

Axillary Bud Development of Poinsettia 'Eckespoint Lilo' and 'Eckespoint Red Sails' (*Euphorbia pulcherrima* Willd.) Is Inhibited by High Temperatures

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Abstract. The effect of temperature on axillary bud and lateral shoot development of poinsettia (*Euphorbia pulcherrima* Willd.) 'Eckespoint Lilo' and 'Eckespoint Red Sails' was examined. Rooted 'Eckespoint Lilo' cuttings were transplanted and placed into growth chambers maintained at 21, 24, 27, or 30 °C for 2 weeks before apex removal. The percentage of nodes developing lateral shoots after apex removal was 68%, 69%, 73%, or 76% at 21, 24, 27, or 30 °C, respectively. Cuttings were removed from the lateral shoots, rooted, and placed into a 21 °C greenhouse, and the apices were removed. The percentage of nodes developing into lateral shoots on cuttings taken from plants held at 21, 24, 27, and 30 °C were 74%, 65%, 66%, and 21%, respectively. Of the cuttings in the 30 °C treatment, 83% of the nodes not producing a lateral shoot had poorly developed axillary buds or no visible axillary bud development. Visual rating of axillary bud viability decreased from 100% to 0% when 'Eckespoint Red Sails' plants were transferred from a 21 °C greenhouse to a greenhouse maintained at 27 °C night temperature and 30 °C for 3 hours followed by 33 °C for 10 hours and 30 °C for 3 hours during the 16-hour day. Transfer from the high-temperature greenhouse to a 21 °C greenhouse increased axillary bud viability from 0% to 95%. Axillary buds of leaves not yet unfolded were sensitive to high temperatures, whereas those of unfolded leaves (i.e., fully developed correlatively inhibited buds) were not. Sixteen consecutive days in the high-temperature treatment were required for axillary bud development of 'Eckespoint Red Sails' to be inhibited.

The commercial success of poinsettia is due, at least in part, to the development of the 'Annette Hegg' family of cultivars that branch freely on removal of the shoot apex (pinching) (Ecke et al., 1990). However, certain cultivars, including 'Eckespoint Lilo' (Lilo) and 'Eckespoint Red Sails' (Red Sails), occasionally branch poorly after pinching; some plants develop no lateral shoots after pinching.

Poorly branched poinsettias can cause significant economic losses. Poinsettias are vegetatively propagated from shoot-tip cuttings; therefore, poorly branched stock plants do not produce the projected number of cuttings. Market specifications for the finished product require five or more laterals on pinched plants at flower. Plants that produce fewer than five flowering laterals after pinching are sold at a reduced price; those that produce fewer than three are discarded.

Poinsettia cultivars differ in their capacity to branch after pinching, and cultivars are often referred to as free-branching or restricted-branching. Reciprocal grafting of free-branching and restricted-branching plants suggests that the branching factor is graft-transmissible (Stimart, 1983). A virus has been proposed as the branching factor, since poinsettias regenerated following heat treatment (Dole and Wilkins, 1994) or suspension culture (Preil, 1994; Preil and Engelhart, 1982) do not have the free-branching characteristic; however, the specific factor has not been identified (Dole and Wilkins, 1991, 1992; Dole et al., 1993).

The cause of inconsistent branching in the normally free-branching cultivars Lilo and Red Sails is not known, although the

problem may be temperature related since poor branching occurs more frequently in the southern United States (personal communication, David Hartley). High temperature has been linked to the inhibition of axillary bud development of chrysanthemum (Faust and Heins, 1992; Schoelhorn et al., 1995) and peach (Boonprakob et al., 1993). Visual observations indicate that axillary buds often fail to develop properly in the leaf axils of poorly branching cultivars (Faust and Heins, 1993). Poor axillary bud development ranges from the absence of any differentiation (i.e., a "blind" leaf axil) to the appearance of undifferentiated tissue that, with time, develops a necrotic surface.

To our knowledge, no data are available to determine if poor branching of Lilo and Red Sails poinsettias is a result of poor axillary bud development or correlative inhibition by the apex or if axillary bud development is predetermined by factors occurring during stock plant production, propagation, or finished plant production. Our objective was to test the hypothesis that high temperature inhibits axillary bud development in poinsettia, resulting in poor lateral shoot development, and, if the hypothesis is true when during plant development is exposure to high temperature effective.

