Meristem Ontogenetic Age as the Controlling Factor in Long-day Floral Initiation in Poinsettia

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Abstract. The poinsettia [*Euphorbia pulcherrima* (Willd. ex. Klotzsch)] is a short-day plant (SDP) for floral initiation that will also initiate floral structures (cyathia) under long days (LD) after the apical meristem produces a cultivar-dependent number of nodes (long-day node number). Leaf removal, root restriction, and air layering failed to affect the long-day node number (LDNN) of the apical meristem. Repeated rooting of shoots, which resulted in the removal of nodes, did not affect the total number of nodes initiated by the apical meristem before floral initiation, although the number of nodes intact on the plant at the time of floral initiation was reduced. Reciprocal grafting of axillary buds of 'Eckespoint Lilo' and 'Gutbier V-14 Glory' plants did not affect the LDNN of the grafted meristem since the LDNN was the same as for nongrafted buds of the same cultivar. Further, grafting axillary buds from different positions along the main axis that differed in LDNN did not affect the LDNN of the grafted meristems. On the basis of these results, it was concluded that LD floral initiation in poinsettia is a function of the ontogenetic age of the meristem and that the LDNN represents a critical ontogenetic age for floral initiation to occur under LD.

The poinsettia is a short-day plant (SDP) that flowers when the skotoperiod exceeds ≈ 12.5 h (Grueber, 1985; Kristofferson, 1969), depending upon cultivar and temperature. The floral structures of a poinsettia are termed cyathia and consist of a single pistillate flower with numerous staminate flowers enclosed in an involucre cup (Shanks, 1980).

The poinsettia will also initiate cyathia under LD after the apical meristem initiates a cultivar-dependent number of nodes (long-day node number) (Evans, 1987; Hackett and Kofranek, 1971). This type of development is commonly referred to as splitting. However, under LD, the cyathia that are initiated do not develop to anthesis and are subtended by foliar leaves rather than bracts.

For many species, evidence exists that indicates that, under inductive conditions, the leaves are the site of photoperiodic perception and the source of at least the primary floral signal (Bernier et al., 1981). Further, depending on species, leaves can have either promotive or inhibitory effects on flowering under noninductive conditions. Lang (1952) demonstrated that leaf removal promoted flowering in the long-day plant (LDP) *Hyoscyamus niger* L. and in the SDP *Chenopodium amaranticolor* Costen and Reynier under noninductive conditions. Lang concluded that the leaves contained floral inhibitors and that removing the leaves removed the source of an inhibitor and floral initiation resulted. In the SDP *Glycine max* (L.) Merrill (Fisher, 1955), the LDP *Scrofularia arguta* L. (Chouard and Lourtiaux, 1959), and the day-neutral *Lycopersicon esculentum* Mill. (Hussey, 1963), floral initiation was shown to occur only after there was a specific ratio of mature-leaf area to immature-leaf area. Removal of young expanding leaves promoted flow-

ering, thus indicating that young leaves were inhibitory to flowering.

In several species in which node count is important in determining when floral initiation occurs, the roots have been shown to exert correlative control over flowering. In the SDP, *Ribes nigrum* L. 'Wellington XXX', floral initiation occurred under SD only after a minimum of 20 nodes were formed. If plants were placed under SD before they attained the 20th node, they became dormant and did not initiate flowers. When air layers were placed along the stem to reduce the distance between roots and the apical meristem, floral initiation was inhibited even after the plants had formed 20 nodes (Schwabe and Al-Doori, 1973). Further, when shoot tips from shoots that had formed 20 nodes were rooted, flowering was delayed on these rooted shoot tips. Schwabe and Al-Doori concluded that the size of the plant, and specifically the distance between the apical meristem and the roots, controlled whether floral initiation could occur under inductive SD. *Nicotiana tabacum* L. 'Wisconsin 38', a day-neutral cultivar, forms 30 to 40 nodes before initiating floral structures. As with *R. nigrum* 'Wellington XXX', McDaniel (1980) demonstrated that air layering and rooting of shoot tips delayed floral initiation in *N. tabacum* 'Wisconsin 38'. McDaniel concluded, as did Schwabe and Al-Doori, that the distance between the apical meristem and the roots was the factor that governed when floral initiation occurred. Roots have also been shown to affect floral initiation in other species including *Pharbitis nil* Chois., strain Kidachi (Shinozaki and Takimoto, 1982, 1983) and *Prunus persica* L. (Richards, 1986). In these species restricting lateral root growth was shown to promote floral initiation.

