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ENVIRONMENTAL AND PHYSIOLOGICAL FACTORS INFLUENCING PREMATURE CYATHIA ABSCISSION IN EUPHORBIA PULCHERRIMA WILLD.

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Steven H. Miller

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Royal D. Heins

Major professor

Royal D. Heins

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By

Steven H. Miller

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ABSTRACT

ENVIRONMENTAL AND PHYSIOLOGICAL FACTORS INFLUENCING PREMATURE CYATHIA ABSCISSION IN *EUPHORBIA PULCHERRIMA* WILLD.

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Low irradiance levels, high temperatures, and water stress all promoted cyathia abscission in poinsettia. Low irradiance appeared to be the primary environmental factor promoting abscission. Compared to plants maintained under normal daylight (ND) at 16°C night temperature (NT) abscission was 62% greater on plants placed under 75% shade 4 weeks after the start of short days. Increasing the NT from 16° to 21° while simultaneously moving plants to shade only increased abscission an additional 10%. Repeatedly water stressing plants to - 0.6 MPa usually promoted abscission when plants were grown under ND, but not when placed under shade. Leaf removal on plants with intact bracts promoted abscission prior to anthesis, while bract removal on plants with intact leaves decreased abscission. Carbohydrate levels increased in leaves on plants with bracts removed but carbohydrates decreased when bracts were present.

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Anatomical Aspects of Abscission

Description of abscission zone. At the base of most plant organs is a region called the abscission zone where the changes that preceed abscission occurs. The abscission zone forms during ontogony (55) in leaves, floral parts, and fruits, but may be induced by several factors (89, 188). The leaf abscission zone is usually very conspicuous in some herbaceous species (95, 187) as is the abscission zone for flowers (89, 200) and perianth segments (66).

Cells in the abscission zone do not differentiate to full maturity as do cells of adjacent tissues, which defines the zone as a region of arrested development (8). Cells and structures in tissues distal to the abscission zone (i.e. fibers, laticifers, resin canals) may be absent or much less developed in the abscission zone (8).

In the zone, cells are smaller, more densly filled with cytoplasm (23, 103, 113, 155), with fewer vacuoles and less cell-wall deposition (8). The limited cell-wall development does not mean the zone cells are weak. Often the zone is initially as strong as adjacent tissues but only weakens prior to seperation (46, 120, 174). However, weakness is sometimes found in the abscission zone. A well defined grove is frequently formed at the insertion of some abscising organs which increases the structural weakness of the zone, however the groves do not

necessarily have any relation to abscission (89). Additional weakness can also occur in the zone by a swelling of the cell walls prior to separation (23, 95, 139, 200).

In vascular tissues of the abscission zone, only tracheary elements may be present (54). In the region where separation occurs, there is a lack of sclarification in the cells of the pith with short, broad tracheary elements (185). The concentration of vascular tissue is in the center rather than the periphery which presumably weakens the zone (55). In Phaseolus sp. vascular bundles fuse to form a ring (8). This was also observed in the leaflet abscission zone of Citrus (100).

In the abscission zone, cell division usually occurs prior to cell separation (187). However, careful study of the patterns of separation in the abscission zones of several species led to the conclusion that cell division was not always an essential aspect of abscission (8). Gawadi and Avery (61) reported that leaf abscission in poinsettia occured without cell division. Baird and Webster (15) found that cell division did not occur in the abscission zone of mature fruits, nor was cell division found prior to flower abscission in several solanaceous species (89). However, in cases where cell division occurs prior to cell separation, the purpose of cell division is for the development of the separation and primary protective layers (8). Cell division in the abscission zone commonly occurs in the pith, cortex, epidermis, and living cells of the vascular tissue (188). The result is the formation of several tiers of cells, the distal tier(s) usually becomes the separation layer and the proximal tier(s) forms the

primary protective layer (8).

Separation layer. The separation layer is almost always restricted to a narrow band of cells, often only a single layer thick. These cells secrete the enzymes necessary for the cell-wall hydrolysis and separation. Separation layers in leaves and lateral structures are usually parallel to the surface of the supporting stem, although significant variations can exist. In legumes separation always takes place in a rather abrupt transition region between the pulvinus and the leaf stalk (26). In Sambucus separation occurs following the positional differentiation of special "target" cells in the abscission zone that grow and lose their adhesiveness in response to endogenous ethylene (134).

Cell separation usually occurs after cell division and can initiate in any tissue of the separation layer as considerable variation exists among species (188). In Coleus leaf abscission (110) the usual abscission pattern is for separation to begin in the abaxial side of the petiole through the epidermal and cortical tissue, until the leaf is supported only by the adaxial part of the cortex and xylem elements. In leaflet abscission of Phaseolus, (186) separation may start internally through the pith cells and proceed outward.

Separation of cells in the abscission zone occurs three ways: mechanical breakage involving non-living cells of the vascular tissue (185), dissolution of the middle lamella (95), and dissolution of the middle lamella and primary wall (187). Flower abscission follows these

same general patterns (89, 200) but usually happens faster than leaf abscission (156), and is frequently associated with meristematic activity in the separation layer (66, 76, 86, 104, 105, 200).

Cell enlargement in the abscission zone often occurs prior to and after separation (54, 188). In leaf abscission differential enlargement in the distal and proximal sides of the abscission zone creates shear forces across the cell walls which result in the leaf being forced off the plant by cell expansion in the proximal side (97). The differential enlargement in leaves has been associated with abscission in a number of species (23, 61, 112, 153). However, cell enlargement is normally not observed before abscission of floral parts (89, 104, 105).

Protective layer(s). A primary protective layer develops proximal to the separation layer to protect the new surface from injury and water loss (54). In herbaceous species, the layer usually consists of little more than the tissues exposed by separation with suberin and lignin deposited between the outermost cells. There may be little or no cell division (61). However, in most species, cell division occurs well before abscission, resulting in several tiers of cells proximal to the separation layer which form the primary protective layer (8). Next, a periderm develops beneath the protective layer, which usually becomes continuous with the periderm of the stem (187). In some cases, the outermost cells of the protective layer may collapse shortly after exposure to the air, but still form what appears to be an effective protective layer (8).

One or more secondary protective layers can develop beneath the primary protective layer in several woody genera (95). In Cornus, Tilia, and Gleditsia a separation layer can develop distal to the secondary protective layer by abscission of the primary protective layer (8). Secondary protective layers across leaf scars usually become continuous with the periderm of the stem (95). The development of protective layers often involves expansion of parenchyma tissues which can crush and close off the functional phloem (8).

Hormonal Regulation

The involvement of hormones in abscision was first postulated by Laibach and Maschmann in 1933 (93). Since then extensive research has been conducted to determine the role of plant hormones in the abscission of plant organs. Several hypothesis have been developed which associates each of the known plant hormones with abscission.

Auxin. Auxin (IAA) was the first of the major plant hormones to be identified. Mai (107) showed that orchid pollen (known to be a source of auxin) delayed the abscission of debladed petioles. La Rue (94) confirmed Mai's work with Coleus and Ricinus by applying synthetic IAA. Other workers also concluded that auxin plays only an inhibitory role in abscission (110, 175). However, auxin inhibits abscission only when applied distally to the abscission zone (6). Proximal applications of auxin accelerate abscission (33, 84, 101, 102, 167, 180). As separation approaches, the ratio of free-extractible auxin on the proximal verses

distal sides of the abscission zone decreases in bean (158) and cotton (29). Abscission can be accelerated if distal IAA application is delayed (33). High concentrations of naphthalene acetic acid (NAA) inhibited abscission while a low concentration promoted abscission in bean explants (145). An early application regardless of concentration, inhibited while a late application promoted abscission of bean explants (145) and in apple leaf petioles (17). This was the basis for a two-stage hypothesis (146). In stage I auxins tend to retard or inhibit abscission and in stage II auxins accelerate abscission (146). Later research with explants identified the role of auxins and ethylene in these two stages (83). Stage I is the auxin dependent stage when the tissue is relatively insensitive to ethylene and a period during which normal auxin inhibition of abscission gradually diminishes and is lost (8). The length of stage I was found to decrease with leaf age (33). During stage II, auxin and ethylene accelerate abscission (33, 200). The active biochemical and structural changes of separation take place in stage II. Senescing tissue produces large amounts of ethylene which generally promotes abscission (184).

The auxin gradient concept was later developed to summarize the aspects of auxin physiology and abscission in bean leaf explants (8). The concept involves two main fluxes of auxin in bean explants; a flow of auxin from the leaf, and a flow of auxin down the stem. This creates an auxin concentration gradient across the abscission zone and appears to be the primary controlling factor in leaf abscission (8, 9, 84). This would explain why a high concentration of auxin distal to the abscission

zone tends to delay leaf abscission and a high concentration proximal to the zone promotes abscission. As the ratio of proximal to distal auxin concentration increases (as auxin moves across the abscission zone) the process of abscisssion proceeds (8).

Ethylene. Early work on ethylene grew out of observations that illuminating gas induced leaf abscission in greenhouse crops (205). Shull (159) first observed that ethylene induced leaf abscission in pot roses. Addicott (6) states that ethylene is not always required for abscission to develop (24) although it is involved with abscission in several species.

Much of the recent information on ethylene-induced abscission has come from working with plant explants. Jackson and Osborne (82) reported that very little ethylene was released from explant tissues distal to the abscission zone until immediately after abscission. Bean explant sensitivity to ethylene depends on the explants stage of sensitivity (83). During stage I, explants are relatively insensitive to applied ethylene, however, during stage II, explants begin to abscise as ethylene levels increase (8, 184). Evidence for stage I explant insensitivity to ethylene compared to stage II show ethylene-mediated increases in protein synthesis occured in stage II explants, but not in stage I explants (3). Ethylene treatment during stage I increased the effectiveness of a treatment during stage II by reducing break strength in the explant (2). Exogenous ethylene applied in stage I explants inhibits polar transport of auxins, increases IAA oxidase activity, and decreases the level of diffusible auxin (71, 118, 132, 173). During

stage II, applied ethylene enhances pectinase activity (119), increases cellulase activity (78), and decreases break strength (37).

Osborne (131) has suggested that the initial stimulus for abscission is a hormonal imbalance due to environmental changes and endogenous competition; this hormonal imbalance would mediate localized senescence of cells in the abscission zone, leading to an increase in ethylene synthesis which would be the signal for abscission. Ethylene only affects cells in the abscission zone by promoting synthesis of hydrolytic enzymes or enzymes involved in growth of cells in the proximal tissue (131).

Abscisic acid. Okhuma et al (129) first demonstrated that abscisic acid(ABA) was an abscission regulator in rapidly abscising cotton bolls. The activity of ABA was equal to or slightly greater than ethylene (22). Application of ABA has promoted abscission in leaves (35, 50, 52, 136, 147, 162), branches (152, 194), flowers (7, 111, 137, 178) and fruit (11, 36, 51). Application of ABA accelerated leaf abscission in explants (1, 14, 23, 37). Many studies have established or strongly indicated a hormonal role of ABA in the promotion of abscission (50, 163, 176, 177) as high levels of endogenous ABA have been found in abscising organs (47).

It is now however beleived that ABA has little or no direct effect on leaf abscission of explants or to intact plants (111). The rise in ABA could be the result of waterstress, which is known to cause a sharp increase in ABA (86, 195, 201). Applied ABA was only effective in inducing leaf abscission when a high dosage was applied (111).

However, it is beleived that ABA stimulates leaf abscission due to an indirect affect of unphysiologically high concentrations of ABA stimulating ethylene production (111). Abeles et al (2) reported that ABA plus saturating levels of ethylene was more promotive of abscission than ethylene alone. The abscission promoting effects of ABA occur during stage II (37) by reducing IAA transport in explants (32) but there is no evidence that ABA effects abscission if applied during stage I (37, 72). Craker and Abeles (37) observed that ABA increased cellulase activity in the abscission zone.

Gibberellins. Applications of gibberellins have caused little or no abscission from intact plants (165, 192) even though it has been tested on hundreds of plants (8). However, gibberellins have been shown to accelerate leaf abscission in explants at high concentrations (19, 29, 34), but to retard abscission at low concentrations (103). In most cases applied gibberellins stimulated fruit development and reduced abscission of young fruits (39, 138, 182).

Applied gibberellins inhibit or delay abscission because the gibberellins intensify the ability of an organ to function as a nutrient sink (8). Gibberellins can influence abscission by increasing the synthesis of IAA in plant tissue promoting abscission (121). However, this effect may be responsible for the abscission retardation at low dosages of gibberellin (8). It is likely that gibberellin-induced increase in auxin intensifies the activity of nutrient sinks (8).

Cytokinins. The effect of cytokinins affect on abscission is not well documented in the literature, although two modes of action have been

noted (8). First is the ability of cytokinins to enhance the sink strength of organs to which it is applied. Cytokinins stimulated growth, induced parthenocarpic development and decreased fruit abscission (38, 98). Kinetin induced an incease in soluble reducing sugars, soluble proteins, dryweight, and chlorophyll (202, 203). Cytokinins also delayed senescence in portions of leaves to which it was applied (96, 120).

Secondly, cytokinins can inhibit abscission (64). Cytokinin applied directly to the abscission zone inhibited bean explant abscission (133). However, cytokinin applied to areas distant from the abscission zone accelerated abscission.

Biochemical Regulation

The main biochemical activities related directly to the separation process are the production, secretion, and action of enzymes which attack and degrade the middle lamella and cell walls (8). A second biochemical activity which involves the deposition of cell wall materials is occuring simultaneously with the degrading activity (8). Molisch (114) was the first to suggest the possibility that separation was the result of enzymatic activity. However, the knowledge of enzymes accrued slowly and it was not until the last two decades that the present concepts developed. An important advent was the discovery that oxygen is an absolute requirement for physiological separation and that the recognized enzymes of oxidative respiration were also necessary (28).

The discovery of how DNA controls the synthesis of an enzyme led plant physiologists to observe that changes in RNA and protein synthesis preceded abscission. The activity of DNA and RNA are significant in the control of abscission, since these changes lead to changes in hormone levels exported to plant organs. The hormonal changes appear to be the primary signal for abscisison from the organ to the abscission zone (8). Principle enzymes involved in degredation of cell walls, particularly the cellulases and pectinases have received the most attention in the literature.

Cellulases. Increased cellulase activity has been correlated with abcission in bean explants (78), Citrus (65, 140), and other species (132). Lewis and Varner (99) concluded that increased cellulase activity in bean leaflet abscission zones was due to de novo synthesis and detected two forms of cellulase in the abscission zone. Subsequent investigations disclosed the existance of several isozymes of cellulase in the abscission zone (63, 99, 141). However, only one of the isozymes appears closely correlated with abscission (155). In contrast, other researchers have found that cellulase activity was not associated with abscission (73). From electron micrograph studies, cell separation was acheived almost entirely by dissolution of the middle lamella, with little cellulose breakdown apparent at the time of separation (8). Cellulase appears to function in the development of the protective layers, however its involvement in cell separation remains in question (8).

Pectinases. Molisch (114) was the first to point out that an enzyme might be involved in the dissolution of the middle lamella. The dissolution of the middle lamella and/or cell walls have been associated with the abscission of floral parts (89, 104 155, 200).

A reduction in Pectin methlyesterase (PME) activity has been correlated with increased abscission in Coleus (113), and in flower abscission of Nicotiana (197). These results suggest that abscission is facilitated in some way by a reduced ability of PME to esterify pectic substances (8). In studies with two cultivars of Nicotiana, Yager (198) found that the cultivar that retained flowers longer had higher levels of PME. However, a number of workers have reported their inability to find changes in PME correlated with abscission (2, 73, 113, 140).

Another pectic enzyme, polygalactonuronase (PGU) was found to rapidly increase immediately prior to the abscission of bean leaflets (119). Similarly, PGU has been identified in leaflet abscission zones of Citrus (143) and in fruit abscission of Citrus (65). Again, other workers have not been able to confirm PGU involvement in abscission (18, 73).

Physiological Regulation

Respiration. Carns (28) was the first to recognize that oxygen was an absolute requirement for physiological separation and that the recognized enzymes of oxidative respiration were necessary for abscission. Oxidative respiration is essential for abscission to occur

by providing the needed energy for enzymatic processes (8). Lowering the oxygen level to 5% inhibited abscission in Coleus explants (144). Measurement of respiration rates in bean explants by oxygen uptake showed that the abscised explants exhibited a "climacteric" rise in respiration while those that did not abscise showed a slow decline in respiration (29). The loss of carbohydrates in abscising apple flowers was attributed to increased respiration (79).

Oxygen is also needed in the process of ethylene biosynthesis for the conversion of the intermediate 1-aminocyclopropane-1-carboxylic acid (4, 5) to ethylene.

Carbohydrate metabolism. Abscission of leaves, flowers, and fruits are directly related to the carbohydrate status of the plant (8). Abscission does not occur as readily under high levels of carbohydrates (8, 10, 151). High carbohydrate levels in the plant in general will contribute to increased vigor of fruits and leaves and will enable such organs to synthesize hormones which apparently inhibit abscission (8). Decreased carbohydrate levels promote abscission in fruit (31, 150, 151), leaves (30, 70, 115, 127) and flowers (92, 166).

The effect of added sugars on organ abscission depends on the carbohydrate reserves within the plant or explant (20, 26). When the carbohydrate level is high, the addition of sugars helps maintain the integrity of cell wall polysaccharides inhibiting abscission; when the level is low, additional sugars promote abscission by providing a substrate for this energy requiring process (10, 20). When carbohydrate levels were high applications of sucrose strongly retarded leaf

abscission in bean explants (20, 26), however, sucrose stimulated leaf abscission in bean explants when carbohydrate levels were low (170).

