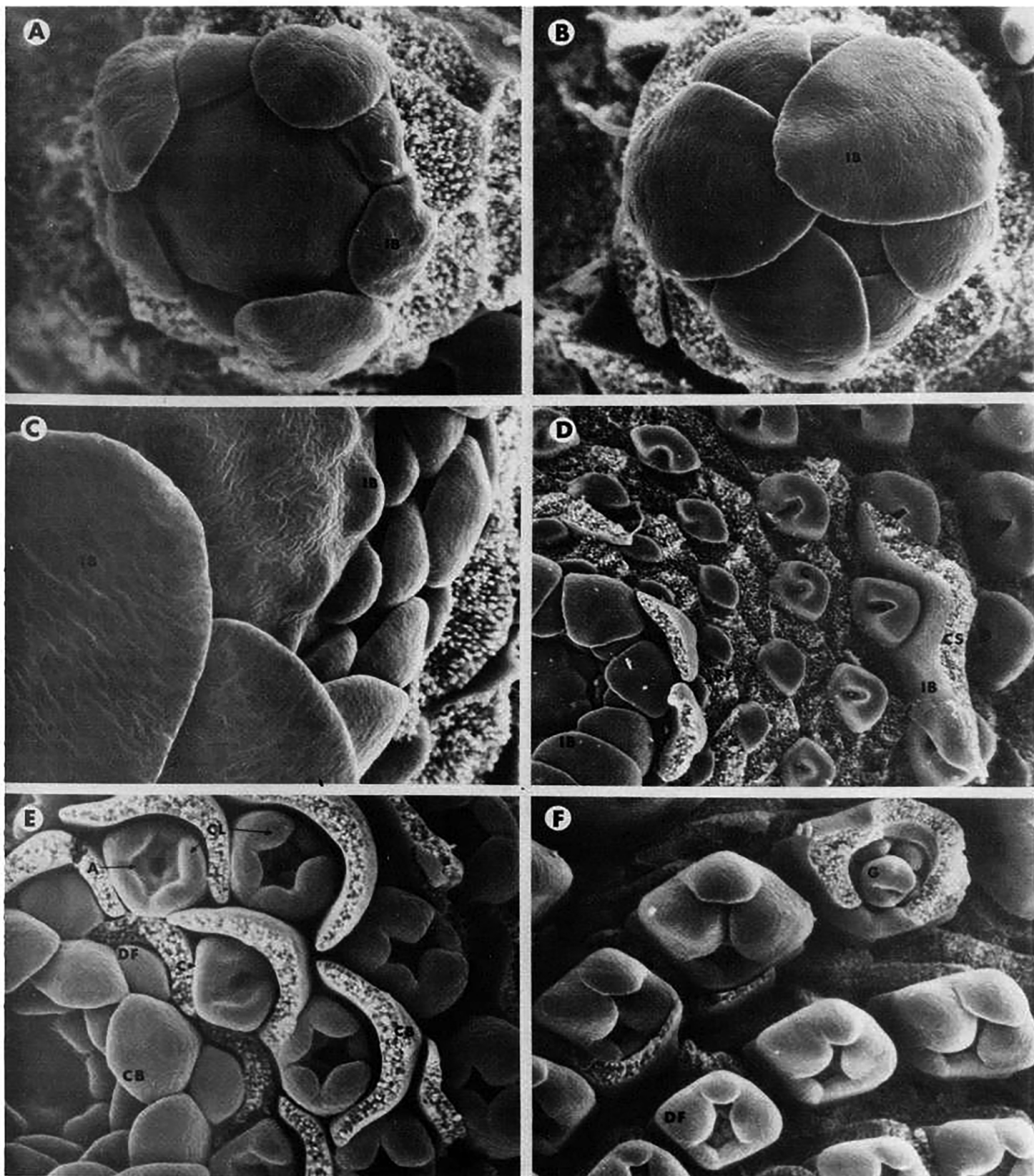


Fig. 2. Scanning electron micrographs of reproductive shoot apices from *Dahlia* 'Miramar'. A. Inner involucrate bract primordia (IB) being formed, all outer involucrate bract primordia (OB) removed,  $\times 77$ . Plant had 7 leaf pairs separated. B. Imbricate IB, all OB removed,  $\times 57$ . Plant had 7 leaf pairs separated. C. IB on periphery of meristematic mantle, large no. compared to A, outer IB removed,  $\times 93$ . Plant had 8 leaf pairs separated. D. Ray floret (RF) formation, capitulum apex in lower left, larger IB removed, cut surface (CS), corolla (C) forming on outer RF,  $\times 48$ . Approx 8 mm bud. E. Disk floret (DF) formation, apex at left, note that few chaff bract (CB) primordia are forming, larger CB removed, corolla lobes (CL) and anthers (A) present on some DF,  $\times 95$ . 22 mm bud. F. Same capitulum as E, most proximal DF at top, apex is out of picture at bottom, all CB removed, 3 CL removed from DF at top to reveal gynoecium (G),  $\times 56$ .



