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Major professor

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GROWTH AND DEVELOPMENT OF *DICENTRA SPECTABILIS* IN RELATION TO STORAGE TEMPERATURE AND HARVEST DATE

By

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ABSTRACT

GROWTH AND DEVELOPMENT OF *DICENTRA SPECTABILIS* IN RELATION TO STORAGE TEMPERATURE AND HARVEST DATE

By

Anne M. Hanchek

Herbaceous perennials overwinter perennating buds at or below the soil surface and can exhibit distinct patterns of seasonal growth. In the fall of 1985 and 1986, field-grown crowns of seven genera , including *Dicentra spectabilis* (L.) Lem. were harvested weekly from western Michigan fields and stored bare-root in polyethylene-lined crates at 0C. Regrowth after storage was superior at later harvests.

In continued work to characterize the chilling requirements of *D. spectabilis*, four separate regrowth responses were observed: eye etiolation, budbreak, stem elongation, and flowering. Unstored crowns harvested in October took 77 days from potting to break bud. Storage at -2.5, 0, 2.5, or 5C for 2 weeks promoted budbreak. After 8 weeks of chilling, buds broke in 10-20 days. Crowns required 4 weeks of $\leq$5C for stem elongation and 8 weeks for faster flowering. At $\geq$10C, eyes etiolated in storage but budbreak was not hastened; essentially no stem elongation was observed after these treatments. At later harvests, less chilling was needed to achieve the same response. By mid-November in 1986, minimum field soil temperatures were below 5C, and harvested crowns broke bud in 5-15 days after

only 2 weeks storage at ≤15C. Constant exposure to 20C delayed budbreak.

In 1987, D. spectabilis eyes were excised from October-harvested crowns stored for 0, 4, 8, or 12 weeks at 5, 7.5, or 10C. The eye was identified in stained fresh sections as an overwintering structure of scales enclosing primary and secondary buds. Etiolation of the eye without budbreak occurred by cell elongation in the basal region. During storage, the domed vegetative meristem observed at harvest lengthened into a spike bearing floral primordia. After 12 weeks at 10C, eyes were three times their original length and contained few leaves but many flower buds. Floral primordia were first observed microscopically in eyes from crowns held 4 weeks at 10C and 8 weeks at 5C. Despite more rapid floral development, crowns held at 10C grew very slowly when planted and usually failed to produce expanded flowers. After exposure to 5C for 8 weeks, most crowns flowered in 40 days and inflorescence size was larger.

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INTRODUCTION

Dormancy in perennials is a familiar phenomenon, especially in the world's temperate zones, where we most often associate it with winter survival. A leafless tree, although very visible, is not the only example of bud dormancy. Herbaceous perennials also have perennating buds, not on aerial stems, but on roots, crowns, stolons, rhizomes, and in bulbs. These buds can exhibit distinct patterns of dormancy.

The definitions used in the study of dormancy are subject to discussion and continuing revision (5). Several systems of terms have been proposed, some for both buds and seeds, some for a particular organ or tissue only. The American Society for Horticultural Science at its 1988 annual meeting proposed this general definition of dormancy: "the suspension of (visible) growth of any plant structure(s) containing a meristem(s) in response to external or internal control" (2).

One growth cycle of herbaceous perennials is typified by Coreopsis lanceolata, which is killed back to a leafy rosette by cold weather. With protection, it can remain evergreen all winter. By some definitions, the plant is quiescent rather than at rest since regrowth can occur in a

heated greenhouse when crowns are defoliated in the months of September, October, and November (Chapter 1). Since growth can resume at any time that temperature and moisture are favorable, we can also call such Coreopsis ecodormant (5).

On the other hand, many perennials completely lose all aboveground structures during part of the year. Spring-flowering bulbs and ephemerals die back early in summer, apparently in a pre-programmed response to the seasonaly unfavorable conditions under which they evolved (7). They are generally described as "summer-dormant" but this refers more to lack of above-ground parts than to cessation of growth. In fact, some authors claim there is no true dormancy in certain bulbs such as tulip and daffodil since the flowering apex continues to develop during the leafless period (3,4).