Carbohydrate translocation. Primary sources of carbohydrates are usually leaves (128, 135, 164). Regions that utilize sugars are sinks, such as growing points of roots and shoots, storage organs (i.e. fruits and seeds), and vegetative tissues both above and below ground (128). Translocation of sugars occur down a concentration gradient, the concentration being higher at sources than at sinks (128). Studies have confirmed this source/sink phenomenon with radioactively labeled ^{14}C applied to source leaves (154, 168). The labeled ^{14}C tends to translocate towards developing sinks such as the root, apex of the shoot or unexpanded leaves (48, 117, 168).

It has been observed that the presence of developing fruits hastened the senescence of leaves and stems in bean and that removal of fruits and flowers delayed the onset of leaf senescence (114, 124, 154). Molisch (114) suggested that formation of flowers and fruits exhausts organic reserves in the plant. Developing flowers and fruits act as competing sinks for nutrients from source leaves. Leaves abscise as the flowers and fruits develop (8). Flowers and fruits are in some degree of competition with other flowers and fruits on the same plant. Often first-set fruits (150) and flowers (166) have a clear advantage over similar later forming organs which cause them to prematurely abscise (8, 12). In Lilium (49), the youngest flower buds prematurely abscise presumably as a result of competition for available carbohydrates, the youngest buds being the weakest sinks (56). Some species do not produce

flowers until there is substantial vegetative growth to support some reproductive activity (8). Cultivars of Phaseolus that produce fewer flowers per day have less flower abscission than heavier bearers (166). This is also true in many fruit species (40, 176, 196).

As discussed above the development of abscission zones in the plant can be regulated by the hormone status (8). It has been suggested that translocation of carbohydrates is hormone-directed (8, 135, 154). Developing parts of the shoot and root (sinks) produce their own specific hormonal signals (148). Carbohydrate translocation was promoted to the site of applied benzyladenine (BA) (12, 62, 157, 158), IAA (21, 62) or gibberellin (GA) (8, 157). Applied ethylene has both promoted (122) and inhibited (67) carbohydrate translocation. Abscisic acid has only shown inhibitory effects (8, 122, 194). These studies tend to support the hypothesis that carbohydrate translocation to a sink is under some form of hormonal control directly (154) regulating growth and abscission of organs in relation to their ability to attract carbohydrates (8). Addicott (8) proposed that strong sinks have a high IAA/GA/CK to moderate ABA ratio and weak sinks have a low IAA/GA/CK to moderately low ABA ratio. However, others beleive hormones do not directly affect carbohydrate translocation (62, 122, 142). Light has a promoting efect on carbohydrate translocation from source leaf to sink (168). Studies showed that light can promote vegetative (169) or reproductive (106, 116) sinks. Greenhouse rose flowering is influenced by the amount of carbohydrate available from photosynthesis for flower bud development (116). Shading vegetative or reproductive sinks

decreased ^{14}C translocation to the sinks (116, 151, 168). Shading flowers and pods of soybean reduced their subsequent sink strength and promoted abscission (76). Decreased carbohydrate translocation caused fruit abscission (151) and improper flower bud development (91, 106, 116, 171).

Differences in light quality (particularly red and far red light acting through the phytochrome system) are known to regulate plant development (59, 160). Curtis (41) and Decoteau and Cracker (45) have implicated phytochrome as a light sensing mechanism active in inhibition of dark-induced leaf abscission in mung bean. Abscission could be inhibited by red light and the inhibition reversible with far red light. Red light prevented or delayed flower and fruit abscission in apple (25, 87) and soybeans (75). Red light promoted ^{14}C-sucrose uptake in pea epicotyles (183) and rose shoots (117) but far red light inhibited uptake. Adding far red to red further enhanced uptake in rose shoots over red light alone (117). Far red light inhibited axillary shoot growth in rose (117), tobacco (88), and tomato (172), thereby promoting apical dominance, whereas red light promoted axillary shoots in rose (117). Mor and Halevy (117) believe far red light promoted greater sink activity in the apical shoot of the rose, thereby inhibiting axillary bud growth. Light may effect the unloading process at the sink by influencing membrane transport (85).

Environmental Regulation

Irradiance. The irradiance intercepted by the plant directly affects photosynthesis and subsequent carbohydrate supply (8). Irradiance levels high enough to promote accumulation of carbohydrates increases the vigor of leaves and fruits enabling such organs to synthesize hormones which inhibit abscission (8). High irradiance levels increase the amount of carbohydrate in source leaves to be translocated to developing vegetative (169) or reproductive sinks (116, 117). Supplemental lighting in the lower canopy of soybeans increased pod set, seeds per pod, and seed yield and decreased flower and pod abscission (76). Additional irradiance decreased flower bud abscission in Lilium (48).

Low irradiance levels provide low to moderate carbohydrate levels in the plant which tend to promote abscission (8). Low irradiance levels are commonly found in tree canopies where leaves are competing for carbohydrates causing less competative leaves to abscise (110, 149). Flower bud abscission in Iris (58), Gladiolus (69), Rosa (204), and tomato (90) increased due to poor irradiance conditions in greenhouses in the winter. In Lilium (49) flower bud abscission coincided with peak ethylene production. As photoperiod decreased, ethylene production increased (175). Shading decreased the amount of ^{14}C translocated to shaded areas (76, 116, 151, 168) and reduced the subsequent sink strength of flowers and pods in soybean promoting abscission (76).

A shortened photoperiod was found to be an important trigger for autumnal defoliation of many trees (60). However, increasing the

daylength prevented defoliation in Acer (130) and Plumaria (123). The correlation of leaf abscission sensitivity to photoperiod suggests that leaf abscission in the autumn in some species may be under the control of phytochrome (8). Curtis (41) and Decoteau and Cracker (45) found that red light inhibited dark-induced leaf abscission in mung bean; red light inhibition could be reversed by a brief exposure to far red light.

Temperature. Early workers had difficulty in distinguishing whether temperature imposed stresses that served as initiating factors of abscission or if temperature determined the rate of the abscission process (8). In extensive work with petal abscission, Fitting (57) recorded increasing rate of abscission as the temperature increased, as was more recently observed in petal abscission in the seed geranium (15). High temperatures also eliminated the effect of Ag^+ (a known inhibitor of ethylene action (18)) in inhibiting petal abscission in the seed geranium (112). As temperature increases, ethylene production increases. The ethylene production response to temperature behaves consistant to an enzyme activated system (27). More recent work defined temperature response curves which have been determined for explants of bean (199), cotton (108), and for petal abscission in Linum lewisii (190). The characteristic maxima for each species occured at 25°C, 30°, and 35° respectively. A Q-10 of ca. 2 was found for most temperature response curves, characteristic of most chemical reactions (8).

Leaf abscission is a common response to cold temperatures. Severe cold will kill the cells in the abscission zone thus, physiological separation is not possible (8). Light frosts that do not

injure the abscission zone can cause considerable leaf abscission in Citrus and Gossypium (8). Depending on species, varying degrees of cold are sufficient to induce abscission, and in some cases cold is the primary factor initiating autumnal defoliation of deciduous trees (8).

Excessively high temperatures also contributes to abscission, however, some of the high temperature effects may be the result of water stress rather than temperature itself (8). Weisner (189) observed that well-watered trees showed little or no leaf abscission at high temperatures. Leaf abscission that occured was on the lower and innermost leaves, not the leaves that received the most direct rays (189), which supports water stress rather than high temperatures that induced abscission (8). Flower buds, flowers, and young fruits abscise in response to high temperatures in crops such as snap beans (193).

Water stress. Leaf, flower, or fruit abscission often is in direct proportion to the severity of a water stress (181). Leaf abscission varies considerably among species and with leaf age (125, 161). Water stress induces chemical and biochemical changes that tend to promote abscission by affecting hormone levels (8). Water stress increased the activity of IAA-oxidase (42), decreased diffusible auxin (74), and decreased auxin transport (43). Itai (80), and Itai and Vaadia (81) reported a decrease in cytokinin activity in response to water stress. Water stress also increases endogenous ethylene levels (44, 67). Rapid increases in ABA levels were found in response to water stress (68, 86, 195, 201).

Conclusions

The abscission of organs from the plant body occurs in a region at the base of the organ called the abscission zone. Cells in the abscission zone are smaller and more densly filled with cytoplasm. Prior to abscission, the cells undergo considerable meristmatic activity forming a separation layer, protective layer(s), or both. Cells in the separation layer secrete the hydrolytic enzymes (cellulases and pectinases) necessary for cell-wall hydrolysis, separation, and protectve layer formation. Cells can separate three ways; dissolution of the middle lamella, dissolution of the middle lamella and primary wall, or mechanical breakage involving non-living cells of the vascular tissue. A primary protective layer consisting of periderm usually forms proximally to the separation layer to protect the newly exposed surface from injury or water loss. In some woody species a secondary protective layer may form. Cell enlargement often occurs prior to and after separation. Differential cell enlargement in the distal and proximal sides of the abscission zone creates shearing forces across the cell walls which results in abscission.

The initial stimulus for abscission appears to be a hormonal imbalance due to environmental changes and endogenous competition. This hormonal imbalance mediates localized senescence of cells in the abscission zone, leading to an increase in ethylene synthesis, which could be the signal for abscission. Ethylene enhances pectinase and

cellulase activity. For abscission to occur, all hormones probably modify the organs sensitivity to ethylene or promote ethylene synthesis. Auxin both inhibits and promotes abscission depending on the stage of sensitivity of the organ to ethylene and in the auxin concentration gradient across the abscission zone. Abscisic acid has been shown to promote abscission as ABA levels increase during water stress which enhances ethylene production. Gibberellins and cytokinins usually inhibit abscission by intensifying the plant organs ability to function as a carbohydrate sink, however, if levels of either hormone are low, ethylene is able to circumvent their inhibitory effect.

Oxidative respiration is essential for abscission to occur by breaking down energy-rich carbohydrates for the numerous enzymatic reactions involved.

Hormones play either a direct or indirect effect on controlling carbohydrate translocation from source to sink, therefore the level of carbohydrate at the abscission zone will determine whether the organ abscises or not.

Low irradiance levels or short photoperiods in long day plants decreases the sink strength of organs, promoting ethylene synthesis and abscission. Irradiance levels sufficiently high to accumulate carbohydrate increase the vigor of the organ enabling the organ to synthesize hormones that inhibit abscission. Leaf abscission in some species appears to be under the control of phytochrome.

High temperatures or water stress appear to induce abscission by increasing the rate of ethylene synthesis.

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Section I

Environmental Factors Influencing Premature Cyathia Abscission In Poinsettia 'Annette Hegg Dark Red'

Environmental Factors Influencing Premature Cyathia Abscission in Poinsettia 'Annette Hegg Dark Red'

Steven H. Miller and R. D. Heins[1]

Department of Horticulture, Michigan State University,

East Lansing, MI. 48824

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Abstract. While low irradiance levels, high temperatures, and water stress all promoted premature cyathia abscission in poinsettia 'Annette Hegg Dark Red', low irradiance appeared to be the primary factor promoting abscission in the greenhouse. Abscission was greater in plants placed under 75% shade at 16°C night temperature (NT) than on plants placed under normal daylight (ND) at 16° or 21° NT. The earlier plants were placed under shade after flower initiation, the lower the final plant dry weight, the earlier cyathia abscission started, and the greater the severity of abscission. A - 0.6 MPa water stress had no

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[1]Research Assistant and Associate Professor respectively.

consistant effect on abscission of plants grown under shade, while on plants grown under ND, water stress promoted abscission as NT increased from 13° to 21°. Under controlled experimental conditions at a constant irradiance, cyathia abscission increased as NT increased.

Introduction

Premature poinsettia cyathia abscission ("center drop") defined as premature abscission of the poinsettia cyathia prior to normal marketing, can be a major problem for poinsettia growers in the midwest and northeastern United States. Abscission of the cyathia in the greenhouse can occur either before anthesis (pre anthesis) or after anthesis (post anthesis) While not affecting growers every year, when the problem occurs, economic losses can be significant. Entire semi-loads of poinsettias have been rejected by buyers when cyathia abscission was found in the shipment (2).

Pre anthesis cyathia abscission has been observed on plants grown in the greenhouse under low irradiance levels (50% shade) (13) and on plants placed in a controlled environment under low irradiance and high temperatures before the bracts had completely developed (13, 17). Post-anthesis cyathia abscission has been observed on plants placed in postharvest environments (10, 11, 13), and on plants held in a dark storage (10, 11). The longer the dark storage, the greater the abscission. However, there have been no systematic investigation into environmental conditions that promote premature cyathia abscission or methods suggested to control the problem.

In preliminary experiments, low irradiance levels, high night temperatures late in crop development (finishing temperature) and water stress were found to promote cyathia abscission (Miller and Heins, unpublished data). Ethylene at 10 $\mu l\ l^{-1}$ had no effect on abscission when applied at anthesis. Chemical sprays at anthesis of napthalene acetic acid, 6-benzylamino purine (BA), or silver thiosulphate did not prevent abscission, however, gibberellic acid (GA-3) or Promaline(GA-4 + GA-7 +BA) prevented abscission as previously reported (12) but resulted in undesirable plant quality when applied at anthesis and delayed flowering when applied earlier in crop development.

The objective of the current studies was to determine the influence of irradiance, temperature, and water stress on premature cyathia abscission.

Materials and Methods

Greenhouse experiments.

General experimental conditions. Rooted cuttings of 'Annette Hegg Dark Red™' (AHDR) were received on Aug 25, 1983, from Paul Ecke Poinsettias, Encinitas, CA. One cutting was planted per 10 cm plastic pot (an experimental unit) in VSP medium (Michigan Peat Co., Houston, TX) composed of 2 peat : 1 perlite : 1 vermiculite (v:v:v) ammended with dolomitic limestone, superphosphate and trace elements. Plants were placed in a glass greenhouse and grown single stem at a spacing of 33

plants m^{-2} under normal daylight (ND) for 1 week. Short days (SD) were started on Sept 1. Black sateen cloth was pulled over the plants from 1600 hr to 0800 hr daily.

The initial night temperature (NT) setpoint was 18°C. Day temperature (DT) and venting temperature setpoints were 3° and 6° above the NT respectively in all experiments irrespective of NT. Temperatures were lowered during the first 2 weeks of SD to 16° NT. After 2 weeks of SD, plants were moved to different greenhouse sections depending on experimental temperature. Plants were fertilized with 260 mg l^{-1} N, 130 mg l^{-1} K, and 0.1 mg l^{-1} Mo. Chlormequat was applied at 1500 mg l^{-1} as a foliar spray for height control the day SD started and 1 week later. A third application of chlormequat at 750 mg l^{-1} was applied after 3 weeks of SD.

Data collection. The date of anthesis and the number of abscised cyathia were recorded on all plants daily for 25 days past anthesis. The total number of cyathia per plant was determined at the end of each experiment by counting the number of cyathia greater than 1 mm in diameter still present plus the number of stubs remaining from previously abscised cyathia. The percent abscission per plant was calculated by dividing the number of abscised cyathia by the total number of cyathia formed.

Expt. 1: Influence of temperature and irradiance on abcission. Every 2 weeks, starting 2 weeks after the start of SD until 8 weeks of SD plants were moved among 4 greenhouse environments: (1) 16° NT and ND, (2) 16° NT and 75% shade, (3) 21° NT and ND, or (4) 21° NT and 75% shade.

Treatments are outlined in Figure 1. There were 25 treatments resulting from plants being moved among environments, 10 plants per treatment. At the end of the experiment, shoot dry weight was measured on 5 plants per treatment by removing the above ground portion of the plant and oven drying the tissue at 60° for 3 days prior to weighing.

Mean percent abscission and mean dry weight were determined for each treatment and statistical significance was determined by analysis of variance. The experiment was analyzed as a completely randomized 5 X 5 factorial design.

Expt. 2: Influence of finishing temperature, irradiance, and water stress on abscission. Two weeks after the start of SD, plants were placed at initial temperatures of 16° or 18° NT. All plants were then grown for an additional 4 weeks. Plants were moved from the 16° and 18° initial temperature houses to greenhouses with NT of 13°, 16°, 18°, or 21° NT. Plants were kept at these finishing temperatures through data collection. For each finishing temperature, half of the plants remained under ND and half were placed under shade. In all temperature and irradiance treatments, half of the plants were repeatedly water stressed to a plant water potential of ca. - 0.6 MPa, the other half were watered daily to maintain a water potential of ca. 0 MPa. Plant water potential was measured using a pressure bomb (PMS Instrument Co., Corvallis, Oregon). Ten extra plants were used per treatment to take water potential readings with an average of 2 plants used each time a reading was taken. The same 2 plants were not used again. When the average water

potential was ca. - 0.6 MPa, all plants in the corresponding treatment were watered to container capacity. The water stress treatment plants were repeatedly stressed until all plants in a treatment reached anthesis. The number of times plants were stressed prior to anthesis varied from 2 to 5 depending on irradiance and finishing temperature.

The experiment was analyzed as a completely randomized design, split, split, split plot, with initial temperature as the main plot, and final temperature, irradiance, and water stress, as subplot factors. There were 32 treatments (2 initial temperatures X 4 finishing temperatures X 2 irradiance levels X 2 water stresses), with 10 plants per treatment. Mean percent abscission was determined daily and statistical significance determined by analysis of variance.

Controlled environment experiment. After planting as described above for the greenhouse experiments, equal numbers of plants were placed in two controlled environment chambers and grown single stem at a spacing of 33 plants m^{-2} for 2 weeks under 125 $\mu mol\ s^{-1}\ m^{-2}$ photosynthetically active radiation (PAR) (0600 hr to 2200 hr) from 215 W VHO deluxe cool white fluorescent lamps. Short days were started Sept 9 with an 8 hr light span from 0800 hr to 1600 hr daily.