Materials and Methods

Experiment 1. Fifty rooted Lilo cuttings were received from a commercial grower (Paul Ecke Poinsettia Ranch, Encinitas, Calif.), transplanted into pots 15 cm in diameter (1200 cm³), and placed in a greenhouse that was maintained at 21 ± 1 °C. Shade cloth reducing photosynthetic photon flux (PPF) by 50% was placed above the plants for 1 week.

After 2 weeks, 25 plants were placed in each of five growth chambers (model E-15; Conviron, Asheville, N.C.) maintained at 21, 24, 27, 30, or 33 ± 1 °C. Plants were exposed to a PPF of 600 ± 30 μmol·m⁻²·s⁻¹ from fluorescent and incandescent lamps for 16

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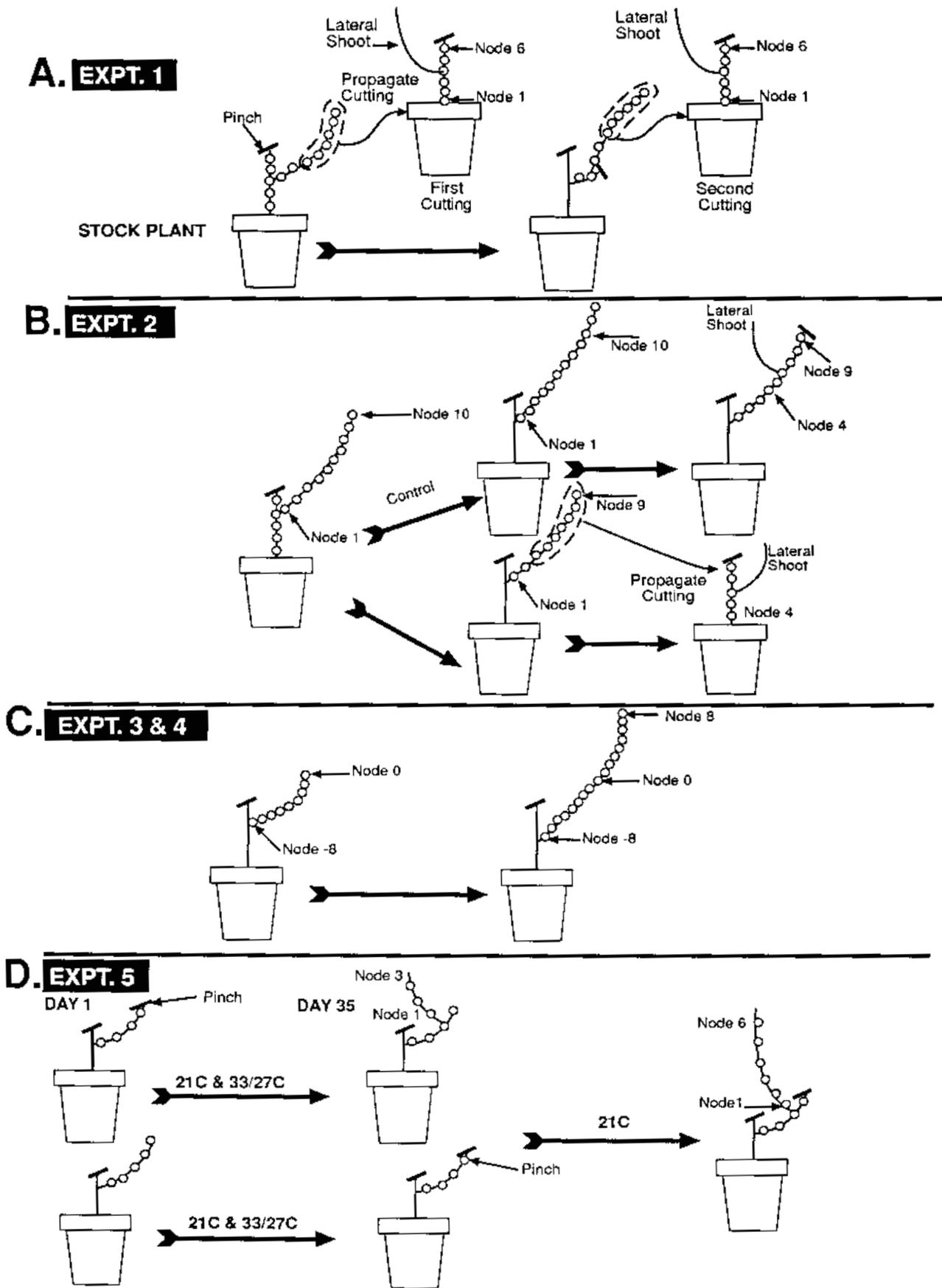