Somewhere between these two extremes is the growth cycle of Hosta, which emerges from the soil in spring, attains full growth and flowering during the summer, and dies back in fall. Defoliation in late summer does not induce new growth. This basic pattern also describes Dicentra spectabilis (Lam.) L., the old-fashioned bleeding heart (6,8). Dicentra has a spreading, tuberous root system with adventitious crown buds or "eyes" that elongate rapidly in spring (Figure 1.0; 1).

In a preliminary study in 1985-86, when crowns were harvested, defoliated, and potted immediately, the eyes did

not elongate even after seven months in the greenhouse. Those same crowns grew well after exposure to cold temperatures in storage, supporting Lopes and Weiler's (6) observation that Dicentra requires chilling to overcome bud dormancy. The first of the following studies was begun to examine the relationship between harvest date and regrowth after storage of selected fall-harvested herbaceous perennials. Further experiments were designed to explore the relationship between harvest date, storage temperature, and growth responses of Dicentra spectabilis.

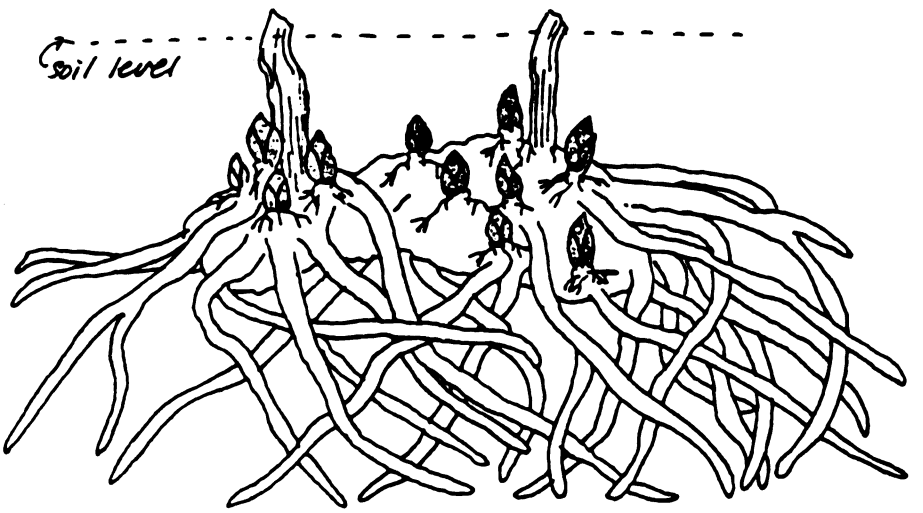

Figure 1.0 Gross morphology of <u>Dicentra spectabilis</u> crown showing eyes and tuberous roots.

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CHAPTER 1

EFFECT OF HARVEST DATE ON STORAGE QUALITY OF HERBACEOUS PERENNIALS

Many herbaceous perennials are grown commercially in southwest Michigan fields. The basic production scheme is to plant seeds or cuttings in the spring, lift and divide the crowns in the fall, and store them bareroot in polyethylene-lined crates at -2 to +2C for several months until shipped (3,7,8).

The recent surge in popularity of herbaceous perennials has meant an increased demand upon growers by retailers for quality material. Many of these retailers are located in warmer areas of the U.S. where fall planting is popular. Retailers find a definite advantage in having two marketing seasons, but have difficulty filling fall orders since the major Michigan producer prefers not to ship at that time. In the growers' experience, plants harvested before November in Michigan generally do not store well, often rotting completely and are of lower overall quality.

USDA recommendations do not address harvest date as a factor in the storage of herbaceous perennials (11) although the reader is referred to Mahlstede and Fletcher (12) who stress the importance of maturity for successful handling of

all nursery stock. Certain perennials which are summer-dormant such as iris and oriental poppy can be lifted early in the fall. The recommendation for most other herbaceous perennials is to dig as late as possible in the season. In an experiment with Alcea (hollyhock), plants dug before October 5 and held at 2C regrew poorly (12). Plants harvested later in the digging season regrew much better. Langhans and Weiler (9) also emphasized the importance of maturity in storage of lily bulbs, with late September or early October harvests for best quality.