Although the attainment of a critical node number is required for LD floral initiation to occur in poinsettia, it is not known whether this represents the attainment of a certain plant size, number of leaves, or plant age. The objective of this study was to determine the developmental basis of the long-day node number (LDNN) for floral initiation in poinsettia.

Materials and Methods

Unless otherwise indicated, materials and methods for all experiments were as follows. Vegetatively propagated plants were

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Abbreviations: LD, long day(s); LDNN, long-day node number; LDP, long-day plant; SD, short day; SDP short day plant.

received from Encinitas, Calif., and potted into $51 \times 31 \times 8$ cm containers with a synthetic medium of 2 peat : 1 perlite : 1 soil (by volume). After 1 week, plants were decapitated to five nodes. The axillary shoot originating from the fifth node was removed, with all nodes intact, when the shoot was ≈ 7.5 cm long. The shoots were rooted under intermittent mist. After rooting, these plants were potted into 0.45-liter pots containing the same growing medium as noted. After 1 week, plants again were decapitated to five nodes. The axillary shoot from the fifth node was used as the experimental unit after all shoots below the fifth node were removed. At all times plants were maintained at a minimum of 21C and under LD, the latter by use of incandescent lighting from 1700 to 2200 HR (minimum of $10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to extend the daylength. Plants were fertilized at each watering with a $\text{Ca}(\text{NO}_3)_2$ and KNO_3 or 20N-4.3P-16.6K solution at a concentration of 250 mg/N per liter.

The poinsettia cultivars used in these experiments have about seven unexpanded leaf primordia enclosing the meristems of terminal and axillary buds. These leaves and nodes were accounted for in all treatments that were conducted at given node counts and when data was taken.

Ten plants were used per treatment. The number of nodes produced by the meristems of interest before floral initiation under LD was recoded and will be referred to as the LDNN.

Leaf removal (Expt. 1). 'Annette Hegg Brilliant Diamond' ('Brilliant') and 'Gutbier V-14 Red' ('V-14') plants were subjected to the following treatments that were continued until the plants initiated floral structures: 1) 50% of each leaf removed perpendicular to the midvein, 2) every other leaf removed, 3) all leaves removed except the five most basipetal leaves, 4) all leaves removed except the five most acropetal expanded leaves, 5) intact control group. Treatments began immediately after the first leaf unfolded. Leaves were either removed or cut in half before the expansion of the leaf to an area of $\approx 1 \text{ cm}^2$.

Air layering (Expt. 2). Air layers were placed along the stems of 'Brilliant' and 'V-14' plants to induce rooting and reduce the distance between the apical meristem and the roots. Air layers were constructed of sphagnum peat wrapped with 0.01 cm thick black polyethylene film. Where a layer was to be constructed, the leaves were removed and a small V-shaped notch was made in the stem immediately below the node. Because wounding and auxin were required for rooting, controls were included that were wounded and treated with auxin. In these controls, the wound was wrapped with plastic and allowed to heal. Auxin was applied by lightly brushing a powder containing 0.1% indole-3-butyric acid (Hormex Rooting Powder #1, Brooker Chemical, North Hollywood, Calif.) on the wound. Plants were either layered once at 10 cm above the soil line or twice at 10 and 20 cm above the soil line. The first layer was constructed when the plants were ≈ 15 cm tall and the second when the plants were ≈ 25 cm tall. A second group of plants was subjected to a different type of air layering, in which bottomless 10-cm diameter plastic pots were placed around the plant stem and filled with soil as the plant grew (McDaniel, 1980). As each pot was filled with growing medium, another pot was placed on top of the previous pot so that a continuous air layer was constructed. Wounding and auxin treatments were performed at each node as previously described. Treatments began when the plants were ≈ 8 cm tall.