The initial NT setpoint was 18°. At the start of SD the NT was lowered to 16° in one chamber and raised to 21° in the other chamber. Plants remained at 16° or 21° for 3 weeks when one-third of the plants at 16° were moved from 16° to 21° and one-third of the plants at 21° were moved from 21° to 16°. Plants were finished at the new

temperatures. Similarly after 5 weeks of SD, another third of the plants were moved between chambers, with the remaining third of the plants were grown continuously at 16° or 21°. Plants remained in respective chambers during data collection. Chlormequat was applied at 1500 mg^{-1} for height control on Sept 2 and Sept 9. Plants were fertilized and data was collected as described in the greenhouse experiments.

The experiment was analyzed as a completely randomized 2 X 3 factorial design. There were 6 treatments (2 temperatures X 3 moving times), with 10 plants per treatment. Mean percent abscission was determine daily and statistical significance determined by analysis of variance.

Results

Expt. 1. Moving plants from normal daylight (ND) to 75% shade or from 16° to 21° NT resulted in earlier and greater cyathia abscission compared with plants maintained at 16° under ND (Tables 1, 2). Abscission was greater on plants under shade at 16° than on plants at 21° under ND (Figure 2). Exposing plants to shade and 21° NT simultaneously resulted in earlier abscission than on plants under shade at 16° or the 21° NT alone. Cyathia abscission was greater at all times under shade at either NT compared with plants at 21° NT and under ND for each date plants were moved (Table 1). The earlier plants were moved to shade the earlier abscission occured and the greater the severity

(Figure 3). On some plants moved from ND to shade after 2 or 4 weeks of SD anthesis never occured as abscission occured before anthesis (Figure 3) and complete abscission of all cyathia occured in a short time span of 4 to 5 days. A move to shade after 6 or 8 weeks of SD induced less abscission, and abscission did not start until a minimum of 5 days after anthesis.

The earlier plants were moved to shade the greater the reduction in final dry weight (Table 3). Final plant dry weight was significantly reduced under shade, but moving plants from 16° NT to 21° NT had no significant effect on dry weight.

Expt. 2. Cyathia abscission was promoted by increasing the initial temprature from 16° to 18° , by increasing final temperature from 13° to 21°, by reducing irradiance, and by water stressing the plants (Tables 4, 5). Plants grown at a 16° initial temperature had less abscission than plants grown at 18° initial temperature irrespective of finishing temperature. In addition as the finishing temperature increased from 13° to 21°, abscission increased regardless of the initial temperature. Irrespective of irradiance or water regime, plants grown at a 16° initial temperature and finished at a 21° finishing temperature had greater abscission than plants grown at a 18° initial temperature and finished at a 13° finishing temperature (Table 4).

Plants under shade had greater abscission than plants under ND in all treatments (Table 4). A significant interaction between irradiance and finishing temperature which resulted in greater

abscission under shade as finishing temperature increased (Table 5). During the period from 55 to 60 days after the start of SD , cyathia abscission was promoted by high initial temperatures, but not after that time. Moving plants from 16° to 21° NT did not increase abscission as much as moving plants from ND to shade while keeping NT constant at 16° (Figure 4).

Water stress increased cyathia abscission on plants grown under ND but had little effect on abscission in plants grown under shade (Table 4, Figure 5). A greater response to water stress occured when the NT was lowered from 18° to 13° under ND (Figure 5) than if maintained at 16° (Figure 6).

Controlled environment experiment. Under controlled conditions, cyathia abscission was greater on plants grown at a constant 21° NT compared to a constant 16° NT (Figure 7). One week after anthesis 62% of the cyathia had abscised at a constant 21° (day 59) compared to only 20% abscission at a constant 16° (day 77). Plants moved after 5 weeks of SD from 16° to 21° had greater abscission than if moved from 21° to 16°. Plants moved from 16° to 21° had abscised 38% of the cyathia before anthesis compared to 3% on plants grown at a constant 21°. However, abscission was eventually greater on plants grown at a constant 21°.

Comparing treatments at a common physiological stage of development (anthesis), plants moved from 21° to 16° after 3 weeks of SD had less abscission than plants moved at 5 weeks of SD to 16° or the control (21° constant) (Figure 8).

Discussion

Low irradiance levels, high temperatures and water stress all promoted cyathia abscission. However, low irradiance appeared to be the primary factor promoting abscission on plants in the greenhouse. When plants were moved from ND to shade at 16° NT after 4 weeks of SD, 74% of the cyathia had abscised 10 days after normal anthesis while only 12% of the cyathia had abscised at the same time when plants remained under ND but were moved from 16° to 21° NT (Table 1). Increasing temperature and decreasing irradiance simultaneously only increased abscission 10% to 84%. In general, the earlier plants were placed under shade, the earlier abscission occurred. On plants under shade, water stress had no consistant effect on abscission while under ND, water stress promoted abscission (Table 4).

Woodhead and Einert (17) reported cyathia to abscise when plants were placed in a postharvest harvest environment before the bracts were half-colored. Decreasing the amount of available PAR to the plant (by shading) decreases photosynthesis and subsequent carbohydrate supply in the plant which tends to promote the abscission of leaves, flowers, and fruits (1).

There was a greater decline in nonsoluable carbohydrate over time in bracts and leaves in plants grown under shade than on plants grown under ND (6). Carbohydrate levels are most likely declining in the cyathia at the same time, especially under shade. A decline in carbohydrate supply was evident in shade grown plants as they had lower

final dry weight compared with plants grown under ND (Table 3).

The developing bracts and cyathia, both being carbohydrate sinks, compete for available photosynthates. The bracts appeared to be stronger sinks than the cyathia (6). Cyathia sink strength is further modified by cyathia shading. On inflorescences growing under shade or covered by neighboring bracts or leaves, the cyathia frequently do not fully develop and abscise either before or shortly after anthesis (personal observation). Abscission may be due to the cyathia's inability to mobilize sufficient carbohydrates to complete development and flowering especially when carbohydrates are limiting. Decreased carbohydrate translocation as a result of low irradiance has caused fruit abscission (9) and improper flower bud development in rose (7), tomato (3), iris (4), and Bougainvillea (14).

Temperature also influenced cyathia abscission. As the initial temperature or finishing temperature increased, cyathia abscission was promoted, especially if plants were grown under shade (Tables 1, 2). Under controlled conditions, cyathia abscission also increased with increasing finishing temperature (Figure 7). Conversely, there was less abscission on plants moved from a 21° to 16° finishing temperature after 3 weeks of SD compared to moving at 5 weeks of SD (Figure 8). The increase in abscission as finishing temperature increased may have been due to carbohydrate depletion. As temperature increases, respiration rates increase (8), which decreases the carbohydrate supply in the plant. Abscission has been reported to increase as the temperature increased in explants of bean (18), and cotton (5), and in petal

abscission in Linum lewisii (15). Flower buds, flowers, and young pods of snap bean are also known to abscise in response to high temperatures (16).

Plants water stressed under ND had greater abscission than plants growing under shade (Table 4, Figure 5). Under shade, significant abscission had already occured due to the low irradiance level at the time a water stress occured, so there were few additional cyathia to abscise. However, many cyathia were still present on plants growing under ND so water stress had the potential for causing more abscission. These results suggest that premature cyathia abscission is primarily promoted by low irradiance levels, commonly found in greenhouses as natural irradiance levels decline in the Fall. Irradiance levels to the leaves are further reduced as bracts expand or if plant density is high resulting in shading of the leaves. Decreased carbohydrates available to the cyathia promote abscission. If temperatures are high, respiration rates will probably increase, further reducing carbohydrate levels in the plant. Under water stress, hormonal changes may occur that would decrease available auxin to the abscission zone and increase endogenous levels of abscisic acid and ethylene which could promote abscission.

Preventative measures appear to be the only means of controlling the problem of premature cyathia abscission. Early flower initiation in late September will allow the cyathia to develop under higher irradiance levels. Proper night temperature control in October and early November will allow lower finishing temperatures to be used. Spacing plants as they are marketed will allow for greater irradiance penetration to the

leaves, resulting in greater carbohydrate levels potentially available to the cyathia.

Table 1. Mean percent cyathia abscission 50 to 80 days after the start of short days influenced by irradiance and/or temperature modifications imposed 2, 4, 6, or 8 weeks after the start of short days. The irradiance change consisted of reducing irradiance 75%, the temperature change consisted of raising the night temperature from 16° to 21°. Expt. 1.

Days after the start of SD[x]	Control[z]	Weeks after the start of short days												Analysis of variance		
		Time of irradiance change				Time of temperature change				Time of Irradiance[y] and temperature change				Time of temperature change	Time of irradiance change	Interaction
		2	4	6	8	2	4	6	8	2	4	6	8			
50	0	0	2	0	0	0	0	0	0	2	2	0	0	--	--	--
55	0	0	5	0	0	0	0	0	0	3	7	0	0	NS[v]	**	NS
60	0	5	19	1	0	0	1	1	0	65	71	29	0	NS	**	NS
65	0	65	74	40	1	11	12	11	2	80	84	67	2	**	**	**
70	1	85	94	73	36	31	26	33	11	84	97	90	30	**	**	**
75	9	91	96	85	69	46	43	45	29	86	97	91	61	**	**	**
80	14	96	97	92	82	48	50	50	40	88	97	91	76	*	**	**

[z]Remained under 16° NT and normal daylight (control).
[y]Irradiance and temperature change occurred on the same date.
[x]Average days to anthesis at a constant 16°C and ND was 56 days.
[v]Nonsignificant (NS) or significant at 1% (*), or .1% (**).

Table 2. Mean percent cyathia abscission on poinsettia 'Annette Hegg Dark Red' 65 days after the start of short days (SD) initially grown at 16°C night temperature (NT) and normal daylight (ND) and then moved to 21°C NT (temperature change) and/or 75% shade (irradiance change) at 2, 4, 6, or 8 weeks after the start of SD. Expt. 1.

Weeks after the start of short days					
Time of temperature change	Time of irradiance change				
	2	4	6	8	No change[z]
2	78	85	55	10	9
4	94	82	63	4	7
6	88	91	62	12	9
8	86	85	61	0	2
No change[y]	56	66	33	0	0[x]
Contrasts					
Irradiance change over time					
linear					**[w]
quadratic					**
cubic					NS
Temperature change over time					
linear					**
quadratic					*
cubic					NS

[z]Remained under normal daylight, subjected to temperature change.
[y]Remained at 16° NT, subjected to irradiance change.
[x]Remained at 16° NT and normal daylight (control).
[w]Nonsignificant (NS) or significant at 1% (*) or .1% (**).

Table 3. Mean final dry weight (g) and analysis of variance of poinsettia 'Annette Hegg Dark Red' initially grown at 16°C night temperature (NT) and normal daylight (ND) and then moved to 21°NT (temperature change) and/or 75% shade (irradiance change) at 2, 4, 6, or 8 weeks after the start of short days. Expt. 1.

	Weeks after the start of SD							
Time of temperature change	Time of irradiance change				No irradiance change	Mean	Analysis of variance	
	2	4	6	8				
2	3.4	3.5	5.6	4.5	5.7	4.5		
4	3.0	4.0	4.8	6.1	6.7	4.9	Temperature change	NS[z]
6	3.0	4.0	4.8	5.4	5.7	4.6	Irradiance change	**
8	3.7	4.1	4.2	5.8	8.2	5.2	Interaction	NS
No temperature change	4.9	4.4	5.0	6.0	7.5	5.6		
Mean	3.6	4.0	4.9	5.6	6.8			

[z]Nonsignificant (NS) or significant at .1% (**).

Table 4. Mean percent cyathia abscission 70 days after the start of short days for poinsettia 'Annette Hegg Dark Red' grown at 16°C or 18°C NT under normal daylight from 0 to 6 weeks of short days. Plants were then moved to a 13°, 16°, 18°, or 21° NT greenhouse and/or placed under 75% shade. Half of the plants at each temperature and irradiance treatments were water stressed to ca. -.6 MPa. Expt. 2.

Initial temperature (°C)[y]	Finishing temperature (°C)[z]															
	13				16				18				21			
	Normal daylight		75% shade		Normal daylight		75% shade		Normal daylight		75% shade		Normal daylight		75% shade	
	C[x]	WS	C	WS	C	WS	C	WS	C	WS	C	WS	C	WS	C	WS
16	3	11	28	12	5[w]	3	63	61	8	11	62	52	29	36	69	72
18	8	24	39	48	4	29	82	80	21	37	78	87	46	56	92	98

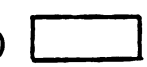
[z]Finishing temperature from 6 weeks after the start of short days through the end of data collection.
[y]Initial temperature from 0 to 6 weeks after the start of short days.
[x]C = no water stress (ca. 0 MPa), WS = ca. -.6 MPa.
[w]Control treatment.

Table 5. Analysis of variance 55 to 80 days after the start of short days (SD) for poinsettia 'Annette Hegg Dark Red' grown at 16°C or 18°C night temperature (NT) under normal daylight from 0 to 6 weeks after the start of short days. Plants were then moved to a 13°, 16°, 18°, or 21° NT greenhouse and/or placed under 75% shade. Half of the plants at each temperature and irradiance treatment were water stressed to ca. -.6 MPa. Expt. 2.

Analysis of variance

	Days after the start of short days					
	55	60	65	70	75	80
Initial temperature (IT)	****[z]	****	****	****	****	****
Final temperature (FT)	****	****	****	****	****	****
Irradiance (I)	****	****	****	****	****	****
Water stress (ws)	***	NS	*	**	**	**
IT x FT	**	NS	NS	NS	NS	NS
IT x I	**	****	NS	NS	NS	NS
FT x I	***	****	****	****	****	****
IT x WS	*	NS	NS	NS	NS	NS
FT x WS	****	NS	NS	NS	NS	NS
I x WS	**	NS	*	***	****	****
IT x FT x I	NS	NS	NS	NS	NS	NS
IT x FT x WS	*	NS	NS	NS	NS	NS
IT x I x WS	NS	NS	NS	NS	NS	NS
FT x I x WS	*	NS	NS	NS	NS	NS
ITx FT x I x WS	NS	NS	NS	NS	NS	NS

[z]Nonsignificant (NS) or significant at 5% (*), 1% (**), .1% (***), or <.1% (****).

Figure 1. Twenty-five treatments resulting from moving poinsettia 'Annette Hegg Dark Red' among four greenhouse environments: (1) 16°C night temperature (NT) and normal daylight (ND)  , (2) 16° NT and 75% shade  , (3) 21° NT and ND  , and (4) 21° NT and shade  at 2, 4, 6, and 8 weeks after the start of short days.

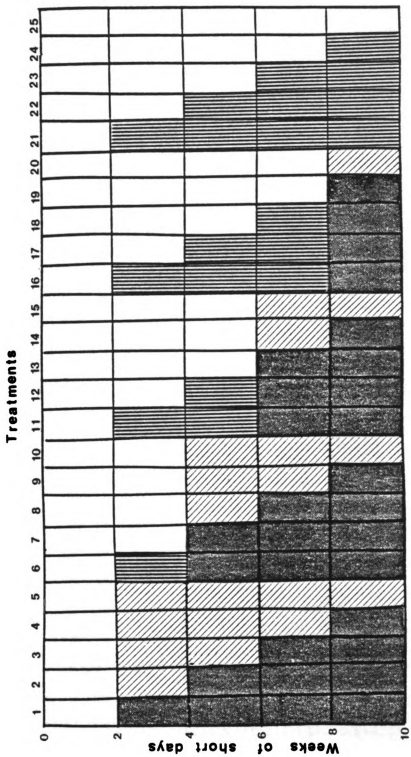

Treatments
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
0
2
4
6
8
10
Weeks of short days

Figure 2. Mean percent cyathia abscission 49 to 77 days after the start of short days (SD) for poinsettia 'Annette Hegg Dark Red' remaining at 16°C night temperature (NT) and normal daylight (ND) or moved to 16° NT and 75% shade (SHD) , 21° NT and ND, or 21° NT and SHD at 2 weeks after the start of SD. Average day of anthesis for each treatment indicated by ⟶ . Expt. 1.