Fig. 1. Diagrams of plant morphology for experiments (A) 1, (B) 2, (C) 3 and 4, and (D) 5.

h-day⁻¹. The shoot apex was removed 1 d after plants were placed into the growth chambers, leaving five nodes on the plants (Fig. 1A). Severe interveinal chlorosis had developed on the leaves by the 12th day after apex removal, especially at 30 and 33 °C. Therefore, the PPF was reduced to 300 μmol·m⁻²·s⁻¹ in all growth chambers, and the night temperature in the 30 and 33 °C chambers was reduced to 21 °C.

The number of lateral shoots that developed on each stock plant was recorded. When seven to eight leaves had unfolded, 72 to 104 cuttings per temperature treatment were taken from these lateral shoots, leaving two nodes per lateral. The number of lateral shoots that developed from these two nodes was recorded, and a second group of 28 to 66 cuttings per temperature treatment was removed from the stock plants.

Half of the cuttings removed from the stock plants were shipped via overnight delivery to the Paul Ecke Poinsettia Ranch, and the other half were rooted at the Michigan State Univ. Research Greenhouses, East Lansing, Mich., in oasis strips maintained at 26 °C. The rooted cuttings were transplanted 3 to 4 weeks later into 15-cm pots and placed in a greenhouse maintained at 21 ± 1 °C. These plants were pinched 1 to 2 weeks after being transplanted, and the number of lateral shoots that developed was recorded after 60 d. Experimental results from Michigan- and California-grown plants did not differ statistically (Table 1); therefore, the data presented have been pooled for this paper.

The following grading system was used to describe lateral shoot development from the first and second flush of shoots from the plants grown in Michigan: 1) shoot > 3 cm long, 2) shoot < 3 cm long, and 3) no shoot developed.

Experiment 2. One-half of the lateral shoots on Lilo stock plants were removed and propagated (Fig. 1B). The other half of the lateral shoots remained on the stock plant in a 21 °C greenhouse for the duration of the experiment (i.e., the control group). Axillary buds on nodes 4 through 9 on the cuttings and the control group lateral shoots were rated according to the following scale: 1) well-developed bud (bud was green, necrosis was not present, and first leaf was visible), 2) poorly developed bud (necrosis affected all or part of the bud and/or no visible leaf), 3) axillary bud not visible (leaf axil was devoid of an axillary bud). Twenty or more axillary buds were identified in the cuttings and the control group as fitting into each of the three ratings.

The cuttings were propagated, transplanted into pots 15 cm in diameter (1200 cm³) and placed in a greenhouse maintained at 21 °C. The propagated cuttings and the lateral shoots remaining on the control group were pinched above node 9 two weeks after the rooted cuttings were transplanted. Six weeks later, the number of lateral shoots that developed from the rated axillary buds was recorded.

Experiment 3. Thirty-six Red Sails plants (six per treatment) grown under long days at 21 °C were moved into a high-temperature treatment for 0, 2, 4, 8, 16, or 32 d, then returned to the 21 °C greenhouse. The high-temperature treatment, hereafter referred to as 33/27 °C, consisted of a 16-h day in which the temperature was set at 30 °C during the first 3 h, 33 °C for the next 10 h, and 30 °C for the last 3 h. The greenhouse temperature was 27 °C for 8 h during the night. The location of the most recently unfolded leaf (node 0), defined as a leaf longer than 1 cm and reflexed to at least 45° from the lateral shoot axis, was recorded at the time of transfer to the 33/27 °C greenhouse (Fig. 1C). Nodes that unfolded after the start of the experiment were assigned positive numbers, 7 being the youngest node. Axillary buds were rated as viable or not viable, according to the scale used in Expt. 2, after ≈12 leaves unfolded on the shoots beyond node 0. Viable axillary buds were defined by

rating 1, while nonviable buds were defined as ratings 2 and 3. One lateral shoot was examined per plant. Eight nodes were examined per lateral shoot.

Experiment 4. Thirteen Red Sails plants initially were grown in the 33/27 °C treatment for 1 month and then moved into a 21 °C greenhouse. The most recently unfolded leaf was recorded at the

Table 1. Significance of F values from general linear model of treatments on the axillary bud viability rating from Expt. 1.