Rooting of shoot tips (Expt. 3). 'Brilliant' and 'V-14' shoot tips were rooted in a glass-covered greenhouse under intermittent mist. After the resulting plant formed four additional expanded leaves, the shoot tips were removed and rooted. When

these shoot tips formed roots and four additional expanded leaves, the treatment was repeated. Thus, a total of eight nodes were removed during the experiment. The plants were then allowed to grow until cyathia were initiated. This treatment was similar to McDaniel's (1980) treatment of tobacco. Between rootings and following the third rooting, plants were placed in a greenhouse without misting. The number of nodes on the plant at the time of floral initiation and the total number of nodes produced by the apical meristem until floral initiation were recorded. A control group was placed under mist during the times when treatment plants were being rooted and moved to the greenhouse when treatment plants were in the greenhouse. Another control group was maintained in the greenhouse at all times. Twenty plants were initially used in each re-rooting treatment group and 10 in each control group. During the experiment, some of the plants in the re-rooting treatment died. Therefore, a random sample of 10 plants was selected from the treatment groups to serve as the experimental units.

Decapitation (Expt. 4). 'Brilliant' and 'V-14' plants were allowed to grow to ≈ 27 nodes (20 unfolded leaves) and then were decapitated immediately above node 20, 16, 12, 8, or 4, counting from the base of the plant. All axillary shoots, except for the one originating from the node of interest, were removed. The axillary buds at each node had about seven unexpanded leaf primordia enclosing the meristem at the time of decapitation. A group of intact plants was used as a control. The LDNN of the lateral shoot and the total nodes on the plant at the time of cyathium initiation were recorded.

Grafting of axillary buds (Expt. 5). Axillary buds of 'Brilliant' plants were excised and grafted to different nodal positions. Buds from position four, counting from the base, were excised and grafted back to position four or grafted to position 12. Buds from position 12 were treated analogously. Buds from nodal positions four and 12 had about seven unexpanded leaves enclosing the axillary meristem at the time the buds were grafted. After grafting, plants were maintained under intermittent mist for 3 weeks until the grafts had healed. At that time, the grafted plants were placed in a greenhouse with nongrafted controls and all plants were decapitated at node 12. All lateral shoots were removed except for those originating from nodes four and 12. The LDNN of the lateral shoot of interest was counted.

Reciprocal grafting of axillary buds (Expt. 6). Axillary buds from 'Eckespoint Lilo' and 'V-14' were reciprocally grafted by excising buds from the fifth node of one cultivar and grafting them to the fifth node of the other cultivar. Grafted control plants in which buds were excised and grafted back to the same plant and position and nongrafted control plants were included. After grafting, plants were maintained under intermittent mist for 3 weeks until the grafts had healed. At that time, the grafted plants were placed in a greenhouse with nongrafted controls and all plants were decapitated immediately above node six. Each cultivar served as both a bud donor and stock. The bud from the sixth node and the grafted bud at the fifth node were allowed to grow until both meristems had initiated cyathia. Therefore, both the influence of the grafted bud on the stock bud and the influence of the stock on the grafted bud could be determined.

Results and Discussion

Leaf removal did not significantly affect the LDNN of either 'Brilliant' or 'V-14'. 'Brilliant' control plants initiated cyathia after forming 21 nodes, and plants subjected to leaf removal treatments formed 20 to 24 nodes, depending on the specific leaf removal treatment. Control plants of 'V-14' initiated cy-

athia after forming 30 nodes, while plants subjected to leaf removal treatments formed 29 to 32 nodes, depending on the specific leaf removal treatment. Leaf removal also failed to affect floral initiation in *Nicotiana tabacum* 'Wisconsin 38' (McDaniel, 1980) and *Helianthus annuus* L. (Habermann and Sekulow, 1972), both of which flower only after the formation of a minimum number of nodes.