Date of harvest can also greatly affect subsequent regrowth of stored strawberry crowns. Best results were achieved when harvest was delayed until December in the northern temperate zone (1,2,5,22,24). Lift date has also been identified as an important factor in successful storage and establishment of conifer seedlings. The ability to survive cold storage and regenerate roots when planted peaked from October to April in the northern temperate zone for Douglas-fir and ponderosa pine (19,20) and from December to February for lodgepole pine and interior spruce (18). Preliminary experiments by Maqbool (unpubl. data 1983) indicated that a similar pattern could exist for several herbaceous perennials.

This study was designed to examine the relationship between harvest date and regrowth after storage of selected fall-harvested herbaceous perennials, including Dicentra spectabilis.

MATERIALS AND METHODS

1985 experiments. Seven different species were used: Aquilegia L. 'Biedermeier', Coreopsis lanceolata L. 'Sunburst', spring-planted Dicentra spectabilis (L.) Lem., Geum quellyon Sweet 'Mrs. Bradshaw', Gypsophila paniculata L. 'Snowflake', Iberis sempervirens L. 'Snowflake', and Lupinus L. 'Russell Hybrids'. Specific information on root system, storage type, and hardiness is given in Table 1.1.

Each week for twelve weeks, from September 11 to November 27, plants were lifted from commercial fields in western Michigan (Walters Gardens, Zeeland, MI). At each harvest, ten soil temperatures at 10 cm depth were recorded per species at the harvest site. Weather records from the Trevor Nichols Experimental Farm, Fennville, MI were also obtained (15). Soil cores at 5 cm to 10 cm were removed, and the samples were weighed before and after oven-drying to determine percent water content (w/w). Plants were processed by shaking off all loose soil and removing the green tops. The number and average length of eyes (crown buds) on each plant of Aquilegia, Gypsophila, Lupinus, and Dicentra were recorded. Five plants of each of the seven species were then potted and put in a cool greenhouse (19C day/12C night). Twenty crowns of each were stored in bulk at 0C in polyethylene-lined crates to avoid desiccation stress (3,21,24).

On January 8 and on April 9, ten plants per species from each harvest were removed from storage and evaluated

for mold, using a 1 to 4 scale (1=0-25% surface molded, 2=26-50% surface molded, 3=51-75% surface molded, 4=76-100% surface molded). The crowns were then potted and their regrowth was evaluated at 3 and 4 weeks after each potting, using a 0 to 5 scale (0=dead, 0.5=dormant buds, 1=emergent growth, ...5=vigorous growth) following Maqbool (13). Whole plant height was measured and presence of buds or flowers noted.

At three times during the harvest season, ten extra plants were dug and processed, then divided into root and crown. The parts were weighed, oven-dried, and reweighed to give dry weight and moisture content on a fresh weight basis.

1986 experiments. Three species were used: Dicentra spectabilis, Gypsophila paniculata 'Snowflake', and Coreopsis grandiflora Hogg ex Sweet 'Sunray' (Table 1.1). Each week for nine weeks from October 7 to December 2, ten plants of each species were potted immediately, ten were stored at 0C for two months, and ten at 0C for four months. Gypsophila and Coreopsis were held under natural daylength in the greenhouse. Dicentra alone was regrown under 16 hours of 8.5 mol/day-m^2 supplemental light. Regrowth, mold, and flowering were evaluated as before, but height was not measured.

Development of eyes was monitored for Dicentra only. At each harvest, ten plants were washed and all visible eyes ($\geq$2 mm) excised from the crowns. Number, length, and dry

weight of the eyes were recorded. Root and crown weights were not measured for any species.

The data for each year were analyzed as a completely randomized design (14). Least significant differences between treatment means were calculated at the 0.05 level with n=5 replicates per treatment cell (no storage) or n=10 (with storage). Standard errors were calculated for dry weight and water content means.