Source	F value	Significance
Location (L)	0.1	NS
Temperature (T)	142.1	***
Node no. (N)	3.4	**
Flush (F)	272.4	***
L × N	4.7	***
L × T	2.3	NS
T × N	4.5	***
L × F	0.0	NS
T × F	6.3	***
F × N	1.4	NS

NS, **, *** Nonsignificant or significant at $P < 0.01$, or 0.001, respectively.

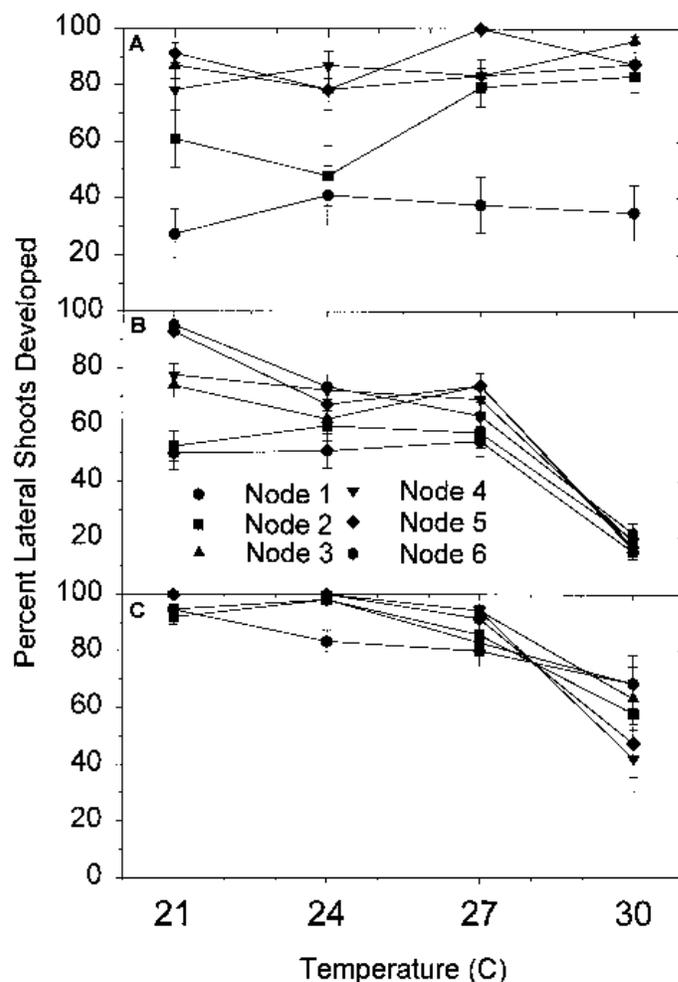


Fig. 2. The effect of temperature and node number on axillary bud development in 'Eckespoint Lilo' poinsettia (Expt. 1). (A) Stock plants after pinching, (B) first-flush cuttings removed from stock plants, and (C) second-flush cuttings removed from stock plants. Rooted cuttings were placed at the indicated temperatures, then pinched. Nodes were numbered from the basal (node 1) to the apical (node 5) part of the shoot. Error bars represent 95% confidence intervals.

time of transfer (node 0) (Fig. 1C). The nodes subtended by leaves that unfolded before the start of the experiment were assigned negative numbers, -8 being the oldest node recorded. Those subtended by the eight leaves that unfolded after the start of the experiment were assigned positive numbers, node 8 being the youngest. Axillary buds were rated in the same manner as in Expt. 3 after ≥ 10 leaves unfolded during the 21 °C treatment. Two lateral shoots were examined per plant. About 17 nodes were examined per lateral shoot. All visible leaf axils examined possessed a viable axillary bud before the start of the experiment.

Experiment 5. Sixteen Red Sails plants that had been grown for 60 d under long days at 21 °C were placed in greenhouses maintained at 21 °C or 33/27 °C. The time of transfer is considered day 1 of the experiment. Four plants in each greenhouse were pinched at the start of the experiment on day 1, while the remainder of the plants were pinched on day 35 (Fig. 1D). Many more nodes were removed on day 35 than on day 1 so that all laterals would