Air layering also failed to affect the LDNN of poinsettia. Control plants of 'Brilliant' formed 32 nodes, while those plants subjected to air layering treatments formed 28 to 31 nodes before initiating a cyathium, depending on the specific treatment. Control plants of 'V-14' formed 37 nodes, while those subjected to air layering treatments formed 32 to 38 nodes before initiating cyathia.

Repeated rooting treatments had no effect on the LDNN (Table 1). The number of nodes present at the time of floral initiation for treated plants was significantly different from the controls. However, counting the eight nodes removed during the repeated-rooting experiment, the total number of nodes produced by the apical meristem before floral initiation was not significantly different from the controls. Therefore, the eight nodes removed during the repeated rooting experiments were integrated into the LDNN count even though they were not intact on the plant at the time of floral initiation.

These results are different from those for *N. tabacum* 'Wisconsin 38' and *R. nigrum* 'Wellington XXX' where plant size, and specifically the distance between the apical meristem and the roots, was important in determining when floral initiation occurred. In the cases of *N. tabacum* and *R. nigrum*, air layering and repeated rooting inhibited floral initiation because they maintained a reduced distance between the apical meristem and the roots. Our results with poinsettia are similar to those obtained by Habermann and Sekulow (1972) with *H. annuus* in which repeated rooting and removal of nodes did not affect the number of nodes formed before floral initiation. In the case of *H. annuus*, Habermann and Sekulow concluded that the ontogenetic age of the apical meristem governed the developmental stage at which floral initiation occurred.

When plants of 'Brilliant' and 'V-14' were decapitated to differing nodes, the axillary shoots developing from these nodes had different LDNN, which depended on the nodal position from which the shoot originated (Table 2). Shoots that originated from the most basipetal node had the highest LDNN. Thus, the more acropetal the nodal position, the fewer nodes the axillary meristem formed before floral initiation.

Table 1. The effect of repeated rootings on LD floral initiation in two *Euphorbia pulcherrima* cultivars.

Treatment ^z	'Brilliant Diamond'		'Gutbier V-14'	
	Nodes ^y	Total nodes ^x	Nodes	Total nodes
Control	31	31	38	38
Control + mist	26	26	32	32
Re-rooted	21	29	27	35
LSD (0.05)	4	NS	5	NS

^zControl plants were grown in a glass-glazed greenhouse at 21°C. "Control + mist" plants were untreated but grown under intermittent mist during those times when treatment plants were under mist. "Re-rooted" plants had the basipetal four nodes removed and the terminal rooted twice so that a total of eight nodes were removed.

^yNodes intact when plants became reproductive.

^xTotal nodes initiated by the apical meristem at the time plants became reproductive (intact nodes + 8 for "re-rooted" plants; intact nodes for "control" and "control + mist" plants).

Table 2. The effect of nodal position on the LDNN of *Euphorbia pulcherrima* 'Brilliant Diamond' and 'Gutbier V-14' axillary shoots.

Nodal position ^z	LDNN ^y		Total nodes from roots ^x	
	'Brilliant'	'V-14'	'Brilliant'	'V-14'
Control	29	34	29	34
4	23	27	27	31
8	20	22	28	30
12	18	17	30	29
16	14	14	30	30
20	12	15	32	35
LSD (0.05)	3	2	NS	NS

^zControl plants were not decapitated. Nodal position indicates the position of the axillary shoot of interest. Nodes are numbered beginning from the roots and moving acropetally.

^yLDNN is the number of nodes formed by the axillary shoot meristem before initiating a floral structure.

^xTotal nodes to roots includes the LDNN of the axillary shoot and the number of nodes below the pinch.