RESULTS

Soil conditions. In the sandy loam soil of Ottawa County, moisture in the upper soil during September, October, and November varied from 5% to 12% (w/w) in response to temporary conditions such as rainfall, snow, cultivation, cloud cover, etc (data not shown). No pattern was obvious. Soil temperature at 10 cm depth declined from near 20 to 2C over both harvest seasons (Figure 1.1).

Soil tests by the MSU Soil Testing Lab showed high levels of phosphorous, calcium, and magnesium, and adequate nitrogen and potassium in all fields. pH ranged from 6.5 to 6.8, cation exchange capacity from 2 to 4 meq/100g.

Plant development before harvest. There were no significant changes over the 12 week harvest season in dry weight or moisture content of the root and crown in any of the seven species harvested in 1985. Average moisture content of roots was close to 70% for all species except Iberis whose roots were only 55% water. Water content of

crowns was generally a little higher than roots (Table 1.2).

Average length of eyes in the four species producing crown buds was 2 to 4-fold greater at later harvests (Figure 1.2). For Dicentra, Gypsophila, and Lupinus, eye length was greatest on the last harvest date. For Aquilegia, length as measured was highest in mid-November. In contrast, the number of eyes per stem did not increase over the harvest season. A sample of Dicentra on September 11, however, was completely lacking in visible eyes, suggesting that eye production was relatively rapid and synchronized between September 11 and 26.

In 1986, sampling was restricted to Dicentra and each eye 2 mm or longer was individually measured. Neither number of eyes nor length per eye varied significantly during October or November (Figure 1.3). Length remained at 10-15 mm throughout the season, similar to the initial 1985 length. Dry weight per eye, however, increased in mid-November.

Post-storage condition. Aquilegia. Plants harvested before November and stored for over 5 months (long storage) were more than 50% covered with mold (Figure 1.4). In general, little to no mold growth was associated with later harvests and shorter storage periods. Neither harvest date nor storage length appeared to affect survival or regrowth quality. The best-looking plants were those harvested in mid-September and immediately potted, or those harvested in November and stored at least 5 months. The latter generally

flowered better as well. None of the plants potted immediately after harvest or after short storage flowered within 8 weeks of observation.

Coreopsis. Coreopsis lanceolata 'Sunburst' crowns lifted anytime during the harvest season in 1985 and potted immediately regrew (Figure 1.5). However, most plants harvested before October 31 did not survive 2 months storage; survival rate was even less for longer periods. All crowns harvested in mid-November or later survived 4 months at 0C. In addition, mold on stored crowns decreased with later harvests ($r=-0.87$, $a=0.0001$) and was barely detectable for the final three harvest dates. Regrowth quality of stored crowns followed the same pattern as mold growth, with the most vigorous plants being those harvested in late November and stored 1 to 4 months.

Coreopsis grandiflora 'Sunray', harvested in 1986, did not support mold growth in storage and 100% of the crowns survived. Crowns potted the day of harvest regrew but were generally of lower and less predictable quality than those stored 2 or 4 months (Figure 1.5d). For 'Sunray', the best plants were those harvested in mid-October or later, and stored 4 months. No plants of either Coreopsis cultivar flowered within 8 weeks of observation.

Dicentra. Plants potted the day of harvest survived, but usually did not regrow, except for a few plants from the latest harvests in 1986 (Figures 1.6, 1.7). Dormant eyes were visible on many non-growing plants. Stored plants

showed an entirely different regrowth pattern. If harvested before October 10 in 1985, Dicentra crowns came out of storage heavily molded, rotted, and dead. Those harvested on or after November 7 showed little mold development in storage and excellent regrowth. The transition from dead to vigorous plants took place over four weeks in October. Results were similar for both storage durations.

In 1986, very little mold developed in storage, even at early harvest dates, and all plants survived. Regrowth, however, paralled that of the previous year (Figure 1.7). In both years, late harvests and long storage at 0C produced higher quality plants which were also more likely to flower.