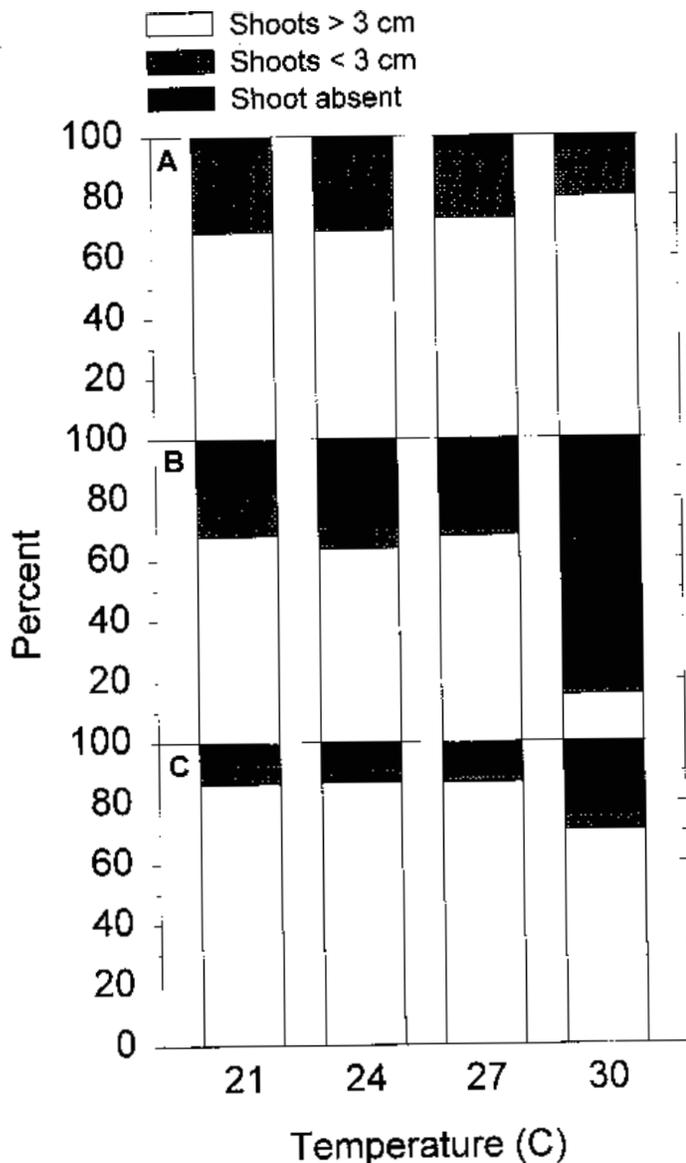


Fig. 3. The effect of temperature on type of axillary shoot developed from 'Eckespoint Lilo' (Expt. 1). (A) Stock plants after pinching, (B) first-flush cuttings removed from stock plants, and (C) second-flush cuttings removed from stock plants. Rooted cuttings were placed at the indicated temperatures then pinched.

have the same nodes released from apical dominance. On day 35, all plants were placed in a greenhouse maintained at 21 °C.

The six basipetal (i.e., lowermost) axillary buds (nodes 1 to 6) on the lateral shoots that developed after pinching on days 1 and 35 were rated in the same manner as in Expt. 3 after six or more leaves unfolded on the lateral shoots. Nine lateral shoots were examined per plant. Six nodes were examined per lateral shoot.

Results

Experiment 1. Although the temperatures at which the shoots developed did not affect the percentage of lateral shoots that developed on the stock plants, nodal position did (Fig. 2A). Thirty-five percent of the basal nodes (Node 1) and 90% of the apical nodes (Node 6) produced lateral shoots. The plants grown at 33 °C developed severe chlorosis and died before data were collected.

The percentage of lateral shoots that developed from the first flush of cuttings removed from the stock plants grown at 30 °C averaged only 21%, while that of cuttings from stock plants grown at 21, 24, and 27 °C averaged 74%, 65%, and 66%, respectively (Fig. 2B). In general, the basal nodes (nodes 1 and 2) on plants from the 21, 24, and 27 °C treatments produced fewer shoots than the apical nodes (nodes 5 and 6).

The percentage of lateral shoots that developed on the second flush of cuttings removed from the stock plants was significantly higher than on the first flush (Fig. 2C). As with plants from the first flush of cuttings, axillary bud development in the 30 °C treatment was significantly lower than that at cooler temperatures. Unlike that of cuttings from the first flush, differences among nodes on the second flush were smaller.

After the initial apex removal on the stock plants, 20% to 30% of the nodes produced no shoots or shoots <3 cm long (Fig. 3A). Less than 7% of the axillary buds failed to produce any shoot, regardless of temperature. In contrast, on the first flush of cuttings (Fig. 3B), 54% of the axillary buds failed to develop into shoots >3 cm long. From the stock plants grown at 30 °C, 83% of the nodes on the first flush of cuttings (Fig. 3B) and 25% of those on the second produced no lateral shoots (Fig. 3C).