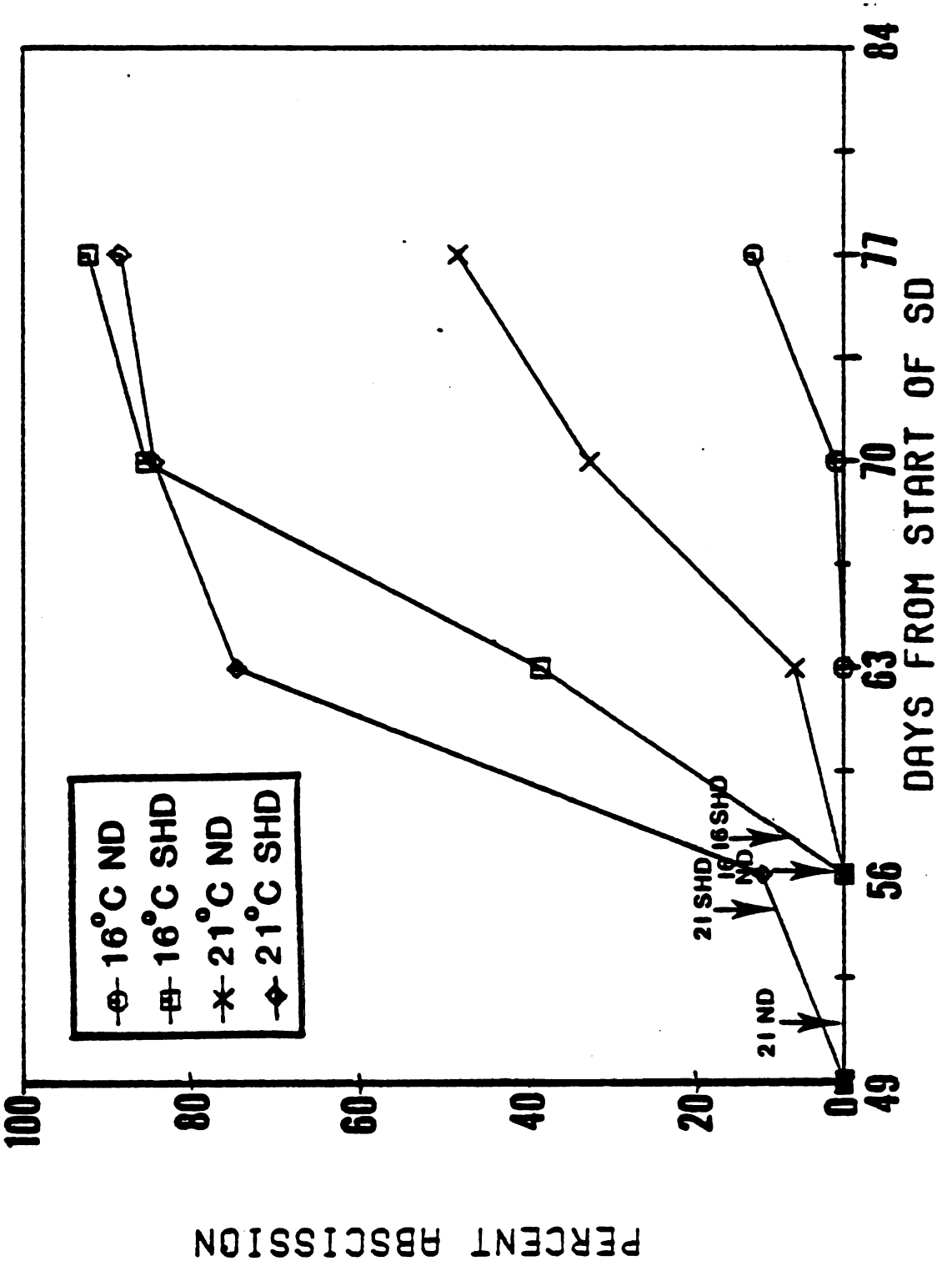

PERCENT ABSCISSION
100
80
60
40
20
0
49
56
63
70
77
84
DAYS FROM START OF SD
16°C ND
16°C SHD
21°C ND
21°C SHD
21 ND
21 SHD
16 ND
16 SHD

Figure 3. Mean percent cyathia abscission 49 to 77 days after the start of short days (SD) for poinsettia 'Annette Hegg Dark Red' grown at 16°C night temperature (NT) and normal daylight (no shift) or moved to 75% shade at 2, 6, or 8 weeks after the start of SD. Average day of anthesis for each treatment indicated by ⟶ (2 = 2 weeks (WKS) of SD, 6 = 6 WKS of SD, 8 = 8 WKS of SD, NS = No shift). Expt. 1.

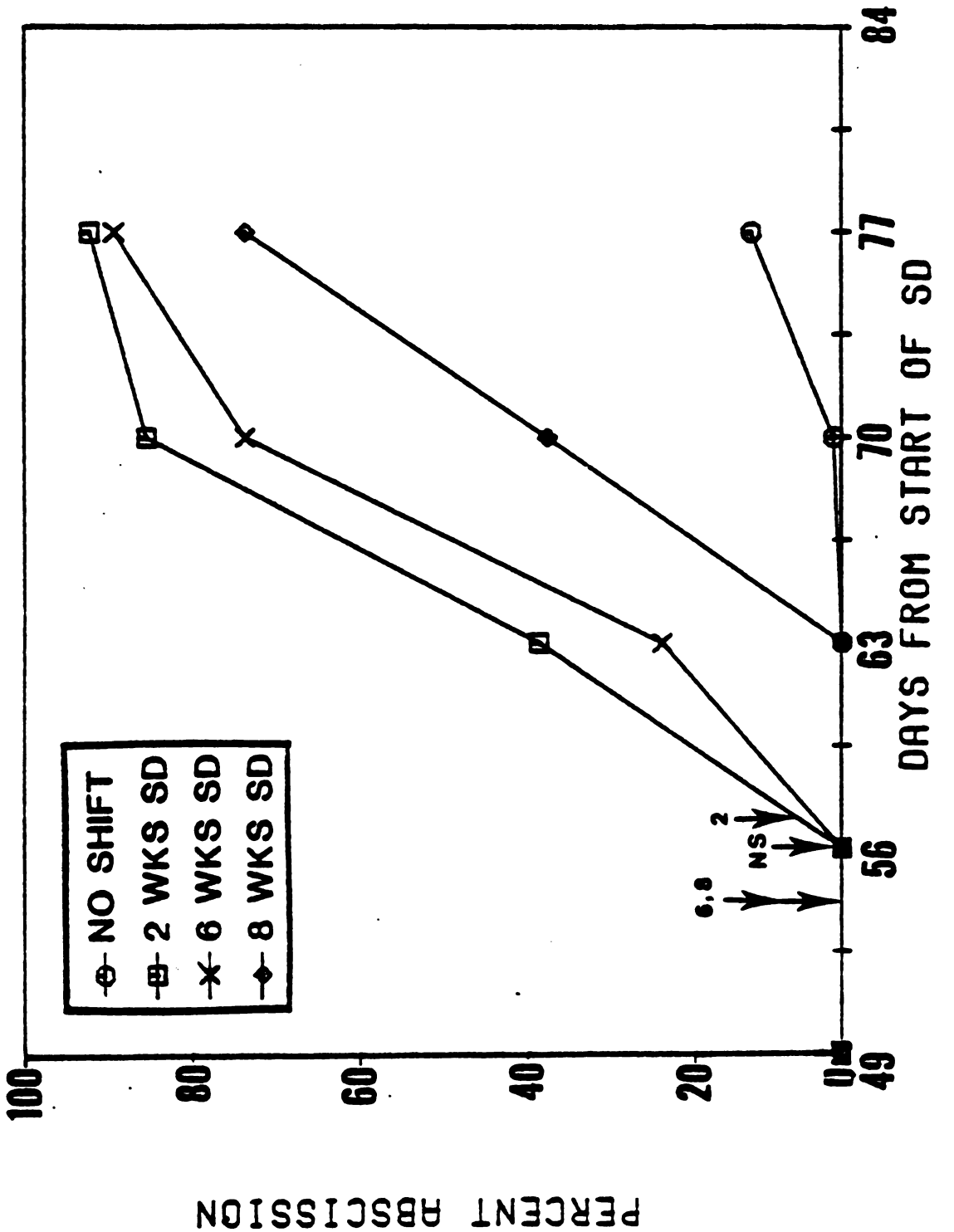

PERCENT ABSCISSION
100
80
60
40
20
0
49
56
63
70
77
84
DAYS FROM START OF SD
NO SHIFT
2 WKS SD
6 WKS SD
8 WKS SD
6.8
NS
2

Figure 4. Mean percent cyathia abscission 49 to 84 days after the start of short days (SD) for poinsettia 'Annette Hegg Dark Red' grown at an initial night temperature (NT) of 16°C or 18°C under normal daylight (ND) from 0 to 6 weeks after the start of short days. Plants were then moved to a finishing NT of 16° or 21° under ND or 75% shade (SHD) or water stressed (WS) to ca. - 0.6 MPa from 6 weeks of SD until anthesis. Day of anthesis was 54 to 55 days after the start of SD for all treatments, indicated by ⟶ . Expt. 2.

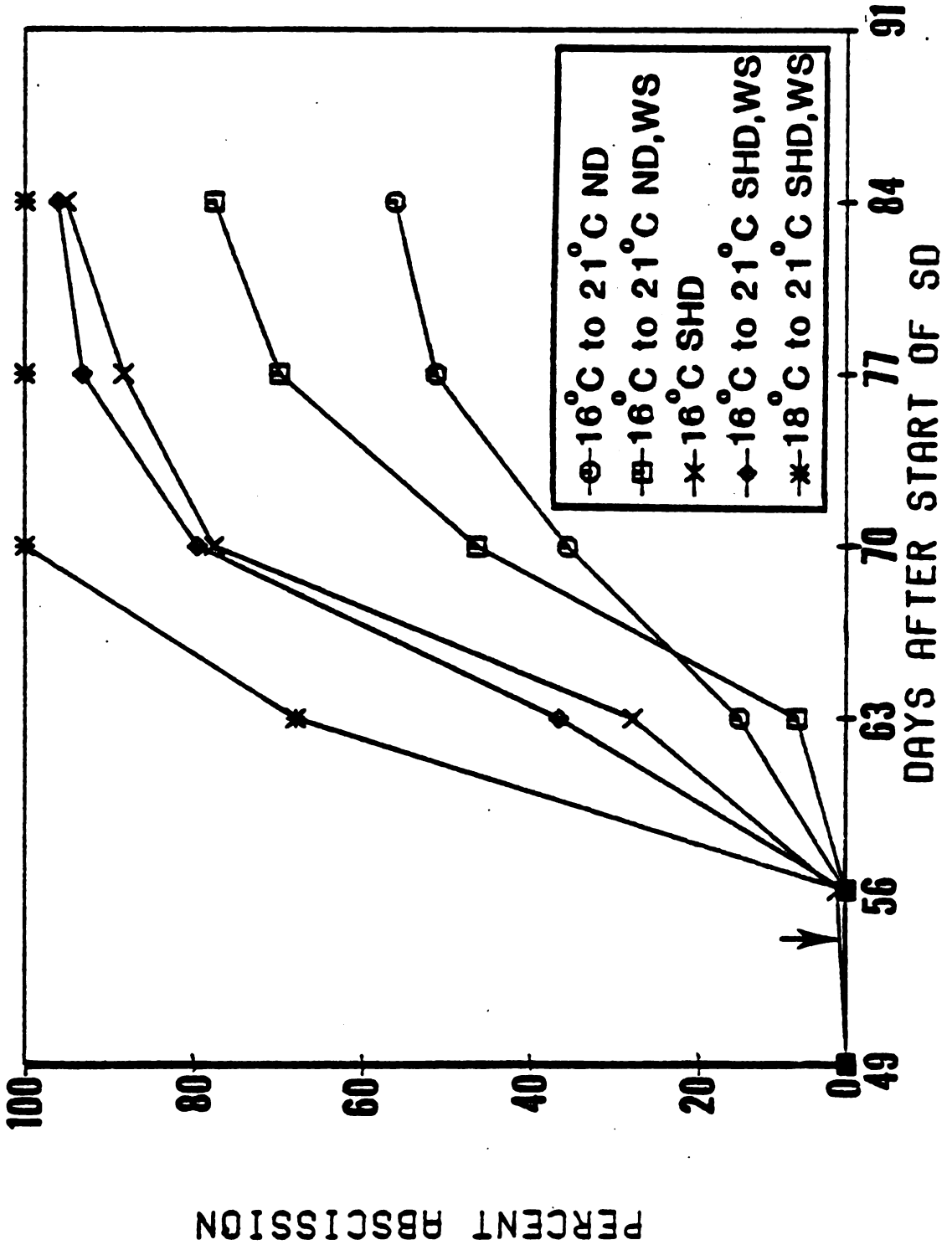

PERCENT ABSCISSION
100
80
60
40
20
0
49
56
63
70
77
84
91
DAYS AFTER START OF SD
16°C to 21°C ND
16°C to 21°C ND,WS
16°C SHD
16°C to 21°C SHD,WS
18°C to 21°C SHD,WS

Figure 5. Mean percent cyathia abscission 49 to 84 days after the start of short days (SD) for poinsettia 'Annette Hegg Dark Red' initially grown at an 18°C night temperature under normal daylight (ND), from 0 to 6 weeks after the start of short days ,then finished at a 13° NT under ND or 75% shade (SHD),or water stressed (WS) to ca. - 0.6 MPa until anthesis. Day of anthesis was 54 to 55 days after the start of SD for all treatments, indicated by ⟶ . Expt. 2.

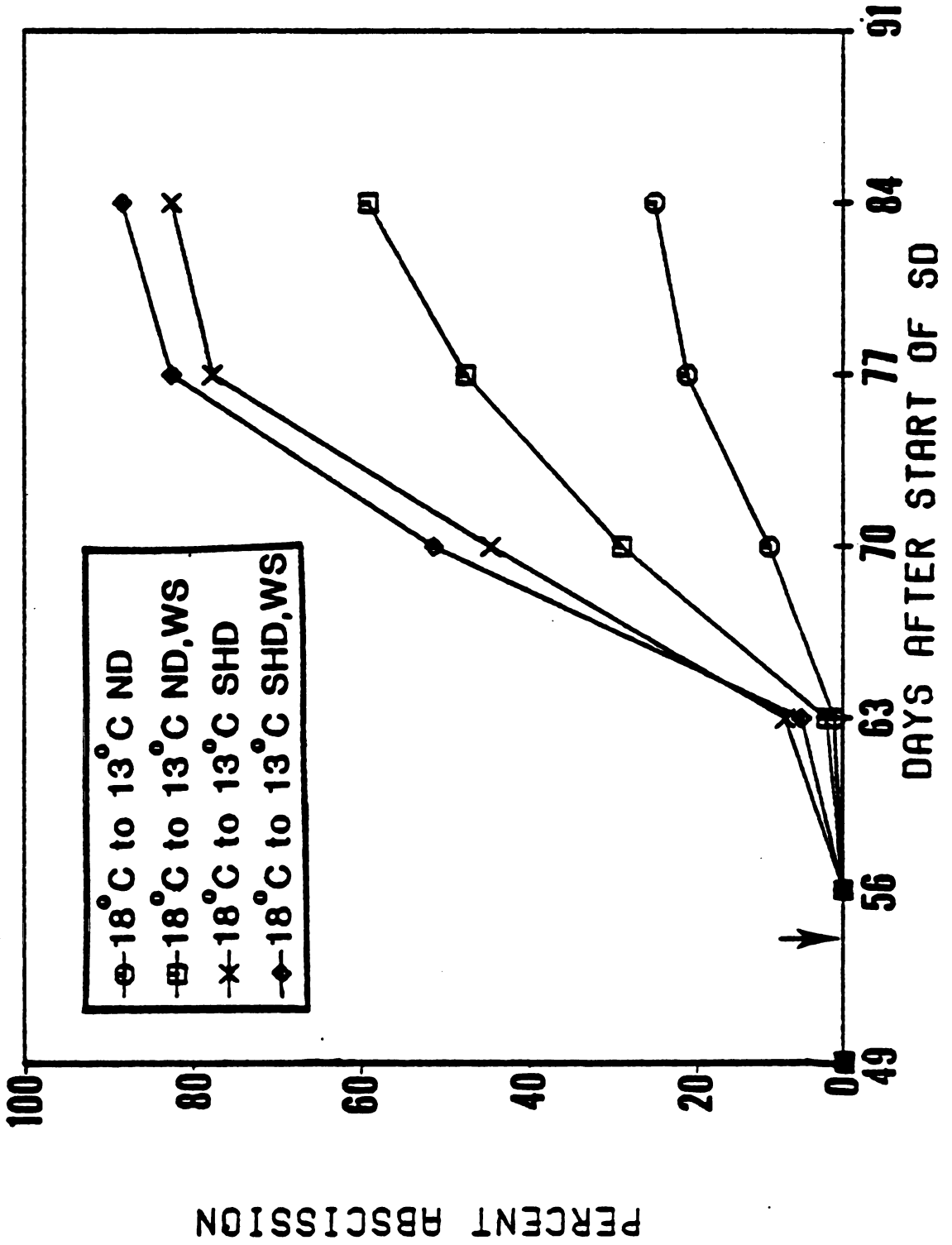

PERCENT ABSCISSION
100
80
60
40
20
0
49
56
63
70
77
84
91
DAYS AFTER START OF SD
18°C to 13°C ND
18°C to 13°C ND,WS
18°C to 13°C SHD
18°C to 13°C SHD,WS

Figure 6. Mean percent cyathia abscission 49 to 84 days after the start of short days (SD) for poinsettia 'Annette Hegg Dark Red' grown at a constant 16°C night temperature under normal daylight (ND) until 6 weeks of SD, then moved to ND or 75% shade (SHD) and/or water stressed (WS) to ca. - 0.6 MPa. Day of anthesis was 54 to 55 days after the start of SD for all treatments, indicated by ⟶ . Expt. 2.