Table 1. Meristem stage of 'Miramar' with varying leaf pair separation, 30 days after planting, 1976.

No. of leaf pairs separated	Meristem stage (%)			
	Vegetative	Prefloral		Reproductive
		Dome	Bract	
0	100	—	—	—
1	100	—	—	—
2	100	—	—	—
3	100	—	—	—
4	36	46	18	—
5	8	34	50	8
6	—	9	—	91

capitulum senesced prior to their anthesis.

Instead of remaining round throughout inflorescence development, the meristematic mantle of 'Park Princess' often was elongated due to differential rates of floret primordia formation at the periphery. Some 'Park Princess' inflorescences reverted back to producing RF after several series of DF had been formed.

**1976 experiments.** The number of leaf pairs separated 30 days after planting had a marked effect on meristematic development (Table 1). 'Miramar' with 0-3 leaf pairs separated were vegetative, but plants with 4-5 pairs separated were mostly in the prefloral stages. Meristems were considered prefloral from doming until the first IB formed. Of the plants with 6 leaf pairs separated, 91% were reproductive. In contrast, when 'Park Princess' had 4 leaf pairs separated they were reproductive (data not presented). These results indicate that when grown under inductive photoperiods dahlias from clumps must reach a certain shoot size before flower initiation occurs. When plants were grown from cuttings, plant size was not a factor in flower initiation, because plants with 4-5 and plants with 15-18 leaf pairs flowered simultaneously after receiving inductive photoperiods (16).

**1977 experiments.** The development of unpinched 'Miramar' plants was about 10 days behind 'Park Princess' (Table 2). For 'Park Princess', the first meristems were prefloral and reproductive at 15 and 20 days after planting, respectively; however, 'Miramar' reached the same stages after 25 and 30 days, respectively. Similarly, the majority of plants were reproductive after 25 and 35 days for 'Park Princess' and 'Miramar' respectively. In this experiment, the average days to flower for 'Miramar' was 4 days longer than 'Park Princess'. In other studies (1, 8), 'Miramar' was 7-10 days later than 'Park Princess'.

These data suggest that the difference between the 2 cultivars in the number of days to anthesis results from the dif-

Table 2. Meristem development of unpinched 'Park Princess' and 'Miramar' at different time intervals after planting, 1977.

Cultivar (days to flower) <sup>2</sup>	Days after planting	Meristem stage (%)		
		Vegetative	Prefloral	Reproductive
Park Princess (65)	10	100	—	—
	15	70	30	—
	20	30	60	10
	25	—	10	90
	30	—	—	100
Miramar (69)	20	100	—	—
	25	40	60	—
	30	40	40	20
	35	—	30	70

<sup>2</sup>Days to flower significantly different at the 1% level.

Table 3. Stage of lateral meristem development from 'Park Princess' and 'Miramar' at intervals after pinching, 1977.<sup>2</sup>

Cultivar	Days after pinching	Meristem stage (%)		
		Vegetative	Prefloral	Reproductive
Park Princess	3	100	—	—
	6	60	40	—
	9	10	40	50
	12	10	10	80
Miramar	3	100	—	—
	6	90	10	—
	9	20	60	20
	12	—	20	80

<sup>2</sup>Plants pinched above node 3 or 4, 25 days after planting.

ference in time of flower initiation. This varies from the chrysanthemum in which variation in the days to flower is due to differences in the rate of development after initiation (9).

When samples of these cultivars were forced in The Netherlands, 'Miramar' flowered before 'Park Princess' (Freriks, personal communication). The reason for this discrepancy is unclear. Although flowering in most dahlia cultivars is partially controlled by photoperiod (5, 6, 10, 12, 13, 14), there is no indication that the photoperiodic differences between The Netherlands and the northern part of the U.S. during the spring would cause a difference in the time of flowering. Possibly, the washing and shipping of clumps utilized in the U.S. affected subsequent shoot growth.