Experiment 2. The axillary bud rating at the time of cutting removal was a good indicator of lateral shoot development after propagation and pinching. Of the buds rated as viable before cutting removal, 83% developed a lateral shoot after propagation. Of the buds that were partially necrotic or had no visible leaf, 38% developed a lateral shoot after propagation. Of the nodes on the control group, 45%, 5%, and 0% of the nodes on the control group developed lateral shoots when the initial nodal rating was 1, 2, or 3, respectively.

Experiment 3. Transferring plants from 21 °C to 33/27 °C for 16 or 32 d reduced the percentage of viable axillary buds on nodes 3 through 7 (Table 2); holding plants at 33/27 °C for 8 d or fewer did not reduce viable axillary bud count. The first two nodes that developed after the initial transfer were not influenced by the 33/27 °C treatment, while node 4 was the first node to be completely inhibited in the 32-d treatment. All buds in the axils of leaves that unfolded before the initial transfer were viable (data not shown).

Experiment 4. Transferring plants from 33/27 °C to 21 °C increased the percentage of viable axillary buds (Fig. 4). Nodes -8 to -4 were not influenced by the temperature change, while nodes -3 to 0 (i.e., the four youngest nodes whose leaves unfolded before transfer to 21 °C) displayed an increase in bud viability. Of the nodes developed after being transferred to 21 °C, 62% to 95% yielded viable axillary buds.

Experiment 5. Plants grown at 21 °C and pinched on day 1 or 35

produce 89% or 83% viable axillary buds, respectively, on the lateral shoot that emerged after pinching (Table 3). Plants placed into the 33/27 °C treatment for 35 d and then pinched produced 75.8% viable axillary buds on the lateral shoot that emerged after pinching. However, plants pinched on day 1 and placed into the 33/27 °C treatment for 35 days produced only 22.2% viable buds on the lateral shoots that emerged after pinching.

Discussion

Results presented in this paper support the hypothesis that high temperatures inhibit axillary bud development in Lilo and Red Sails poinsettia, resulting in poor lateral shoot development. Visual observations of poinsettia leaf axils indicated that, at times, the axil was completely devoid of an axillary bud, while at other times the "bud" consisted of a mass of undifferentiated cells. High temperatures (>27 °C) interrupted or prevented axillary bud initiation, development, or both. Blind leaf axils (rating 3) did not produce lateral shoots, and poorly developed (rating 2) axillary buds did not consistently produce lateral shoots.

Buds developing in the axils of folded leaves were sensitive to high temperatures, but once leaf unfolding occurred, they were no longer sensitive. Viable axillary buds released from apical dominance developed into lateral shoots regardless of temperature. Consequently, one cause of poor branching in poinsettias was exposure of plants to temperatures >27 °C. If plants pinched shortly after propagation fail to branch properly, high temperatures probably occurred during stock plant production. However, other environmental problems, such as drought stress or high media salinity, should also be considered.

Temperatures during propagation often were >27 °C; however, our data show that viable axillary buds will produce a lateral shoot regardless of temperature (Expt. 1) and propagation process (Expt. 2). In other words, viable axillary buds do not degrade during propagation. The percentage of lateral shoots that developed from viable axillary buds on the control group in Expt. 2 was lower than that from the viable buds on the cuttings due to stronger apical dominance of the apical nodes of the control group. The reason for this result is that when a rooted cutting is pinched, typically all five remaining nodes will be released from apical dominance; however, when a lateral shoot is pinched on a multi-stemmed stock plant (the control), typically only the top two to four nodes may be released from apical dominance.

Viable quiescent axillary buds exposed to high temperatures will produce a lateral shoot that also has viable axillary buds if cool temperatures are provided after pinching (Expt. 5). However, lateral shoots that emerge in a high-temperature environment will