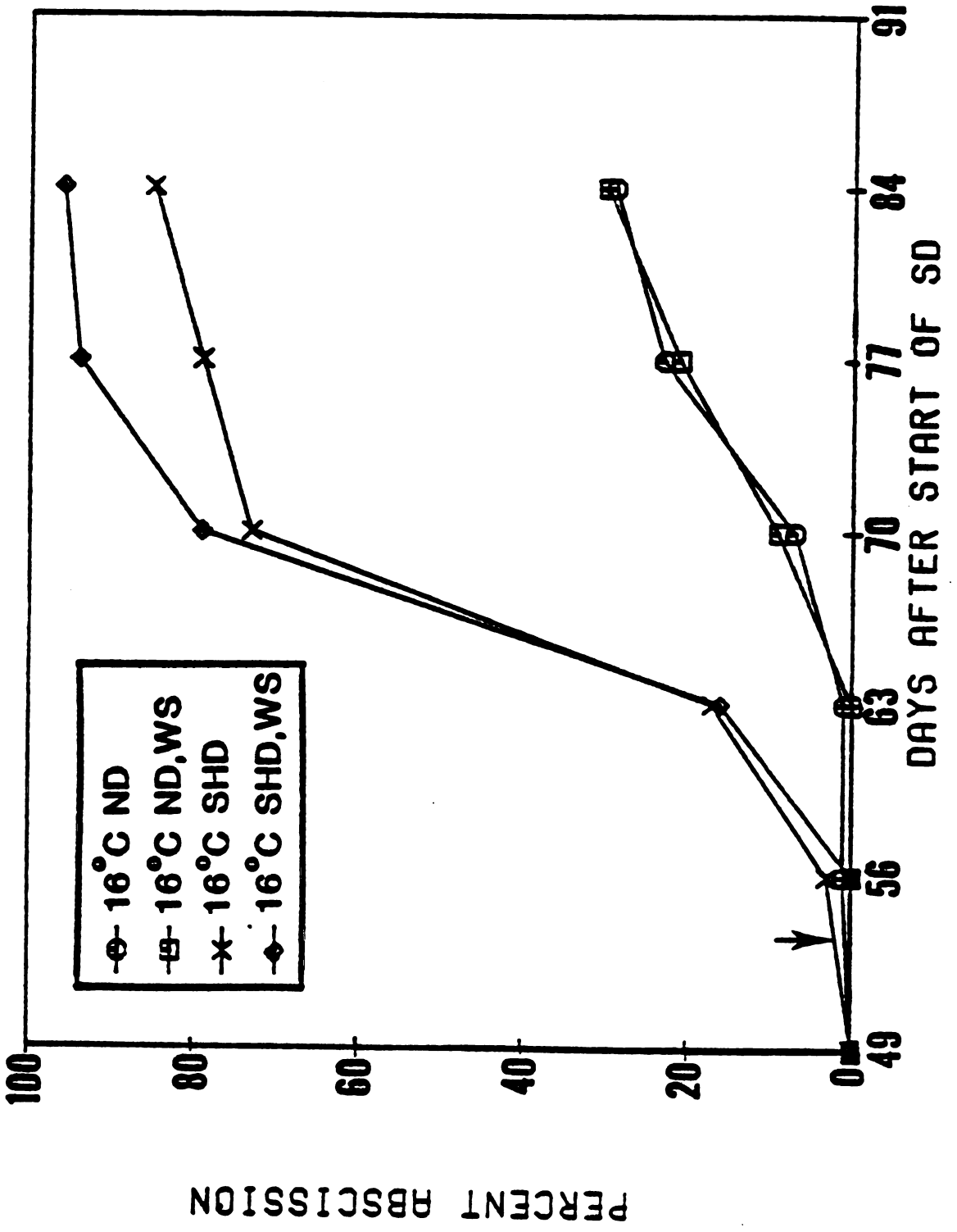

PERCENT ABSCISSION
100
80
60
40
20
0
49
56
63
70
77
84
91
DAYS AFTER START OF SD
16°C ND
16°C ND,WS
16°C SHD
16°C SHD,WS

Figure 7. Mean percent cyathia abscission 49 to 77 days after the start of short days (SD) for poinsettia 'Annette Hegg Dark Red' grown in a controlled environment chamber (125 μmol s^{-1} m^{-2} from 0800 hr to 1600 hr) at 16°C or 21°C night temperature (NT) or moved after 5 weeks of SD from the 16° or 21° NT chamber to the 21° or 16° chamber respectively. Day of anthesis for each treatment indicated by ⟶ .

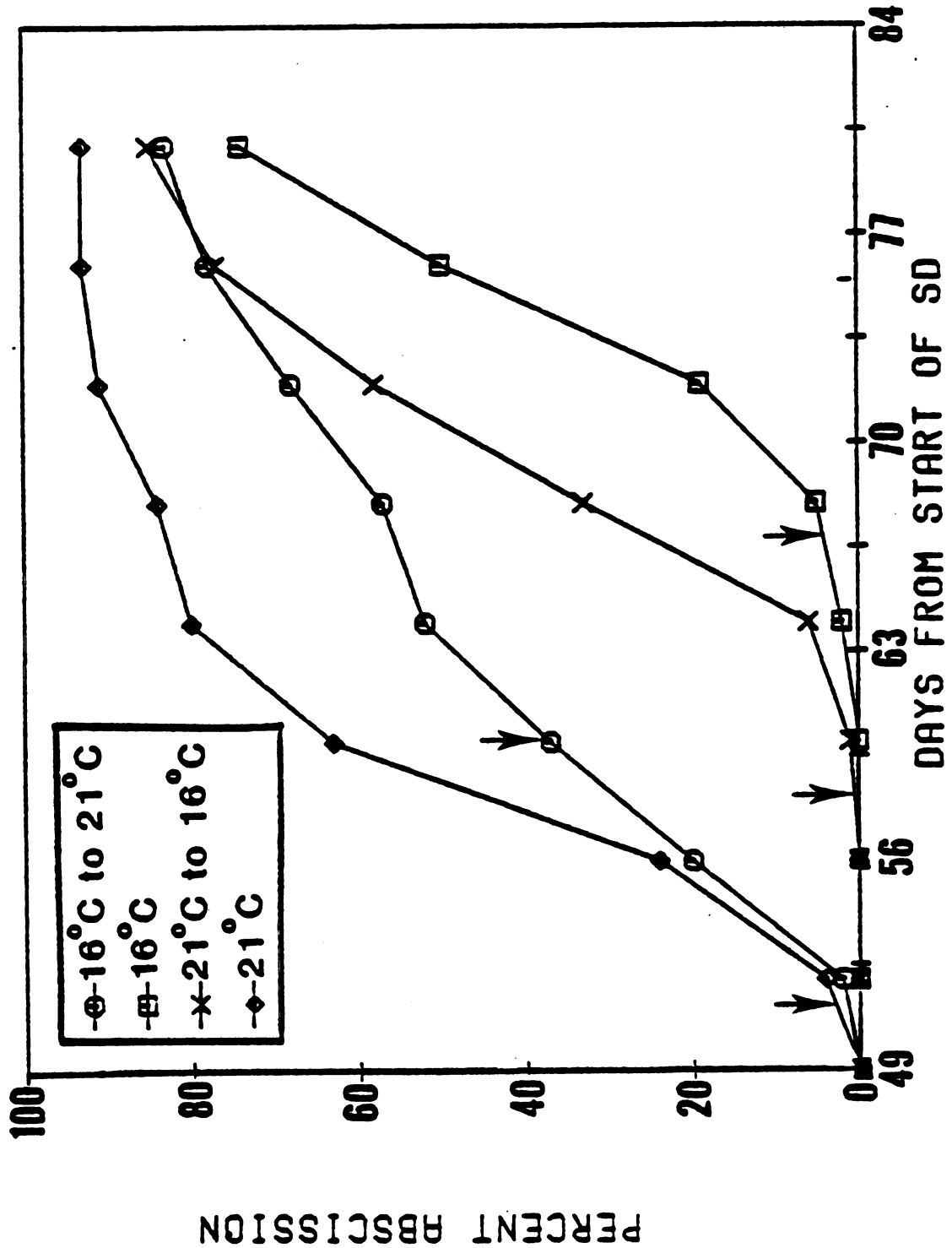
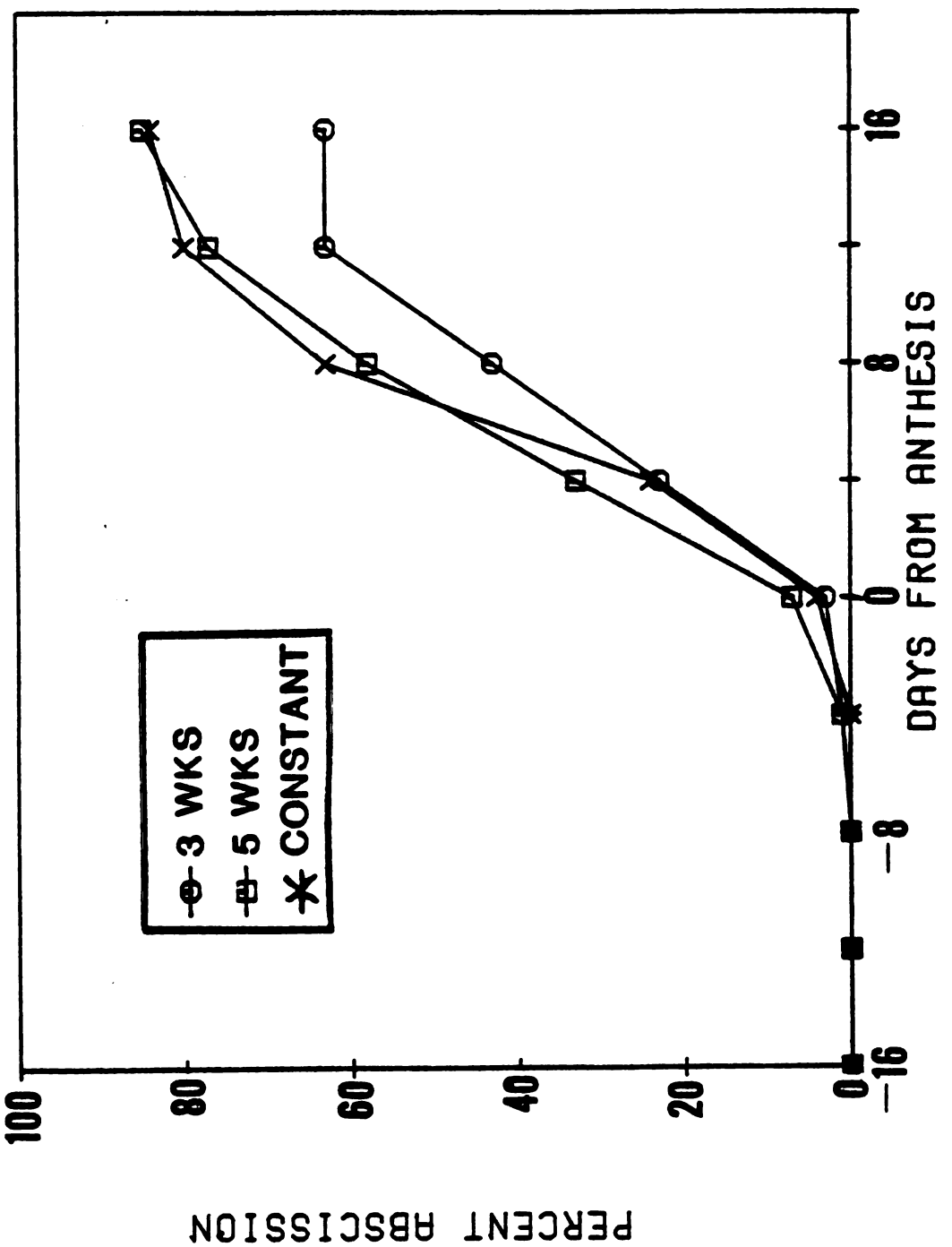

PERCENT ABSCISSION
100
80
60
40
20
0
49
56
63
70
77
84
DAYS FROM START OF SD
16°C to 21°C
16°C
21°C to 16°C
21°C

Figure 8. Mean percent cyathia abscission 16 days before anthesis to 16 days after anthesis for poinsettia 'Annette Hegg Dark Red' grown in a controlled environment chamber (125 $\mu mol\ s^{-1}\ m^{-2}$ from 0800 hr to 1600 hr) at a constant 21°C night temperature (NT) or moved to a 16° NT after 3 or 5 weeks of short days.


PERCENT ABSCISSION
100
80
60
40
20
0
-16
-8
0
8
16
DAYS FROM ANTHESIS
3 WKS
5 WKS
CONSTANT

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Literature Cited

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Section II

Physiological Factors Influencing Premature Cyathia Abscission in Poinsettia 'Annette Hegg Dark Red'

Physiological Factors Influencing Premature Cyathia Abscission in Poinsettia 'Annette Hegg Dark Red'

Steven H. Miller and R. D. Heins[1]

Department of Horticulture, Michigan State University,

East Lansing, MI. 48824

Additional index words. Euphorbia pulcherrima, center drop, cyathium, carbohydrate depletion, source/sink relationships

Abstract. As plant density increased, transmission of photosynthetically active radiation (PAR) through the bracts to the leaf canopy decreased significantly while cyathia abscission increased concomitantly. More than 90% of the PAR above the bracts was absorbed or reflected 5 cm below the bracts on 20 cm tall plants spaced at 65 or more plants m^{-2}. Reducing natural irradiation 75% by shading leaves of poinsettia promoted cyathia abscission while removing immature bracts decreased abscission. Leaf removal on plants with intact bracts promoted

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[1]Research Assistant and Associate Professor respectively.

abscission to a degree that 100% of the cyathia abscised prior to anthesis while bract removal on plants with intact leaves decreased abscission sufficiently that only 23% of the cyathia had abscised 25 days after anthesis. Measurements of nonsoluable carbohydrate showed a significant increase in leaf carbohydrate on plants with bracts removed while carbohydrate decreased in leaves of plants with bracts intact. Carbohydrate depletion appears to be the primary factor responsible for premature cyathia abscission.

Introduction

The problem of premature poinsettia cyathia abscission and the resulting economic losses have been reported (6). Premature cyathia abscission, occuring either before or after anthesis is promoted by low irradiance levels, high temperatures, or water stress in the greenhouse or postharvest environment (6, 12, 13, 15, 19). However, low irradiance appears to be the primary factor promoting abscission in either environment (6). Although high temperatures or water stress alone will promote abscission, they intensify the problem if plants are under low irradiance levels in the greenhouse (6). Low irradiance levels are often found in greenhouses during fall production due to declining solar radiation levels. Irradiance levels in the canopy are further reduced as bracts expand, covering the leaves or if plant density is high. Under these situations premature cyathia abscission can be observed when the leaves or cyathia are shaded by the developing bracts, or by neighboring leaves.

Under low irradiance levels, photosynthesis is reduced in source leaves. The reduction in photosynthesis reduces the amount of carbohydrate available for translocation to developing sinks (1). Covering vegetative or reproductive sinks has been shown to decrease ^{14}C translocation to these sinks (7, 10, 16). Covering flowers and pods of soybean reduced their sink strength and promoted abscission (5).

Competition between sinks can causes the younger, less developed sinks to abscise (3, 4, 15). In species that bear a small number of flowers or fruit, there is less abscission than in heavier bearing species (2, 15, 17, 19).

Even though it is known what environmental factors promote premature cyathia abscission in poinsettia, there has been no investigation into physiological factors such as source/sink relationships in the plant that may also control abscission. Based on previous source/sink work, the objective of this study were to: (1) determine if abscission was promoted by covering the cyathia; (2) determine if abscission was promoted by shading or removal of source leaves; (3) determine if removing bracts reduced cyathia abscission by eliminating competition between two sinks; (4) measure abscission at different plant densities; and (5) measure carbohydrate content in bracts and leaves over time under different environments to determine if carbohydrate levels differed in plants grown under diferent irradiance levels or night temperatures.

Materials and Methods

General conditions. Rooted cuttings of 'Annette Hegg Dark Red™' (AHDR) were received on Aug 25, 1983, (Expt. 1-2), Sept 22, 1983, (Expt. 3), and Jan 25, 1984, (Expt. 4-5) from Paul Ecke Poinsettias, Encinitas, CA. One cutting was planted per 10 cm plastic pot (an experimental unit) in VSP medium (Michigan Peat Co., Houston, TX) composed of 2 peat : 1 perlite : 1 vermiculite (v:v:v) ammended with dolomitic limestone, superphosphate and trace elements. Plants were placed in a glass greenhouse and grown single stem at a spacing of 33 plants m^{-2}. Plants for Expt. 1-2 were grown under natural photoperiods (ND) for 1 week and plants for Expt. 3-5 were grown for 2 weeks under ND plus a 4 hr night interruption (2200 hr to 0200 hr) of 5 μmol s^{-1} m^{-2} photosynthetically active radiation (PAR) from 60 W incandescent lamps. Short days (SD) were initiated Sept 1 (Expt. 1-2), Oct. 1 (Expt. 3), and Feb 8 (Expt. 4-5). Black sateen cloth was pulled over the plants from 1600 hr to 0800 hr daily under SD.

The initial night temperature (NT) setpoint was 18°C. Day temperature (DT) and venting temperature setpoints were 3°C and 6°C above NT respectively in all experiments irrespective of NT. Temperatures were lowered during the first 2 weeks of SD to 16° NT. Plants were then moved to different greenhouse sections depending on experimental temperature. Plants were fertilized with 260 mg l^{-1} N, 130 mg l^{-1} K, and 0.1 mg l^{-1} Mo. Chlormequat was applied at 1500 mg l^{-1} as a foliar spray for height control the day SD started (Expt. 1-2), after 1 week of SD (Expt. 1-5), and/or after 2 weeks of SD (Expt. 4-5). A third

application of 750 mg l^{-1} chlormequat was applied after 3 weeks of SD (Expt. 1-5).

Data collection. The date of anthesis and the number of abscised cyathia were recorded on all plants daily for 25 days past anthesis (Expt. 1-3), or every 2 days for 16 days (Expt. 4). The total number of cyathia per plant was determined at the end of each experiment by counting the number of cyathia greater than 1 mm in diameter still present plus the number of stubs remaining from previously abscised cyathia. The percent abscission per plant was calculated by dividing the number of abscised cyathia by the total number of cyathia formed.

Expt. 1: Cyathia shading. Plants were initially grown for 5 weeks under SD at 16° NT. After 5, 6, or 8 weeks of SD , the inflorescence on a group of plants was covered with an aluminum foil "cap". One group of plants was left as a control. The experiment was analyzed as a completely randomized design with 4 treatments, 5 plants per treatment. Mean percent abscission was determined for each treatment and statistical significance determined by analysis of variance.