When plants were pinched above node 3 or 4 and the meristems of the most vigorous growing laterals at the distal nodes were examined at 3 day intervals, 80% of 'Park Princess' and 'Miramar' were reproductive 12 days after pinching (Table 3). The main shoot apex on 'Park Princess' with 3 or 4 leaf pairs separated would have been either prefloral or reproductive at the time of removal, but with 'Miramar' at the same stage of leaf development the apex would have been primarily vegetative (Table 1). At the time of pinching, 25 days after planting, the lateral buds at nodes 3 and 4 on both cultivars were vegetative and measured about 0.15 × 0.08 mm. When the main shoot of unpinched plants flowered, the lateral buds at nodes 3 and 4 were still vegetative.

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## Growth and Development of Forced Tuberous-rooted Dahlias<sup>1</sup>

J. E. Barrett<sup>2</sup> and A. A. De Hertogh<sup>3,4</sup>

Department of Horticulture, Michigan State University, East Lansing, MI 48824

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**Abstract.** For the first 35 days following planting, the dry weights of the tuberous roots (TR) of *Dahlia* 'Park Princess' and 'Miramar' decreased, but simultaneously the dry weights of the fibrous roots (FR) and shoots increased. During the 2nd half of the forcing period shoot and TR dry weights increased rapidly. New TR developed from adventitious roots which formed at the basal nodes of the stem. Ancymidol (0.75 mg/plant) reduced shoot dry weight as well as total height but did not alter TR or FR growth. Plant quality measured by shoot dry weight was reduced when the distal half of each TR was removed before planting. It was not reduced where half of the TR were left intact or when only 1 cm was removed from each TR. The number of days to flower was inversely correlated with plant height measured at 14 and 28 days after planting but not with clump fresh weight.

Within a cultivar the rate of early shoot growth of tuberous-rooted (TR) dahlias is variable, and the shoots must reach a certain minimum size before flower initiation occurs (2). Thus, the 2 week variation in the time of flowering of a population of plants within a cultivar (5) may be related to the variation in early shoot growth.

In other bulbous species, the size of the storage organ can affect the growth and development of the shoot. Below a critical size, tulip, hyacinth, and iris bulbs will not form flowers (13, 20). There is a direct relationship between *Lilium longiflorum* bulb size and the number of flowers and leaves produced (6). Also, the larger the potato (*Solanum tuberosum* L.) seed piece the earlier the flowering with a greater no. of shoots and flowers (3, 14). Small sweet potato roots produce more shoots per unit weight than larger roots (7). The effects of photoperiod and growth regulators on TR development in dahlias have been

studied (9, 18, 19, 23, 25), but no detailed studies have been reported on the relationship of the storage organs to shoot growth and flowering. This latter aspect was investigated in this study.

### Materials and Methods

**Cultural procedures.** Unless otherwise noted, the shipping, handling, and forcing of clumps were the same as previously described (2). In experiments 1 and 4, the planting medium consisted of equal parts of soil, peat, sand, and Perlite; and 0.5 mg of ancymidol was applied to each pot in 100 ml of solution 14 days after planting. In experiments 2 and 3, the planting medium was soil, peat, sand, and Turface (1:1:1:6); and ancymidol at 0.75 mg/pot was applied 13 and 14 days after planting, respectively.

**Experiment 1.** In order to determine the changes in the dry weight of the TR, fibrous roots (FR), shoots, and total plant during forcing, 90 uniformly sized clumps each of 'Park Princess' and 'Miramar' were planted on April 9, 1976. Dry weight determinations were made on 15 randomly selected plants of each cultivar at 0, 14, 21, 35, 49, and 63 days after planting.

**Experiment 2.** Two hundred randomly selected 'Park Princess' clumps were planted March 8, 1977 to determine the effect of ancymidol on the growth of the various plant parts. At intervals, the dry weight and plant height were determined for 20 plants either with or without ancymidol.

**Experiment 3.** During harvesting, handling, and shipping clumps are often damaged to varying degrees. Sometimes, a portion of a TR must be removed before the clumps will fit into a pot. To determine how much of the clump can be removed without affecting shoot growth, 90 randomly selected

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<sup>2</sup>Present address: Ornamental Horticulture Department, University of Florida, Gainesville, FL 32611.

<sup>3</sup>Present address: Department of Horticultural Science, North Carolina State University, Raleigh, NC 27650.

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