Geum. Stored crowns were rarely free of mold (Figure 1.8). Early harvests and long storage periods aggravated the problem. Survival, however, was excellent despite mold growth. Death in storage was only notable ($\geq$25%) for very early harvests stored for 5 months.

Crowns potted the day of harvest always showed excellent regrowth. Stored plants did not regrow as well, except for late harvests and 1 to 2 month storage. Quality tended to decrease with storage duration. No plants flowered within 8 weeks of observation.

Gypsophila. Mold on Gypsophila roots increased while percent survival decreased with storage length of 5 months or more for early harvests in 1985 (Figure 1.9). In October, plants were harvested and stored successfully for short periods; November harvests survived longer storage of

4 months. Regrowth quality of October harvests was poor but increased in November. Unstored plants generally regrew well, but stored roots produced taller plants (data not shown).

In 1986, results were quite different. The regrowth quality of plants harvested in October or November and stored for 4 months was consistently high. Two months storage produced good plants only from later harvests, while unstored roots did not regrow well after mid-October. No plants flowered within 8 weeks of observation.

Iberis. Harvest of Iberis began on October 3 rather than September 11. Since these plants are sub-shrubs and were not cut back at harvest or potting, regrowth was defined as greening of existing foliage and extension of lateral branches. Height during regrowth was not measured. Foliage of October-harvested plants was heavily molded after 5 months at 0C (Figure 1.10). Surviving individuals from these treatments also regrew poorly. Shorter storage periods and later harvests produced better quality plants which were free from mold. Unstored Iberis from all harvests grew well in the greenhouse but did not flower. Flowering was best for plants harvested in November and stored at least 4 months.

Lupinus. Mold growth was generally greater for early harvests and longer storage periods (Fig. 1.11). Of the few plants harvested and stored before mid-October that survived, some individuals were diagnosed with Pythium by

the MSU Plant Diagnostic Clinic. However, Lupinus harvested and potted immediately always regrew fairly well. Regrowth after storage improved as harvest was delayed. No plants flowered within 8 weeks of observation.

DISCUSSION

Mold rating was not generally indicative of subsequent regrowth quality. Harvest date was always more highly correlated with mold than was subsequent regrowth, with the exception of Iberis, which was stored as a leafy evergreen. Its damp, compressed foliage provided an excellent medium for growth of surface molds in storage and growing points were often damaged. Yet fungicides such as benomyl can be phytotoxic (6,13). Unpublished work by Heiden (pers. comm.) shows that removal of stems and foliage of Iberis before storage, rarely done in practice, avoids these problems and results in a predictably high-quality plant.

Most crowns of any perennial that came out of storage completely covered with mold regrew poorly, but plants free of mold did not always regrow well. Also, the mold rating refers only to surface mold. In many cases, dead or dying plants were rotted in storage as opposed to molded. The possibility of internal pathogens such as bacteria or the oomycete found in Lupinus cannot be ignored, although the subject was not part of this study (6).

Coreopsis and Geum, plants with fibrous root systems and stored as trimmed rosettes, grew fairly well despite

being cut back when potted immediately after harvest. After storage, however, plants from early harvests were of very low quality, especially after long periods. Beginning in mid-October, regrowth ratings began to equal or surpass those of unstored plants. Plant height followed the same pattern, but showed, in addition, an interesting reduction in height of unstored plants harvested late in November (Figure 1.12a). Fleshy-rooted species (Aquilegia, Dicentra, Gypsophila, and Lupinus), stored as bare roots with dormant crown buds, behaved similarly but did not regrow as well without storage (Figure 1.12b). Additional exposure to 0C not only improved the regrowth rating, but greatly increased height relative to the control.

Although a tall plant did not always receive a high regrowth rating, height and regrowth quality were strongly correlated (r=0.9, a=0.0001) for all the perennials studied except Geum. Mold decreased over as harvest was delayed for both plant types, but increased with storage duration for early-harvested fleshy-rooted species.