Expt. 2: Bract removal and leaf shading. Plants were initially grown under SD at 16° NT for 5 weeks. After 5, 6, or 8 weeks of SD, groups of plants were treated by (1) removing bracts, (2) shading leaves with 75% saran, (3) removing bracts and shading leaves, or (4) leaving them untreated (control). Bracts were removed with a razor blade leaving no petiole. The 4 treatments were arranged in a completely randomized design, 5 plants per treatment. All plants remained at the same temperature.

Mean percent abscission was calculated for each treatment and statistical significance determined by analysis of variance.

Expt. 3: Bract and leaf removal. After 5, 6, 7, or 8 weeks of SD, plants were placed at 18° NT or 21° NT. Plants were treated by removing (1)bracts, (2)leaves, (3)bracts and leaves, or (4) no tissue (control). Treatments were performed all 4 dates at both temperatures. Bracts and leaves were removed using a razor blade, leaving no petiole.

Data were analyzed as a completely randomized split, split plot, with temperature as the main plot, removal treatment and removal times as subplot factors, giving 32 treatments (2 temperatures X 4 removal treatments X 4 removal times), 5 plants per treatment. Mean percent abscission was calculated for each treatment and statistical significance determined by analysis of variance.

Expt. 4: Plant spacing. Six weeks after the start of SD, plants were either moved to a 21° NT greenhouse or remained at 16° NT and were spaced at 11, 33, or 65 plants m^{-2}.

Photosynthetically active radiation (PAR) transmission was measured in the plant canopy at 10, 15, 20, and 25 cm from the bench 1, 2, and 3 weeks after spacing using a Li-Cor LI-185B meter and LI-190S quantum sensor (Li-Cor Instrument Co., Lincoln, NE.). Transmission was expressed as a percent of irradiance above the canopy. For each date, three measurements were made at each height and spacing.

The abscission data were analyzed as a split plot design with temperature as the main plot and spacing as the subplot, giving 6

treatments (2 NT X 3 spacings), 4 plants per treatment. Mean percent abscission was calculated every 2 days and statistical significance determined by analysis of variance. Mean percent PAR transmission at each spacing was determined by averaging all measurements over the 3 measurement dates.

Expt. 5: Nonsoluable carbohydrate determination. Six weeks after the start of SD, plants were placed under ND or SHD at both 16° and 21° NT. Plants were treated by removing (1)bracts, (2)leaves, or (3)no tissue. There were 12 treatments, 4 plants per treatment.

Six weeks after the start of SD and every week for the following 3 weeks at 0800 hr, three 18.8 mm^2 leaf disks were removed from the first 3 leaves below the lowest bract and 3 bract disks were removed from the first fully expanded bracts in each control plant. Likewise, 3 leaf disks were removed from each plant with bracts removed and 3 bract disks were taken from the first 3 fully expanded bracts on each plant with leaves removed. For each plant, the same 3 leaves and bracts were sampled each week. The three bract or leaf disks were boiled in 95% ethanol. The tissue was then ground and diluted with 100 ml distilled water (leaf disks) or 20 ml water (bract disks). A 2 ml aliquot was pipeted out into an 18 X 150 mm test tube. Four mls of anthrone reagent (2 g anthrone dissolved in 1 l of 100% sulfuric acid0 was added to each 2 ml aliquot. The two solutions were mixed thoroughly and the test tubes were placed in a boiling water bath for 3 minutes. A marble was placed on top of each tube to prevent loss of water. The tubes were allowed to cool and the absorbance of the sample was read at 620 nm using a Beckman

325 spectrophotometer. The absorbance of each sample was compared to the absorbance of standard glucose solutions of 15, 30, 60, 120 $\mu g\ l^{-1}$ of glucose.

Analysis of variance with orthogonal contrasts was conducted to compare treatment means.

Results

Expt. 1. Covering the inflorescence with an aluminum foil "cap" at 5, 6, or 8 weeks of SD resulted in non significant increases in cyathia abscission compared to the control (Table 1).

Expt. 2. Removing bracts from plants both delayed and decreased cyathia abscission compared to non-treated plants, while shading of leaves promoted abscission (Table 2). Combined bract removal and leaf shading further hastened and increased abscission. The earlier bracts and leaves were removed or the earlier leaves were shaded, the earlier abscission occured and the greater the total abscission.

Expt. 3. Removing leaves greatly promoted cyathia abscission whereas bract removal delayed abscission (Table 3). Removing both bracts and leaves gave an intermediate effect. Removing leaves caused complete abscission on some plants as early as 1 week after anthesis, and the earlier leaves were removed, the earlier abscission occured. Only 20% of the plants reached anthesis prior to cyathia abscission when leaves were removed after 5 or 6 weeks of SD, compared to 100% of the plants reaching anthesis for all other treatments (Table 3). Removing bracts significantly delayed abscission compared to the non-treated control

plants. Similar results were observed at 21° (data not presented).

Expt. 4. Spacing plants at 11 or 33 plants m^{-2} resulted in less abscission than spacing plants at 65 or more plants m^{-2} (Table 4). Plants spaced in a 21° NT greenhouse had greater abscission than at a 16° NT.

Photosynthetically active radiation transmission into the plant canopy for spacings of 11 to 97 plants m^{-2} is shown in Figure 1. The greatest transmission occured amongst plants spaced at 11 plants m^{-2}. A similar transmission curve was found through the top 10 cm of the canopy for plants spaced at 33 plants m^{-2}, but, PAR transmission dropped off significantly as measurements were made deeper in the canopy. Spacing at 65 or 97 plants m^{-2} had almost identical PAR transmission curves with transmission decreasing to less than 10% of the above canopy irradiance 5 cm into the canopy.

Expt. 5. Leaves. There was a significant increase in glucose equivalents from 6 to 9 weeks of SD in leaves of plants with bracts removed compared to a decrease in leaves of whole plants (bracts present) (Table 5).

Averaged over all treatments, leaves grown under ND had significantly greater glucose equivalents than if grown under shade however, glucose equivalents were similar at 16° and 21° NT.

Bracts. There was significantly greater glucose equivalents in bracts of plants with leaves removed than in whole plants (leaves present) averaged over both NT (Table 5). Bract glucose equivalents decreased in all treatments from 7 to 9 weeks of SD.

Bracts grown under ND had greater glucose equivalents than if

grown under shade, and glucose equivalents were higher at 16° compared to 21° (Table 5). At 16°, there was no difference in glucose equivalents under ND or shade, although glucose equivalents were higher in bracts grown under ND than shade at 21°.

Discussion

Cyathia abscission in poinsettia is influenced by the environment under which the plant is grown which in turn affects the ability of the cyathia to mobilize carbohydrates. Carbohydrates translocated from the source leaves are partitioned to the bracts and cyathia. The bracts appear to be stronger sinks than cyathia, because when leaves are removed, the bracts remain intact while the cyathia never reached anthesis and abscised (Table 3). Removing the bracts had an opposite effect in that little or no cyathia abscission occured and the cyathia become larger than normal and develop far past anthesis (Tables 2, 3). The removal of bracts apparently allowed more carbohydrate to translocate to the cyathia, which accounted for their larger size and abscence of abscission.

Shading leaves or spacing plants at high densities promoted abscission. Both shading and high plant density decreased the irradiance reaching the leaves, decreased photosynthesis and therefore the carbohydrate available to the sinks resulting in cyathia abscission (1). Measurements of PAR in the plant canopy showed that as plant density increased, there was less available PAR penetrating to the leaves (Figure 1). In commercial greenhouses, plant densities can be

sufficiently high that as bracts expand, the leaves become completely shaded by the bracts, decreasing the PAR in the leaf canopy. Further in 'Annette Hegg Dark Red', 3 to 6 inflorescences can develop from a pinch (Miller and Heins, unpublished results) causing many of these inflorescences to shade each other when plants are densely spaced. The shaded inflorescences often have all of their cyathia abscised (personal observation). While covering the inflorescence with an aluminum cap did not significantly promote cyathia abscission in Expt. 1 (Table 1), plants in Expt. 1 were spaced at 33 plants m^{-2} which did not result in excessive crowding. Spacing at a higher density might interact with covering the inflorescence to promote abscission. Spacing plants ata higher density would have increased interplant shading, decreasing carbohydrates, and possibly resulting in a greater abscission response to covering the inflorescence as occurs in plants where bracts shade neighboring inflorescences. Similarly, covering the flowers and pods in soybean decreased sink strength and reduced ^{14}C translocation to the flowers and pods, promoting abscission (5).

Measurements of glucose equivalents confirm that shade significantly reduced nonsoluable carbohydrates in the bracts and leaves (Table 5). Removing bracts (removal of sink competition) increased glucose equivalents in leaves which could explain why there was little or no cyathia abscission (Tables 2,3). Glucose equivalent levels were higher in bracts or leaves at 16° compared to 21° probably due to decreased respiration rates at higher temperatures (8). Cyathia abscission increased as temperature increased (6) probably due to higher

respiration rates consquently reducing carbohydrate in the plant.

Cyathia abscission appears to be promoted by environmental changes which affect competition for carbohydrates. Environmental changes can cause hormonal imbalances are often the initial stimulus for abscission of a plant organ (1). The principle environmental change promoting cyathia abscission was exposing plants to low irradiance levels by shading (6). Under low irradiance levels, an organ does not have the ability to synthesize sufficient abscission inhibiting hormones such as auxins, giberellins or cytokinins (1). It has been suggested that translocation of carbohydrates to sinks is directed by the hormone level in the organ (1, 9, 13). However, if the level of auxin, gibberellin, or cytokinin in the organ is low, the ability of the organ to function as a sink decreases (1). This would explain why weaker sinks are not able to attract large amounts of carbohydrate, causing the organ to abscise. The decreased production of abscission-inhibiting hormones results in a hormonal imbalance causing localized senescence of cells in the abscission zone of the organ; this potentially leads to an increase in ethylene synthesis and abscission (1).

Application of compounds associated with the delay or prevention of abscission (silver thiosulphate, aminooxyacetic acid, gibberellic acid, or 6-benzylamino purine) were not effective in delaying cyathia abscission (6), therefore, preventative measures appear to be the only means of controlling cyathia abscission. Preventative measures would include flower initiation in late September which would allow the cyathia to develop under higher irradiance levels. Proper night

temperature control in October and early November would allow lower temperatures to be used in late November and early December. Spacing plants as they were marketed would increase canopy irradiance levels resulting in potentially greater carbohydrate levels available to the cyathia.

Table 1. Mean percent cyathia abscission and analysis of variance 55 to 85 days after the start of short days (SD) for poinsettia 'Annette Hegg Dark Red' with cyathia covered with an aluminum cover 5, 6, or 8 weeks after the start of SD. Expt. 1.

Days after start of short days[z]	Weeks after the start of short days				Analysis of variance
		Cyathia covered			
	Control	5	6	8	
55	1	1	0	0	--
60	1	1	0	0	NS[y]
65	3	6	12	10	NS
70	8	21	24	20	NS
75	17	27	34	40	NS
80	24	31	44	56	NS
85	31	34	44	56	NS

[z]Normal anthesis 56 days after the start of short days (SD) at 16°C.
[y]No significant (NS) difference.

Table 2. Mean percent cyathia abscission and analysis of variance 55 to 85 days after the start of short days for poinsettia 'Annette Hegg Dark Red' with bracts removed, leaves shaded, or bracts removed and leaves shaded at 5, 6, or 8 weeks after the start of short days. Expt. 2.

Days after the start of short days[z]	Weeks after the start of short days									Analysis of variance		
	Control	Bracts removed			Leaves shaded			Bracts removed leaves shaded			Time	Treatment	Time x treatment
		5	6	8	5	6	8	5	6	8			
55	0	0	0	0	2	0	0	0	0	0	NS[y]	NS	NS
60	0	0	0	0	4	0	0	0	0	0	*	NS	NS
65	0	1	0	0	7	3	0	14	4	0	*	*	NS
70	0	1	0	0	7	9	0	28	11	5	*	**	NS
75	4	1	0	3	10	16	1	37	31	11	NS	**	NS
80	10	1	1	7	16	22	6	43	39	29	NS	**	NS
85	12	1	1	7	18	27	10	44	39	29	NS	**	NS

[z]Average days to anthesis at a constant 16°C was 56.
[y]Nonsignificant (NS) or significant at 5% (*), or .1% (**).

Table 3. Percent of the plants reaching anthesis, mean percent cyathia abscission, and analysis of variance 50 to 85 days after the start of short days (SD) for poinsettia 'Annette Hegg Dark Red' grown at 18°C night temperature with bracts, leaves, or bracts and leaves removed at 5, 6, 7, or 8 weeks after the start of short days (SD). Expt. 3.

Days after start of SD[z]	Control	Weeks after the start of short days: Bracts removed 5	Bracts removed 6	Bracts removed 7	Bracts removed 8	Leaves removed 5	Leaves removed 6	Leaves removed 7	Leaves removed 8	Bracts and leaves removed 5	Bracts and leaves removed 6	Bracts and leaves removed 7	Bracts and leaves removed 8	Analysis of variance: Time	Temp	Trt	Time x Temp	Time x Trt	Temp x Trt	Time x Trt x Temp
50	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-
55	0	0	0	0	0	35	7	0	0	1	0	0	0	**[y]	NS	**	NS	***	NS	NS
60	0	0	0	2	0	83	44	1	0	13	2	0	0	***	NS	***	NS	***	NS	**
65	2	2	0	2	0	100	87	41	0	35	2	4	8	***	NS	***	NS	***	NS	NS
70	10	7	1	16	3	100	93	73	39	54	16	33	43	***	NS	***	*	***	NS	*
75	30	10	2	22	15	100	98	83	79	64	44	61	57	NS	NS	***	*	***	NS	NS
80	40	23	12	31	18	100	100	89	96	77	51	81	77	NS	NS	***	*	*	NS	*
85	46	23	17	35	21	100	100	90	99	77	61	91	93	NS	NS	***	NS	NS	NS	*
% Reaching[x] anthesis	100	100	100	100	100	20	20	100	100	100	100	100	100							

[z]Average days to anthesis at a constant 18°C was 56 days.
[y]Nonsignificant (NS) or significant at 5% (*), .1% (**), or <.1% (***).
[x]Percent of the plants in each treatment that reached anthesis.

Table 4. Mean percent abscission and analysis of variance 56 to 70 days after the start of short days for poinsettia 'Annette Hegg Dark Red' grown at 16°C or 21°C night temperature and spaced at 11, 33, or 65 plants m^{-2}. Expt. 4.

Days from start of short days[z]	Plants m^{-2}						Analysis of variance		
	16°C			21°C			Spacing	Temperature	Spacing x temperature
	11	33	65	11	33	65			
56	0	0	0	0	0	0	--	--	--
58	0	0	0	0	0	1	NS[y]	NS	NS
60	0	0	0	0	0	4	NS	NS	NS
62	0	0	0	0	0	6	NS	NS	NS
64	1	1	1	0	0	8	NS	NS	NS
66	2	2	1	2	5	22	NS	NS	NS
68	4	3	9	3	6	25	***	*	**
70	6	4	15	7	11	30	***	*	**

[z]Average days to anthesis at a constant 16°C and 21°C night temperature was 54 and 51 days.
[y]Nonsignificant (NS) or significant at 5% (*), 1% (**) or <.1% (***).

Table 5. Mean glucose equivalents per 3 leaf or bract disks sampled at 6, 8, or 9 weeks after the start of short days from bracts and leaves of poinsettia 'Annette Hegg Dark Red' grown at 16°C or 21°C night temperatures under normal daylight or 75% shade. Exp. 5.