^{NS}Nonsignificant at $P = 0.05$. Ten plants were used per treatment.

Table 3. The effect of reciprocal grafting of *Euphorbia pulcherrima* 'Brilliant Diamond' axillary buds from different nodal positions on the LDNN of shoots derived from those buds.

Treatment number ^z	Original position	Grafted position	LDNN
1	4	Control	24
2	12	Control	17
3	4	4	25
4	12	12	16
5	4	12	25
6	12	4	17
Significance			
1 vs. 2			**
1 vs. 3 vs. 5			NS
2 vs. 4 vs. 6			NS

^zControl plants were pinched at the indicated node and the resulting shoot was used as the experimental unit.

^{NS, **}Nonsignificant or significant $P = 0.05$ or 0.01 , respectively. Ten plants were used per treatment.

When axillary buds were grafted to new positions on the main stem, the LDNN of the axillary shoots were similar to that of grafted and nongrafted controls (Table 3). Reciprocal grafting buds of 'Lilo' and 'V-14' also failed to affect the LDNN of the grafted buds or the adjacent intact buds (Table 4). Therefore, grafting axillary buds to different nodal positions or to a different cultivar had no effect on the LDNN of the axillary meristem.

McDaniel and Hsu (1976) also reported a nodal position dependence with respect to floral initiation of axillary meristems in *N. tabacum* 'Wisconsin 38'. However, in contrast to our results in poinsettia, McDaniel and Hsu (1976) found that grafting axillary buds of *N. tabacum* 'Wisconsin 38' to different positions altered the expected number of nodes formed by the axillary meristem before floral initiation occurred. They concluded that position dependence was a function of the distance between the axillary meristems and the roots. However, based on results from the re-rooting and reciprocal bud grafting experiments with poinsettia, it is clear that this conclusion does not adequately explain nodal position dependence in poinsettia.

Since minimum leaf count, leaf area, ratio of mature to immature leaves, or plant size are not adequate to explain the developmental basis for the LDNN in the control of LD floral initiation in poinsettia, a different mechanism is required to

Table 4. The effects of reciprocal grafting of axillary buds from two cultivars on LDNN in *Euphorbia pulcherrima*.

Treatment number	Bud graft combination ²	LDNN	
		Scion	Stock
1	'Lilo'	20	20
2	'V-14'	36	36
3	'Lilo'/'Lilo'	20	20
4	'V-14'/'V-14'	37	38
5	'V-14'/'Lilo'	36	20
6	'Lilo'/'V-14'	20	36
Significance			
1 vs. 2		**	**
1 vs. 3 vs. 6		NS	---
2 vs. 4 vs. 5		NS	---
1 vs. 3 vs. 5		---	NS
2 vs. 4 vs. 6		---	NS

²'Lilo' and 'V-14' represent untreated controls. Therefore, the LDNN of the shoot originating from node 6 after decapitation is treated as the stock and the scion for contrast purposes. For budding combinations, the first cultivar was the scion and the second cultivar was the stock.

³LDNN represents the number of nodes on the axillary shoots at the time of floral initiation after decapitation of the main shoot. Scion refers to the bud grafted to nodal position 5 and scion refers to the in situ bud at node 6.

NS,*,** Nonsignificant or significant at $P = 0.05$ or 0.01 , respectively. Six plants were used per treatment.

interpret these results. Meristem ontogenetic age, as measured by the number of nodes formed before LD floral initiation, is a mechanism that can explain all of the responses to the experimental manipulations conducted. When the meristem reaches a cultivar-dependent critical ontogenetic age, as measured by the LDNN, floral initiation occurs. Neither leaf removal, air layering, nor grafting buds to different positions affected the node number at which LD floral initiation occurred because none of these treatments affected the ontogenetic age of the meristem.

Although repeated rooting removed nodes, all nodes that were formed were apparently included into the LDNN count by the meristem whether or not the node remained intact on the plant. Therefore, the critical event for ontogenetic aging in the poinsettia meristem is the initiation of a node and not its presence.