In 1985, all stored crowns were potted on the same days, so storage length varied with harvest date, the later harvests always being stored for shorter periods. This mimicked the industry practice of harvesting the same material at several times in the fall, then mixing harvest dates in the same shipment. Under these conditions, regrowth quality after storage rose as harvest was delayed. If regrowth was mainly a response to time in storage, then

plants from the first harvest after short storage (a total of 17 weeks at 0C) should have behaved as plants from the last harvest after long storage (a total of 18 weeks at 0C), and the two parameters would be well correlated. This was not the case. Late harvest consistently improved regrowth quality after storage.

In 1986, the treatments were designed for constant storage duration. Under those conditions, regrowth was unchanged with respect to harvest date for Coreopsis (a different species than in 1985), slightly better at later dates after short-term storage for Gypsophila, and greatly improved for Dicentra. Clearly, both harvest date and storage duration can affect regrowth.

Over the harvest season, there was a change in the plant response to storage. Early in the season, the shorter the time spent at 0C, the better. At some point, though, in response to field chilling, plants "hardened" and remained undamaged by long storage. Mahlstede and Fletcher (12) reported that decreasing moisture content from 80% to 73% signalled maturity in Alcea. Lily bulb growers recognize maturity when the old stem pulls easily form the bulb (9). Researchers have tried to measure the hardening process by monitoring changes in starch content of roots (2,5) or electrolyte leakage after freezing tests (4,25). In this experiment, dry weight of crowns, moisture content, eye length, and eye number per crown were measured. Only eye length varied significantly with harvest date, but the

relationship was not adequate to predict a complex response such as storage quality.

Overall, the observed changes in plant response to storage in 1985, whether in mold rating, regrowth, height, or crown bud length, occurred in mid-October at the same time as minimum soil temperatures dropped below 10C. Similar changes could be seen in October of 1986, but soil temperatures dropped earlier and stayed low for several weeks. Chilling has long been assumed to drive the hardening process (23), but most authors have worked with woody plants that carry aerial perennating buds (16,17,18). Logically, herbaceous perennials would respond to the temperature of the soil surrounding their terrestrial buds. This may explain why little or no mold was found on stored crowns harvested in 1986. The change from "unstorable" to "storable" may have taken place the first week of the harvest period. This study implies that the critical temperature was below 10C. However, controlled chilling at 0C in storage did not fully replace field chilling for early-harvested plants. There must be other factors at work, such as diurnal temperature cycles or photoperiod effects (9,19,23).

The most striking response, by far, was seen in Dicentra. The drastic changes from dead to living, molded to non-molded, non-growing to growing, and non-flowering to flowering suggest a switch turned on by exposure to cold temperatures, as experienced both in the soil environment

and in the storage room. These results further support the observation that Dicentra requires chilling to overcome dormancy (10), and that dormancy develops as part of the hardening process.

TABLE 1.1. Growth form and hardiness of herbaceous perennials used in harvest date studies.

BOTANICAL NAME (Common name)	ROOT SYSTEM	CROWN CONDITION IN STORAGE	USDA ZONE OF HARDINESS*
Aquilegia 'Biedermeier Strain' (Columbine)	fleshy tap	dormant crown buds	3
Coreopsis grandiflora 'Sunray' (Coreopsis)	fibrous	trimmed leafy rosette	3
Coreopsis lanceolata 'Sunburst' (Coreopsis)	fibrous	trimmed leafy rosette	3
Dicentra spectabilis (Old-fashioned bleeding heart)	fleshy tuberous	dormant crown buds	2
Geum quellyon 'Mrs. Bradshaw' (Avens)	fibrous	trimmed leafy rosette	5
Gypsophila paniculata 'Snowflake' (Baby's breath)	fleshy tap	dormant crown buds	5
Iberis sempervirens 'Snowflake' (Candytuft)	fibrous	leafy sub-shrub	3
Lupinus 'Russell Hybrids' (Lupine)	fleshy tap	dormant crown buds	4

*: R.W. Cumming and R.L. Lee. 1960. Contemporary perennials. MacMillan Co., New York.