LEAVES

Weeks after start of short days	16°				21°			
	Normal daylight		75 % shade		Normal daylight		75 % shade	
	Whole plant	Bracts removed	Whole plant	Bracts removed	Whole plant	Bracts removed	Whole plant	Bracts removed
6	29	--	87	--	34	--	44	--
8	57	75	18	24	20	69	10	18
9	39	89	14	31	24	83	9	34

Contrasts[z]

Whole plant vs Bract removal		***[y]
Normal daylight vs 75% shade		***
16°C vs 21°		NS
Whole plant vs Bract removal	(16°)	**
Normal daylight vs 75% shade	(16°)	***
Whole plant vs Bract removal	(21°)	***
Normal daylight vs 75% shade	(21°)	**

BRACTS

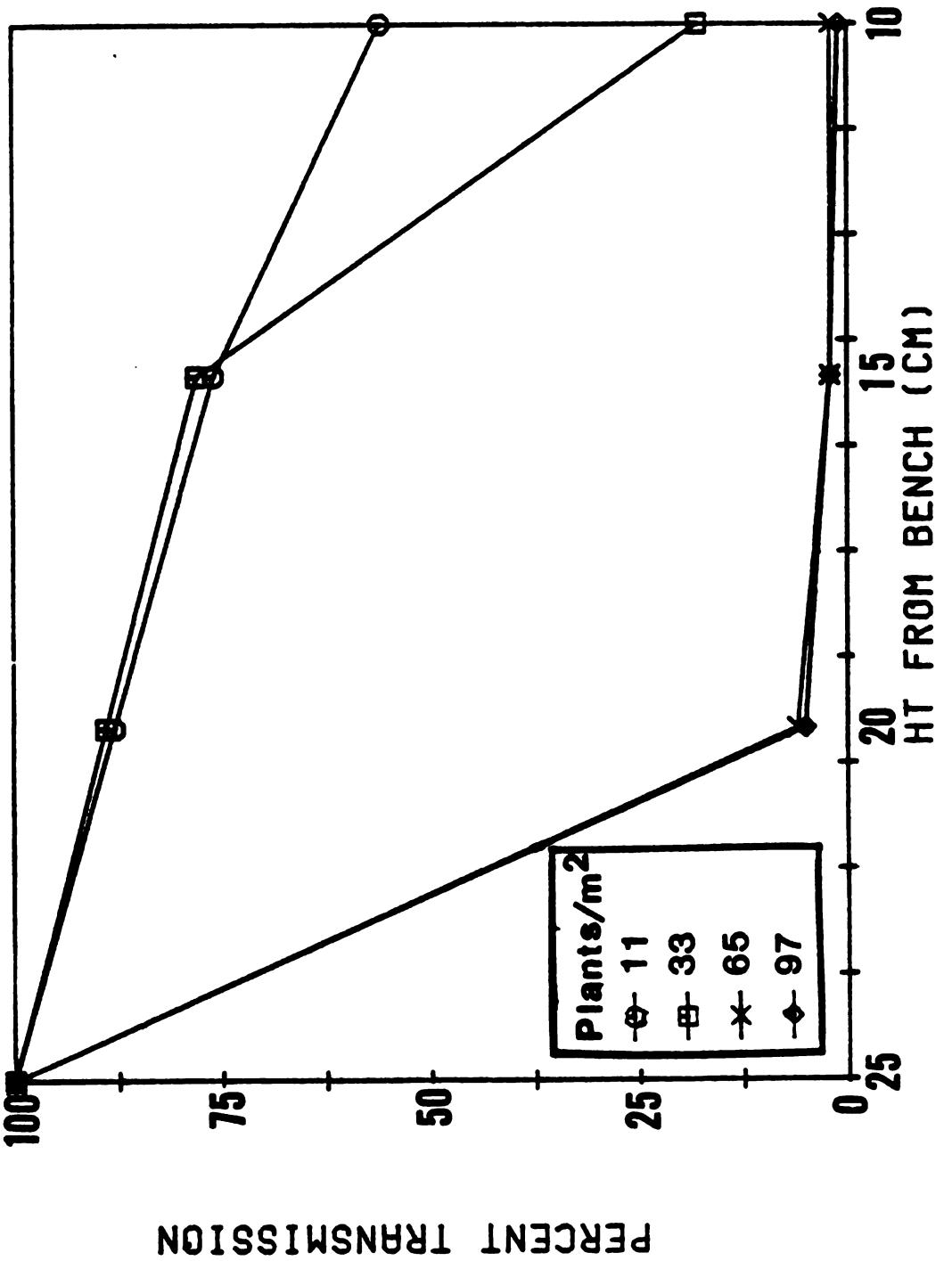
Weeks after start of short days	16°				21°			
	Normal daylight		75% shade		Normal daylight		75 % shade	
	Whole plant	Leaves removed	Whole plant	Leaves removed	Whole plant	Leaves removed	Whole plant	Leaves removed
6	--	--	--	--	--	--	--	--
8	29	31	22	32	17	31	12	21
9	17	25	14	21	10	22	9	8

Contrasts

Whole plant vs Leaf removal		**
Normal daylight vs 75% shade		*
16°C vs 21°		**
Whole plant vs leaf removal	(16°)	*
Normal daylight vs 75% shade	(16°)	NS
Whole plant vs Leaf removal	(21°)	NS
Normal daylight vs 75% shade	(21°)	*

[z]Contrasts on data at 63 days after the start of short days.
[y]Nonsignificant (NS) or significant at 5% (*), 1% (**) or <.1% (***) level.

Figure 1. Percent photosynthetically active radiation transmission into poinsettia 'Annette Hegg Dark Red' canopies at plant spacings of 11, 33, 65, and 97 plants m^{-2}. Expt. 4.


PERCENT TRANSMISSION
100
75
50
25
0
25
20
15
10
HT FROM BENCH (CM)
Plants/m2
11
33
65
97

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Literature Cited

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VARIATION IN POINSETTIA CULTIVAR SENSITIVITY TO CYATHIA ABSCISSION

STEVEN H. MILLER and R. D. HEINS[1]

[1]Department of Horticulture, Michigan State University,
East Lansing, MI. 48824-1112 (U.S.A.)

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ABSTRACT

Miller, S. H. and R. D. Heins. 1984. Variation in poinsettia cultivar sensitivity to cyathia abscission. Scientia Hortic.,

Differences in sensitivity to cyathia abscission on poinsettia cultivars 'Annette Hegg Dark Red' (Dark Red), 'Annette Hegg Lady' (Lady), 'Annette Hegg Brilliant Diamond' (Brilliant), 'Gutbier V-14 Glory' (V-14), and 'Mikkel Triumph' were evaluated in the greenhouse and in a postharvest environment. Abscission was evaluated chronologically based both on the number of days after the start of short days (SD) and on the number of days after anthesis. Seventy-seven days after the start of SD, V-14 had the least abscission of the tested cultivars in the greenhouse or postharvest environment, while Lady had the greatest abscission. In contrast, 7 days after anthesis, V-14 had the greatest abscission in the postharvest environment while Brilliant and Dark Red had the least abscission. The differences in abscission on V-14 based on

keywords: Euphorbia pulcherrima, carbohydrates, cyathium

Section III

Variation in Poinsettia Cultivar Sensitivity to Cyathia Abscission

evaluation method was due to it's reaching anthesis 7 to 10 days later than the other cultivars. Abscission was greater in all cultivars in the postharvest environment than in the greenhouse probably due to the lower photosynthetically active radiation (PAR) levels in the postharvest environment (5.1 mol d^{-1} in the greenhouse compared to 0.29 mol d^{-1} in the postharvest environment).

INTRODUCTION

Much of the potential variation in poinsettia postproduction quality is related to genetic background (Rogers, 1981). Many of the early cultivars had poor bract and leaf retention (Ecke and Matkin, 1976), however later breeding efforts introduced cultivars that decreased this problem (Shanks, 1981). However, cyathia abscission is still a problem in greenhouses and marketing which results in plants looking prematurely aged (Shanks, 1981).

Flower or petal abscission has been attributed to low light (Fortanier and Zevenbergen, 1973; Halevy, 1975; Kinet, 1977), high temperatures (Fitting, 1911; Wittwer, 1954; Armitage et al., 1980), and carbohydrate depletion in the flower (Kofranek, 1951; Subhadrabandu et al., 1978; Durieux, et al., 1983). Information on cyathia abscission is limited and the mechanism which causes it is unknown (Staby and Kofranek, 1979; Miller and Heins, 1984a). Cyathia abscission occurs in plants grown under low light (Staby and Kofranek, 1979) or in plants placed in a postharvest environment with low light and warm temperatures

(Woodhead and Einert, 1973; Staby and Kofranek, 1979). The longer plants were held in dark storage the greater the cyathia abscission (Scott et al., 1983; Scott et al., 1984).

Sprays of gibberellin or gibberellin plus 6-benzylamino purine late in the crop delayed cyathia abscission (Shanks, 1981), but these hormones can cause excessive stem elongation, smaller bracts, and delayed flowering (Miller and Heins, unpublished results).

Information on cultivar sensitivity to cyathia abscission is limited. Scott et al (1984) observed that 'V-14' had less cyathia abscission than 'Dark Red Hegg' or 'Mikkel Improved Rochford' after being held in either a dark or lighted postharvest environment. This was attributed to 'V-14' being more tollerant of stress than other cultivars (Hammer et al., 1981; Shanks, 1981; Scott et al., 1983). The objective of this research was to determine if there were differences in cultivar sensitivity to cyathia abscission both in the greenhouse and in a simulated postharvest environment.

MATERIALS AND METHODS

Experimental conditions. Rooted cuttings of 'Annette Hegg Dark Red™' (Dark Red), 'Annette Hegg Lady™' (Lady), 'Annette Hegg Brilliant Diamond™' (Brilliant), and 'Gutbier V-14 Glory™' (V14) from Paul Ecke Poinsettias, Encinitas, CA. and 'Mikkel Triumph™' from California-Florida Plant Corp., Fremont, CA. were received 25 Aug 1983, (Expt. 1) and 22 Sept 1983, (Expt. 2). One cutting was planted per 10 cm plastic pot (an experimental unit) in VSP medium (Michigan Peat Co., Houston,

Tx.) composed of 2 peat: 1 perlite: 1 vermiculite (v:v:v) ammended with dolomitic limestone, superphosphate, and trace elements. Plants were placed in a single layer glass greenhouse and grown single stem, at a spacing of 33 plants m^{-2}. Plants for Expt. 1 were initially grown under natural daylight (ND) and plants for Expt. 2 were initially grown, under ND plus 4 hr (2200 hr to 0200 hr) of 5 $\mu mol\ s^{-1}\ m^{-2}$ of photosynthetically active radiation (PAR) from 60 W incandescent lamps to prevent flower initiation. Short days (SD) were initiated 1 Sept (Expt. 1) and 1 Oct (Expt. 2). Black sateen cloth was pulled from 1600 hr to 0800 hr daily throughout both experiments.

The night temperature (NT) setpoint during vegetative growth was 18°C. Day temperature (DT) and venting temperature setpoints were 3°C and 6°C above the NT respectively in all experiments. The NT was set at 16° when SD started. Plants were fertilized with 260 mg l^{-1} N, 130 mg l^{-1} K, and 0.1 mg l^{-1} Mo. Chlormequat was applied as a foliar spray for height control at 1500 mg l^{-1} at the start of SD and 1 weeks later, and at 750 mg l^{-1} after 3 weeks of SD. When 50% of each cultivar reached visible, bud half of the plants were moved to a 21° NT greenhouse. Plants remained at the two NT until anthesis. When 50% of the plants in each cultivar reached anthesis, half of the plants were moved and evaluated in a simulated postharvest environment at 18° NT with an 8 hr photoperiod (0800 hr to 1600 hr) under 10 $\mu mol\ s^{-1}\ m^{-2}$ PAR from 40 W cool white fluorescent lamps measured at the top of the bract canopy. The remaining plants were evaluated in the greenhouse.

Data collection. The date of anthesis and the number of abscised cyathia were recorded daily for 25 days past anthesis for each plant. The total number of cyathia per plant was determined at the end of the experiment by counting the number of cyathia greater than 1 mm still present plus the number of stubs remaining from previously abscised cyathia. Percent abscission per plant was calculated by dividing the number of abscised cyathia by the total number of cyathia formed.

Statistical analysis. The experiments were analyzed as a completely randomized design, split, split plot, with NT as the main plot, evaluation environment and cultivars as subplot factors. There were 20 treatments (2 NT X 2 environments X 5 cultivars), 5 plants per treatment. Statistical significance was determined by analysis of variance and Duncans multiple range test was used to compare cultivars within each treatment (Steel and Torrie, 1980).

RESULTS AND DISCUSSION

Through 77 days from the start of SD, V14 had less abcission than the other cultivars, in both the greenhouse and in the postharvest environment (Table 1, Figures 1, 2). Lady consistantly had greater abscission than the other cultivars throughout the evaluation period in both environments. In the greenhouse, Brilliant had less abscission than

Dark Red, Lady, or Mikkel Triumph (Figure 1) while in the postharvest environment, Brilliant and Dark Red had less abscission than Lady or Mikkel Triumph (Figure 2).

When evaluated after a common number of days after anthesis, Brilliant had less abscission than the other cultivars with one exception in the postharvest environment where Dark Red had less abscission (Table 1, Figures 3, 4). Abscission in V14 was equal to or greater than the other cultivars at the same stage of physiological development. In the postharvest environment, V14 had the greatest abscission (Figure 4), while Dark Red had the least abscission. Abscission was greater for all cultivars in the postharvest environment than in the greenhouse (Figures 3, 4).

In Expt. 1, Dark Red, Lady, Brilliant, and Mikkel Triumph reached anthesis in approximately 55 days when plants were grown at 16° while V14 reached anthesis 7 to 9 days later (Table 2). When plants were grown at 21°, all cultivars flowered 3 to 4 days earlier except for Mikkel Triumph which flowered 2 days later. Compared to the "Hegg" cultivars, V14 reached anthesis 7 to 10 days later.

In Expt. 2, plants flowered 4 to 11 days later than in Expt. 1 when grown at 16° and 3 to 5 days later when grown at 21°. Flowering in Mikkel Triumph and Dark Red was delayed more than in the other cultivars. There was more variation in time to flower between cultivars in Expt. 2 than in Expt. 1. However, variation was less at 21° than at 16°.

While V-14 had less cyathia abscission through 77 days after the

start of SD, on a chronological basis, when comparing all cultivars at anthesis, V-14 had equal to or greater abscission than the other cultivars. The reason V-14 had less abscission through 77 days of SD was because it reached anthesis later than the other cultivars, therefore the cyathia were not as physiologically old. In V-14 the cyathia that were typically first to abscise were the younger, outer cyathia (personal observation). Therefore, even though abscission was greater for V-14, it was not as visibly apparent as in the other cultivars, which normally abscised the older inner cyathia first leaving a distinct "open center" in the inflorescence.

There was greater cyathia abscission in the postharvest environment than in the greenhouse probably due to the lower irradiance level in the postharvest room. Actual total irradiance received by plants in the greenhouse during the 25 days past anthesis averaged 5.89 mol d^{-1} in Expt. 1 and 4.36 mol d^{-1} in Expt. 2. This compares with 0.29 mol d^{-1} in the postharvest room. Low irradiance levels have been shown to promote cyathia abscission (Woodhead and Einert, 1973; Staby and Kofranek, 1979; Miller and Heins, 1984a; Scott et al., 1984).

Temperatures higher than the greenhouse are often found in postharvest environments and also promote cyathia abscission (Woodhead and Einert, 1973; Staby and Kofranek, 1979). In contrast plants finished at 21° were evaluated under lower temperatures in the postharvest room (ca. 19°) and still abscised more cyathia than when evaluated in the greenhouse. When cultivars were evaluated in the greenhouse, plants grown at 16° NT had less abscission than plants grown at 21° (Table 1)

however, there was little difference in abscission between plants grown at 16° or 21° and evaluated in the postharvest environment, probably due to the lower irradiance levels. Therefore irradiance appears to be the primary environmental factor controlling abscission.

The cyathia abscission under low irradiance levels in the postharvest environment was probably due to declining carbohydrates in the plant (Addicott, 1982). Bracts and leaves show a steady decline in carbohydrate content as plants approach anthesis, declining faster under reduced irradiance and/or higher temperatures (Miller and Heins, 1984b). Carbohydrates are probably also declining in the cyathia at the same time.

In the greenhouse, declining natural irradiance levels in the fall and expanding bracts shade the leaves and decrease photosynthesis, reducing carbohydrate supply. High temperatures will also increase respiration rates which will also reduce carbohydrates in the plant (Noggle and Fritz, 1976). During expansion, bracts compete with the cyathia for carbohydrates. The bracts appear to be stronger sinks as they do not abscise (Miller and Heins, 1984b). Similarly in Lilium (Durieux et al., 1983), the youngest flower buds, being the weakest sinks prematurely abscise as a result of competition for carbohydrates (Fawazi and El Fouly, 1979).

These results show that through 77 days of SD, V14 was superior to the other cultivars. The delayed abscission in V14 is due to delayed anthesis. Of the "Heggs", cyathia abscission in Brilliant is delayed relative to the other cultivars. Once anthesis is reached, abscission in

V14 progresses as rapidly as in the Hegg cultivars. Under all circumstances, Lady appears to abscise cyathia faster than the other tested cultivars. Warm finishing temperatures and/or low irradiance levels late in crop development or in the postharvest environment promotes abscission.

To decrease the occurance of cyathia abscission, early flower initiation in late September is important to maximize reproductive growth under the higher irradiance levels in early fall. Proper night temperature control in October and early November will permit lower night temperatures in late November and December and hence should help reduce abscission. Spacing plants to maximize light penetration as plants are marketed is another method to help maintain carbohydrate levels in the plant and delay abscission.

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Table 1. Mean percent abscission on plants 70 days after the start of short days and on plants 21 days after anthesis for five poinsettia cultivars. Plants were grown at 16° night temperature until visible bud, then at 16°C or 21°C until anthesis. Plants were evaluated in the greenhouse or in a postharvest environment (18°C, 10 μmol $s^{-1}m^{-2}$).

Cultivar	Evaluation environment							
	Greenhouse				Postharvest room			
	Finishing night temperature (°C)							
	Expt. 1		Expt. 2		Expt. 1		Expt. 2	
	16°C	21°C	16°C	21°C	16°C	21°C	16°C	21°C
	70 days after the start of short days							
'Annette Hegg Dark Red'	1 a[y]	36 a	0 a	36 b	50 c	48 bc	9 a	13 ab
'Annette Hegg Lady'	2 ab	32 a	35 b	48 b	39 bc	69 c	36 b	45 b
'Annette Hegg Brilliant Diamond'	1 a	17 ab	4 a	30 b	11 ab	31 ab	1 a	10 ab
'Gutbier V-14 Glory'	1 a	2 b	0 a	5 a	0 a	0 a	0 a	3 a
'Mikkel Triumph'	6 b	23 ab	2 a	47 b	27 abc	30 ab	0 a	21 ab
	21 days after anthesis							
'Annette Hegg Dark Red'	13 a	40 b	31 b	58 ab	75 bc	55 ab	84 ab	60 a
'Annette Hegg Lady'	15 a	39 b	72 c	72 b	63 bc	82 ab	96 b	74 a
'Annette Hegg Brilliant Diamond'	6 a	17 a	5 a	42 a	28 a	42 a	79 ab	75 ab
'Gutbier V-14 Glory'	36 b	38 b	23 ab	57 ab	67 c	93 b	77 ab	95 b
'Mikkel Triumph'	9 a	34 b	41 b	65 b	48 ab	47 a	66 a	80 b

[z]70 days after the start of SD.
[y]Mean separation within columns using Duncan's multiple range test (5% level).
[x]21 days after anthesis.