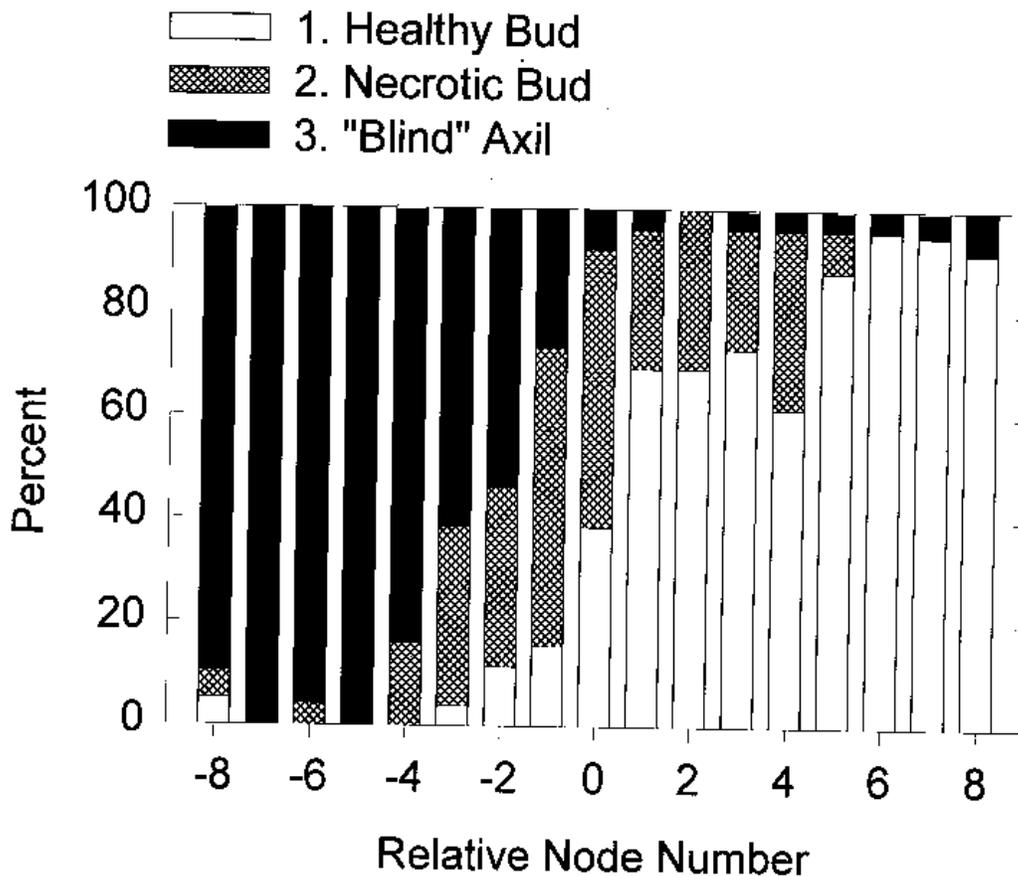


Fig. 4. Effect of high temperature on axillary bud development of 'Eckespoint Red Sails' poinsettias initially grown at 33/27 °C and then transferred to 21 °C. Node 0 indicates the most recently unfolded leaf at the time of transfer. Negative numbers indicate nodes whose leaves unfolded before transfer, while positive numbers indicate nodes whose leaves unfolded after transfer. (Node -8 was the oldest; node +8, the youngest.) (Expt. 4)

produce a high percentage of nonviable axillary buds. Thus, high temperatures that may occur during propagation will not influence branching of a plant pinched 2 to 3 weeks after the propagation phase ends. Also, high propagation temperatures will not affect axillary bud development on the lateral shoots that emerge after pinching. High temperatures affect only axillary buds that are initiating and developing in actively growing shoot tips.

The maximum percentage of axillary bud or lateral shoot development varied among experiments. For example, in Expt. 1, ≈90% of the axillary buds from the second flush of cuttings developed lateral shoots, while only 70% of the axillary buds from the first flush of cuttings developed lateral shoots. The reason for the variability is not clear, although it possibly is due to an interaction with some other environmental factor. For example, axillary bud development may have been influenced by PPF, since the first flush of cuttings was exposed to 600 μmol·m⁻²·s⁻¹ for 2 weeks, while the second flush of cuttings was only exposed to 300 μmol·m⁻²·s⁻¹. The higher PPF may have increased plant temperatures, especially considering that fluorescent and incandescent lamps were used without a thermal energy filter (Faust and Heins, 1996).

Transferring stock plants from 33/27 to 21 °C improved axillary bud development. Of the axillary buds from nodes that developed after transfer, 70% were viable. When stock plants were transferred from 21 °C to 33/27 °C for 32 d, three leaves unfolded after the transfer before bud development was affected. Perhaps the negative effect of high temperatures during early stages of bud development can be overcome by cooler temperatures later in

development, and later stages of bud development are less sensitive to high temperatures.