The position dependence of the LDNN of axillary buds can also be explained by their ontogenetic ages if axillary meristems of different ontogenetic ages are formed by the apical meristem of the primary shoot as it develops and becomes ontogenetically older over time. Because the apical meristem would be at an ontogenetically older state, axillary meristems at more acropetal nodal positions on the main plant axis would be ontogenetically older and, therefore, form fewer nodes before initiating floral structures than more basipetal axillary meristems. That this situation is true, is demonstrated by the fact that the number of nodes formed by an axillary meristem plus the number of nodes below it on the primary stem is a constant number (Table 2). This explanation assumes that the apical meristem of the plants used in these experiments started with constant ontogenetic ages as a result of the source of the plant material and its treatment before being used in the experiment (multiple propagations and decapitations). The consistency and predictability of the LDNN of a given cultivar supports this assumption. In addition, Siraj-Ali et al. (1990a) demonstrated that severe pruning (hedging) of stock plants had a rejuvenating effect on poinsettia plants.

Since position dependence was established at the time the axillary meristem was formed and not as a function of position

per se, the axillary buds may be grafted to different positions without affecting their LDNN (Table 3). Further, since buds of one cultivar can be grafted to another without affecting the LDNN of the meristem of the grafted bud (Table 4), LD floral initiation must be under the autonomous control of the meristem and, as stated previously, determined by the number of nodes formed by the meristem rather than by a chemical signal from some other organ of the plant. The difference in the LDNN between cultivars could either be due to a difference in the required ontogenetic age for floral initiation to occur or due to a difference in the rate of ontogenetic aging per node formed.

Position dependence for floral initiation is seen in both *N. tabacum* 'Wisconsin 38' and poinsettia. However, position dependence appears to be established by two mechanisms: position in relation to the roots in the former and ontogenetic age of the shoot meristem in the later. Position dependence has also been reported in woody perennial species (Hackett, 1985). As with the case of the poinsettia, this pattern has usually been explained in terms of the more acropetal tissues being more mature, or ontogenetically older, than the more basipetal tissues.

The basis of an ontogenetic age requirement for LD floral initiation in poinsettia may be related to meristem competence to respond to chemical signals. The chemical signals required for floral initiation may be present under LD, but the meristem may not be competent to respond to these signals until after a specific ontogenetic age has been achieved. That this may be the case in poinsettia is supported by Siraj-Ali et al. (1990b) who found that poinsettia plants produced from seed vary in their competence to respond to SD depending on age. Further, in *Citrus sinensis* (L.) Osbeck (Furr et al., 1947), *Larix leptolepis* L. Kaempferi., and *Larix decidua* Mill. (Robinson and Wareing, 1969), meristems of juvenile scions grafted onto reproductively mature trees did not respond to a floral stimulus from adjacent mature leaves by flowering, while in situ meristems on the mature stock did flower. Robinson and Wareing (1969) concluded that the mechanism for change from the juvenile to the mature phase of the shoot apex was intrinsic to the apex itself, and the transition may have been related to a minimum number of cell divisions required before the apex could respond to the floral signal. In an analogous way, a given poinsettia meristem, apical or axillary, may need to reach a critical ontogenetic age, as measured by node number, before the meristem is competent to respond.

For all experiments conducted, all plants eventually initiated cyathia. This occurrence is contrary to the assumption that only a fraction of poinsettia plants form cyathia under LD. However, the LDNN of a poinsettia cultivar can be used to predict when a given poinsettia cultivar will form cyathia under LD. Further, since nodes formed by a meristem are integrated into the LDNN count even if the nodes are not intact on the plant, it is important from a commercial perspective to take cuttings from short shoots, with few nodes, rather than taking cuttings from long shoots. The length of the cutting is unimportant since the meristem will integrate into the LDNN count the nodes left behind on the stock plant.