Table 2

Number of days to anthesis for five poinsettia cultivars grown at 16° until visible bud (ca. 28 days), then at 16°C or 21°C night temperature to anthesis

Cultivar	Temperature			
	16°C		21°C	
	Expt. 1[z]	Expt. 2	Expt. 1	Expt. 2
'Annette Hegg Dark Red'	54 a[y]	65 b	51 a	56 a
'Annette Hegg Lady'	56 a	63 b	52 a	57 a
'Annette Hegg Brilliant Diamond'	54 a	58 a	50 a	55 a
'Gutbier V-14 Glory'	63 b	70 c	60 b	64 b
'Mikkel Triumph'	54 a	65 b	56 ab	59 a

[z]Short days started on Sept. 1 - Expt. 1; Oct. 1 - Expt. 2.

[y]Mean separation within columns using Duncan's multiple range test (5% level).

Figure. 1. Mean percent cyathia abscission 56 to 98 days after the start of short days of five poinsettia cultivars finished at 21°C night temperature and evaluated in the greenhouse. Day of anthesis indicated by ⟶ . Expt. 2.

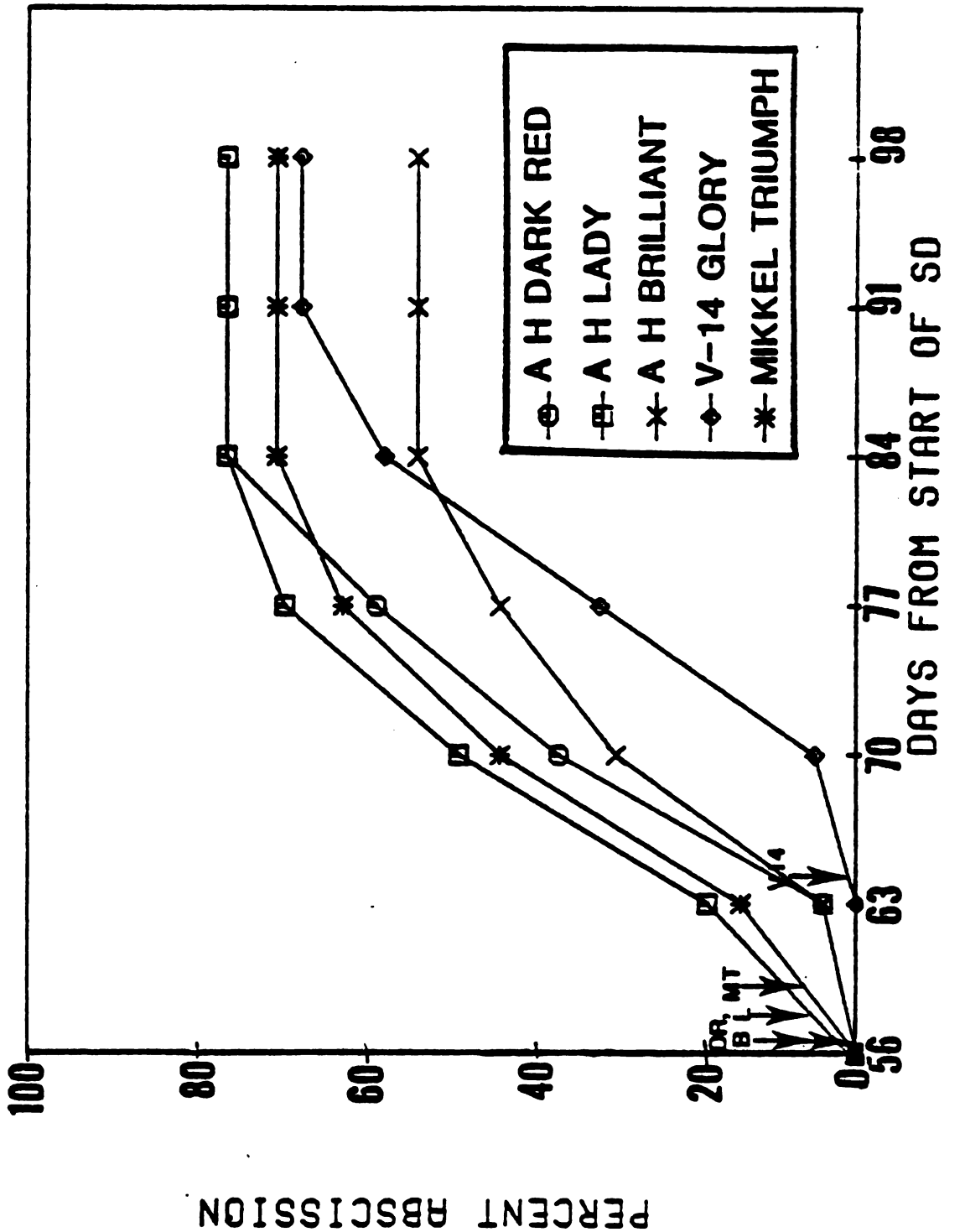

A H DARK RED
A H LADY
A H BRILLIANT
V-14 GLORY
MIKKEL TRIUMPH
PERCENT ABSCISSION
DAYS FROM START OF SD
100
80
60
40
20
0
56
63
70
77
84
91
98
DR.
B
MT

Figure. 2. Mean percent cyathia abscission 56 to 98 days after the start of short days of five poinsettia cultivars finished at 21°C night temperature and evaluated in a postharvest environment. Day of anthesis indicated by ⟶ . Expt. 2.

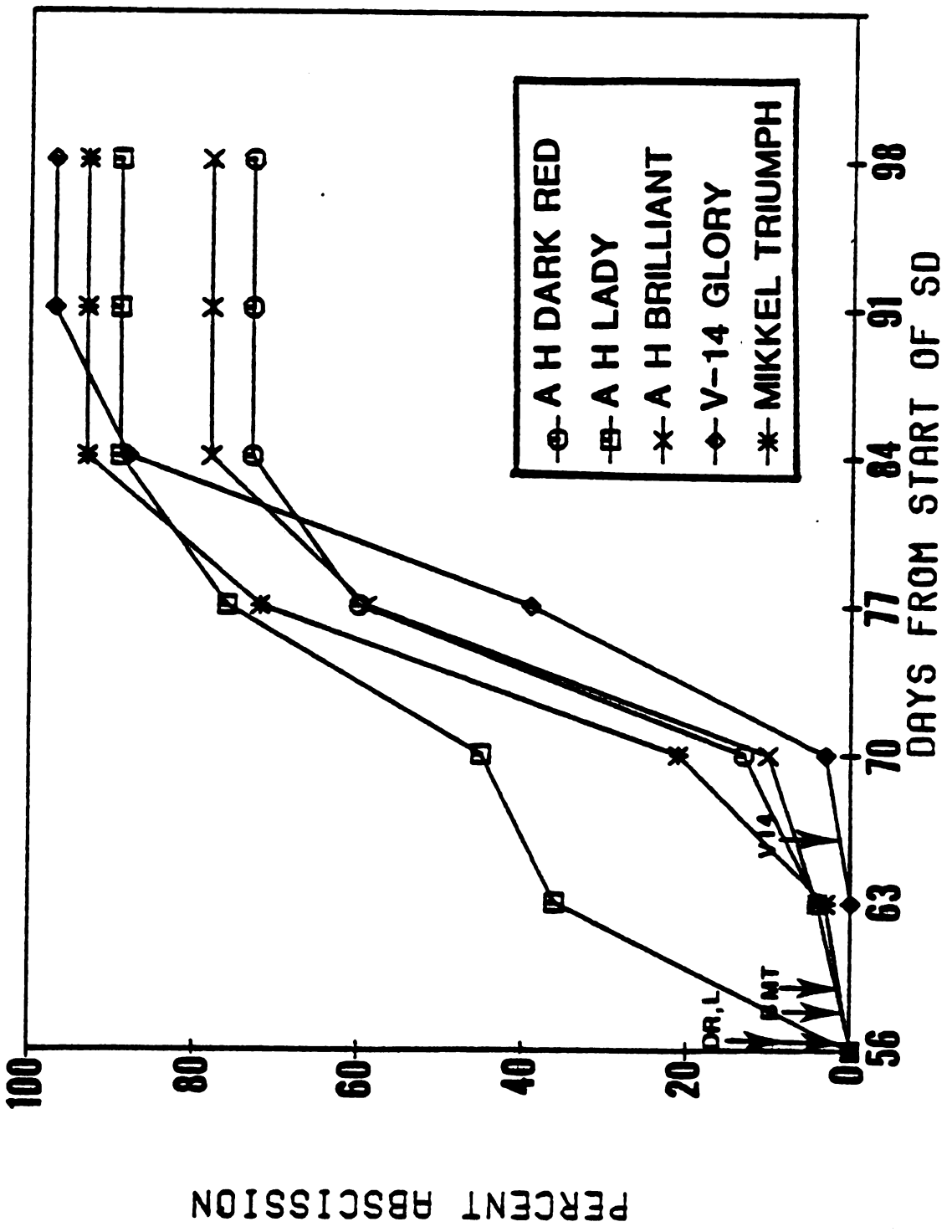

A H DARK RED
A H LADY
A H BRILLIANT
V-14 GLORY
MIKKEL TRIUMPH
PERCENT ABSCISSION
DAYS FROM START OF SD
100
80
60
40
20
0
56
63
70
77
84
91
98
DR,L
EMT
V14

Figure. 3. Mean percent cyathia abscission 7 days before anthesis to 35 days after anthesis of five poinsettia cultivars finished at 21°C night temperature and evaluated in the greenhouse. Day of anthesis indicated by ⟶ . Expt. 2.

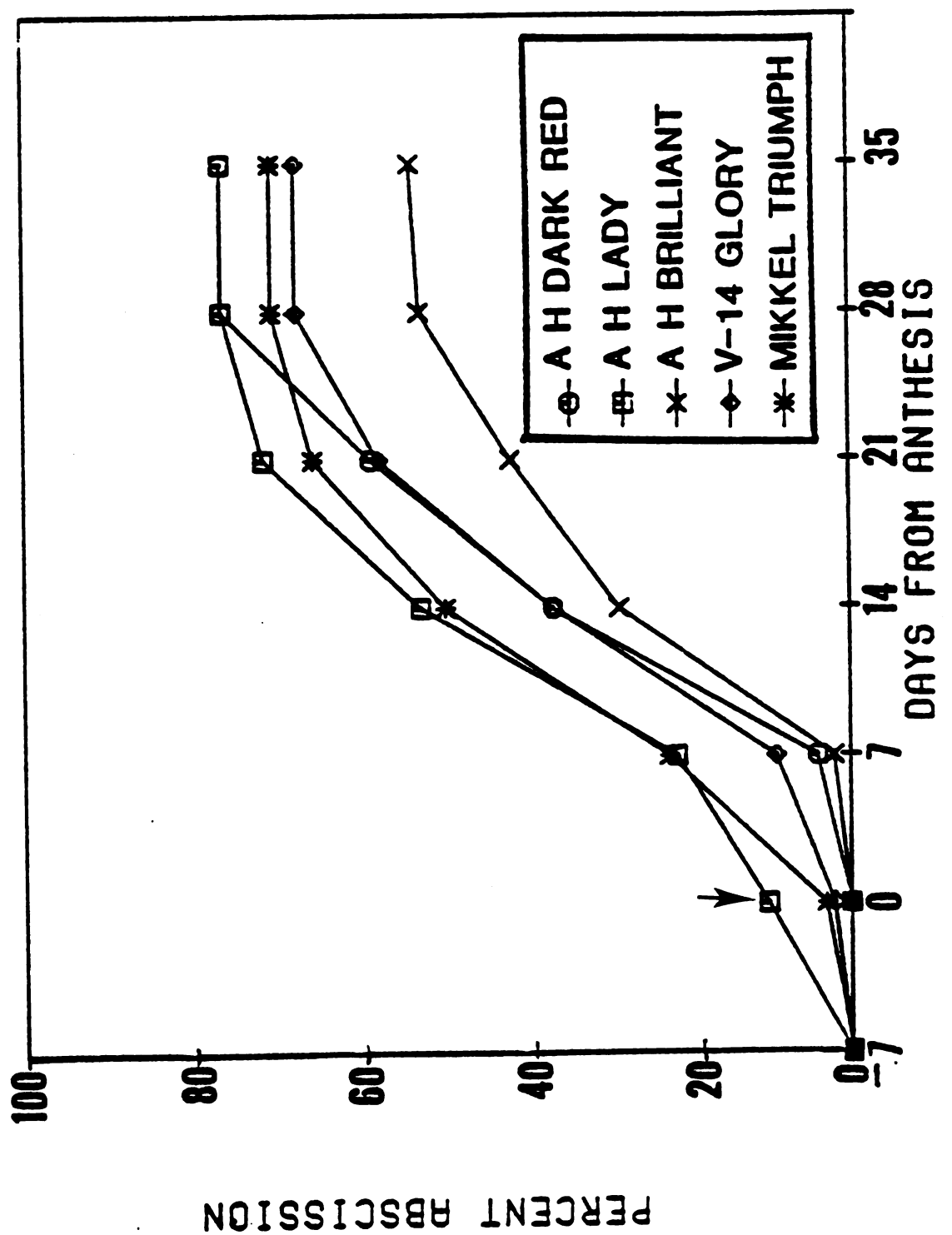
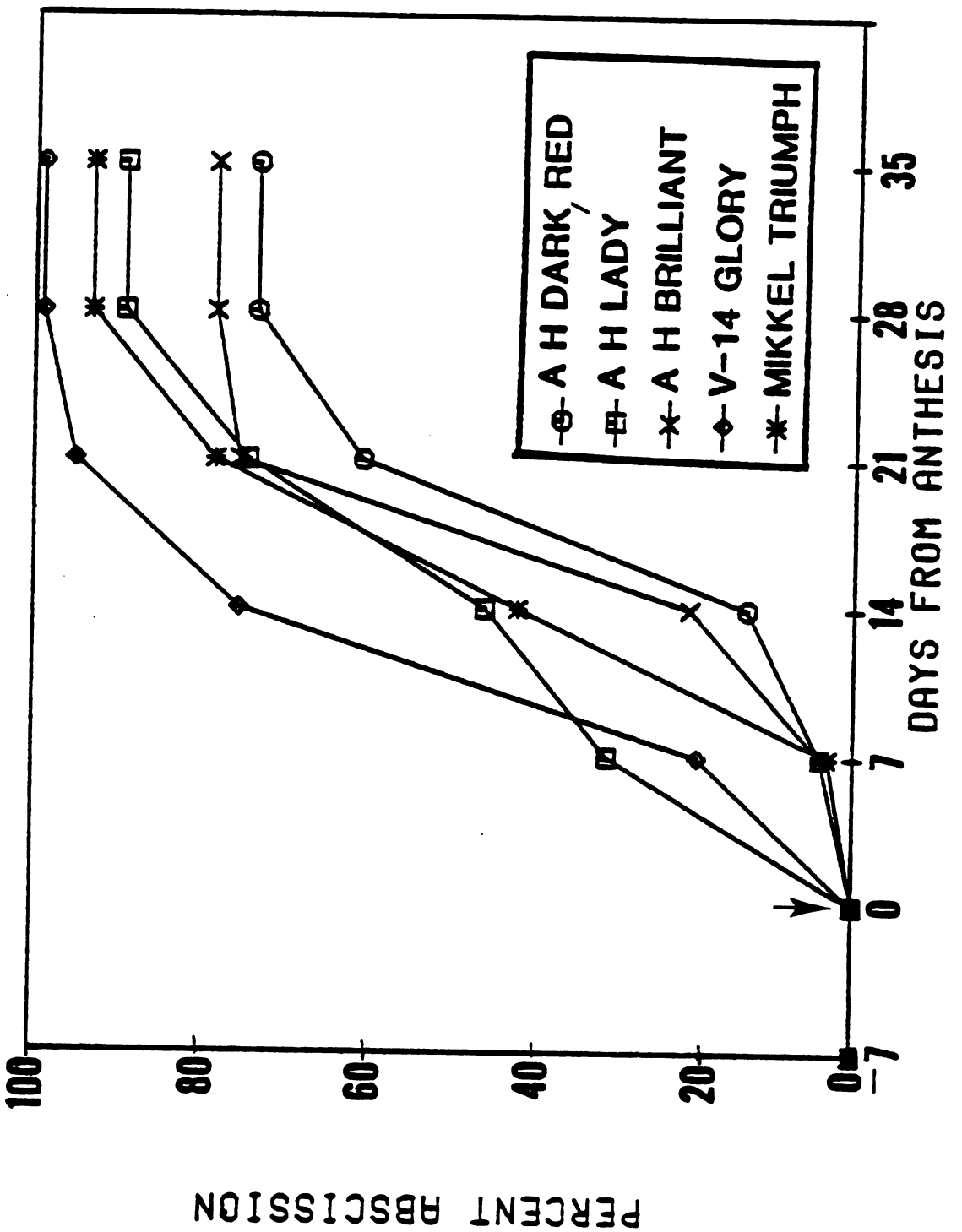

PERCENT ABSCISSION
100
80
60
40
20
0
-7
0
7
14
21
28
35
DAYS FROM ANTHESIS
A H DARK RED
A H LADY
A H BRILLIANT
V-14 GLORY
MIKKEL TRIUMPH

Figure. 4. Mean percent cyathia abscission 7 days before anthesis to 35 days after anthesis of five poinsettia cultivars finished at 21°C night temperature and evaluated in a postharvest environment. Day of anthesis indicated by ⟶ . Expt. 2.


A H DARK RED
A H LADY
A H BRILLIANT
V-14 GLORY
MIKKEL TRIUMPH
100
80
60
40
20
0
-7
0
7
14
21
28
35
DAYS FROM ANTHESIS
PERCENT ABSCISSION

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