Sixteen consecutive days at 33/27 °C were required to inhibit bud development of Red Sails in Expt. 4; however, the response of poinsettias to high temperature may be quantitative. In other words, as temperature increases above the critical 27 °C, fewer days may be required for inhibition. Likewise, different poinsettia cultivars may exhibit different degrees of high-temperature sensitivity. Our results indicate that Lilo would require fewer days at high temperatures than Red Sails (i.e., the former is more sensitive to high temperatures). In separate experiments in which plants were grown continuously at 33/27 °C, 'Eckespoint Freedom' also displayed a reduction in the number of lateral shoots developed; however, 'Eckespoint Freedom' is considerably less sensitive to high temperatures than Red Sails.

In summary, poor branching appears to be a result of at least two factors. First, apical dominance results in a decreased percentage of lateral shoots developing on nodes positioned lower on the stem. Second, incomplete development of axillary buds prohibits lateral shoot development after pinching. Poor axillary bud development is the major problem during commercial production of Lilo and Red Sails when greenhouse temperatures cannot be adequately controlled.

Poinsettias regenerated following heat treatment or suspension culture branch poorly. Although axillary buds on these plants are well-developed (personal communication, Kirsten Rasmussen, Aaslev, Denmark), only one or two shoots develop after apex removal (personal communication, Walter Preil, Ahrensburg, Germany), indicating that these plants possess extremely strong correlative inhibition. Considerable research has been undertaken to identify the factor that promotes branching of poinsettia; however, even if the branching agent proposed by Dole and Wilkins (1994) is identified, this solution may explain only the apical dominance problem, not the axillary bud development problem.

The goal for the commercial poinsettia propagator is to produce viable axillary buds on the stock plants, which can be accomplished by maintaining temperatures at ≤27 °C during stock plant production of Lilo and Red Sails. Since temperatures are often ≥27 °C, increased shading and misting plants with water may help reduce temperature. Bud viability on stock plants may be monitored before harvesting cuttings to prevent propagation of cuttings that will not produce well-branched plants. The soft-pinch leaf

Table 2. Effects of the duration of a high day-temperature treatment on the axillary bud development of 'Eckespoint Red Sails' poinsettias in the leaf axils of nodes 0 to 7. Node 0 refers to the node with the most recently unfolded leaf at the time of transfer, while nodes 1 through 7 represent the nodes that developed after the start of the experiment (Expt. 3).

Days at 33/27 °C	Nodes developing lateral shoots (%)							
	Node (no.)							
	0	1	2	3	4	5	6	7
0	100	100	100	100	100	100	100	100
2	100	100	100	100	100	100	100	100
4	100	100	100	100	100	100	100	100
8	100	100	100	100	100	83	100	100
16	83	100	83	83	33	33	67	83
32	100	100	100	83	0	0	0	0
Source	F value							Significance
Days (D)	93.6							***
Node no. (N)	14.0							***
D × N	11.6							***

***Significant at $P < 0.001$.

Table 3. Effect of temperature and pinch date on the axillary bud viability of 'Eckespoint Red Sails' (Expt. 5). The temperature treatments were delivered during the first 35 days of the experiment. All plants were grown at 21 °C after day 35.

Temp (°C)	Pinch date	Axillary bud viability (%)					
		Node no.					
		1	2	3	4	5	6
21	1	93.2	68.1	80.7	94.3	100	100
	35	80.2	57.8	73.6	91.3	95.9	100
33/27	1	57.0	15.0	4.2	11.5	31.0	14.3
	35	89.7	58.6	78.1	71.1	82.3	75.0
Source		F value				Significance	
Temperature (T)		85.0				***	
Pinch date (P)		210.4				***	
Node (N)		33.7				***	
P × T		135.9				***	
P × N		11.9				***	
T × N		4.8				***	
P × T × N		2.4				*	

***Significant at $P < 0.05$, or 0.001, respectively.

removal technique (Berghage et al., 1989) can be used to improve branching by providing more nodes and, thus, more potential lateral shoots (Hughes et al., 1991) on shoots with improperly differentiated basipetal buds. If temperature control during stock plant production is not possible, then the problem of poor lateral branching in poinsettias must be resolved by selecting cultivars not sensitive to, or only slightly sensitive to, high-temperature-induced axillary bud inhibition. If viable axillary buds are present but poor branching still occurs, other causes may need to be considered, such as drought stress, high media salinity, poor root development, and root diseases.

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