Literature Cited

- Bernier, G., J.M. Kinet, and R.M. Sachs. 1981. The physiology of flowering, vol. 1. CRC Press, Boca Raton, Fla.
 Chouard, P. and A. Lourtoux. 1959. Correlations et reversions de croissance et de mise a fleurs chez la plante amphicarpique *Scrofularia arguta*. Comptes Rendus Academie des Sciences Paris 249:889.
 Evans, M.R. 1987. Precocious floral initiation of *Euphorbia pulcherrima* MS Thesis, Univ. of Minnesota, St. Paul.

- Fisher, J.E. 1955. Floral induction in soybean. *Bot. Gaz.* 117:156-165.
- Furr, J.R., W.C. Cooper, and P.C. Reece. 1947. An investigation of flower formation in adult and juvenile *Citrus* trees. *Amer. J. bot.* 34(1):1-8.
- Grueber, K.L. 1985. Initiation and development of the inflorescence in five cultivars of poinsettia. PhD Diss., Univ. of Minnesota, St. Paul.
- Habermann, H.M. and D.B. Sekulow. 1972. Development and aging in *Helianthus annuus* L. Effects of the biological milieu of the apical meristem on the patterns of development. *Growth* 36:339-349.
- Hackett, W.P. 1985. Juvenility, maturation, and rejuvenation in woody plants, p. 109-155. In: J. Janick (ed.). *Horticultural reviews* vol. 7. AVI Publishing Company, Westport, Conn.
- Hackett, W.P. and A.M. Kofranek. 1971. Analysis of low temperature stimulation of floral initiation in poinsettia cv. Paul Mikkelsen. *J. Amer. Soc. Hort. Sci.* 96(3):308-311.
- Hussey, G. 1963. Growth and development in the young tomato. II. The effect of defoliation on the development of the shoot apex. *J. Expt. Bot.* 14(41):326-333.
- Kristoffersen, T. 1969. Influence of daylength and temperature on the growth and development in poinsettia (*Euphorbia pulcherrima* Willd.) *Acta Hort.* 14:73-89.
- Lang, A. 1952. Physiology of flowering. *Annu. Rev. Plant Physiol.* 3:265-306.
- McDaniel, C.N. 1980. Influence of leaves and roots on meristem development in *Nicotiana tabacum* L. cv. Wisconsin 38. *Planta* 148:462-467.
- McDaniel, C.N. and F.C. Hsu. 1976. Position-dependent development of tobacco meristems. *Nature* 259(5544):564-565.
- Richards, D. 1986. Tree growth and productivity-the role of roots. *Acta Hort.* 175:27-36.
- Robinson, L.W. and P.F. Wareing. 1969. Experiments on the juvenile adult change in some woody species. *New Phytol.* 68:67-78.
- Schwabe, W.W. and A.H. Al-Doori. 1973. Analysis of a juvenile-like condition affecting flowering in the black current (*Ribes nigrum*). *J. Expt. Bot.* 24(82):969-981.
- Shanks, J.B. 1980. Poinsettias, p. 301-326. In: R. Larson (ed.). *Introduction to floriculture*. Academic, New York.
- Shinozaki, M. and A. Takimoto. 1982. Correlation between long-day flowering and root elongation in *Pharbitis nil*, strain Kidachi. *Plant and Cell Physiol.* 23(6):1055-1062.
- Shinozaki, M. and A. Takimoto. 1983. Effects of some growth regulators and benzoic acid derivatives on flower initiation and root elongation of *Pharbitis nil*, strain Kidachi. *Plant and Cell Physiol.* 24(3):433-439.
- Siraj Ali, Y.S., H.K. Tayama, T.L. Prince, and S.A. Carver. 1990a. The relationship between maturity level and splitting in poinsettia. *HortScience* 25:1616-1618.
- Siraj Ali, Y.S., H.K. Tayama, T.L. Prince, and S.A. Carver. 1990b. Identification of the developmental phases in poinsettia. *J. Amer. Soc. Hort. Sci.* 115:728-732.