TABLE 1.2. Season averages for dry weight and moisture content (w/w) of herbaceous perennial roots and crowns harvested in fall of 1985. Data averaged over 3 harvests (10/10,10/31,11/21) with 10 plants per species per harvest. No significant differences between harvests (a=0.05).

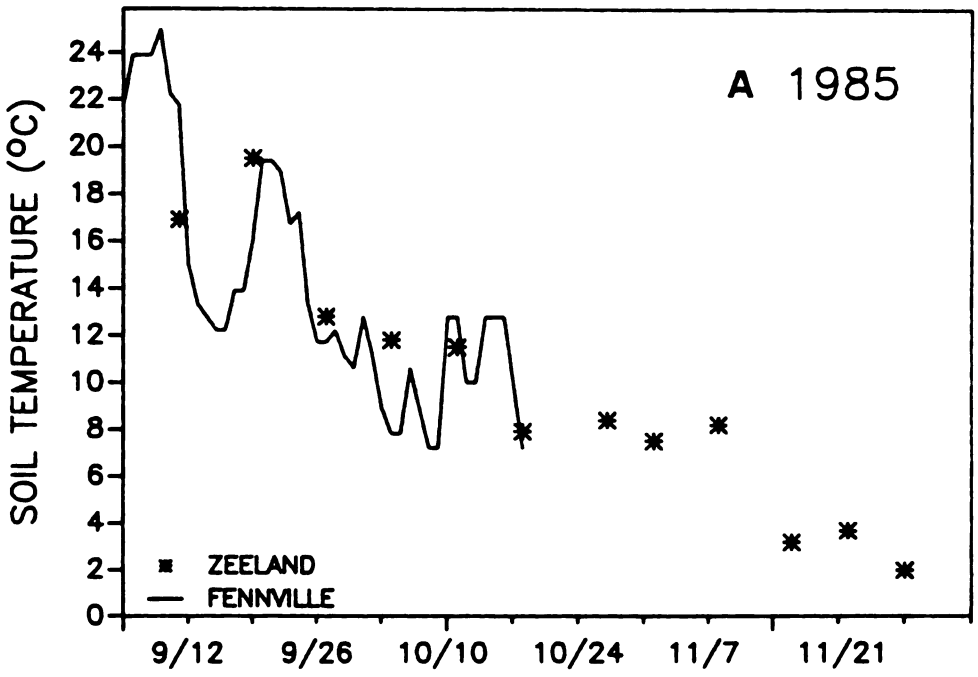
BOTANICAL NAME	ROOT DRY WEIGHT (g)	ROOT % WATER	CROWN DRY WEIGHT (g)	CROWN % WATER
Aquilegia 'Biedermeier Strain'	2.5 (0.3)*	70 (1)	0.7 (0.1)	79 (1)
Coreopsis lanceolata 'Sunburst'	5.4 (0.8)	75 (1)	9.7 (1.5)	80 (1)
Dicentra spectabilis	36.7 (4.1)	75 (1)	27.2 (2.3)	77 (1)
Geum quellyon 'Mrs. Bradshaw'	11.6 (0.8)	70 (1)	15.8 (1.2)	73 (1)
Gypsophila paniculata 'Snowflake'	5.5 (0.4)	68 (1)	0.3 (0.02)	69 (1)
Iberis sempervirens 'Snowflake'	17.0 (2.4)	55 (2)	22.8 (2.0)	74 (1)
Lupinus 'Russell Hybrids'	6.6 (0.8)	75 (1)	3.7 (0.6)	78 (1)

*: one standard error of the mean

Figure 1.1 Minimum daily soil temperatures at 10 cm depth at Trevor Nichols Experimental Farm, Fennville, MI, and average soil temperatures at 10 cm depth at 10:00 am in perennial fields, Zeeland, MI.

A. 1985. Zeeland standard error of the mean=0.3.

B. 1986. Zeeland standard error of the mean=0.4.


A 1985
SOIL TEMPERATURE (°C)
24
22
20
18
16
14
12
10
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4
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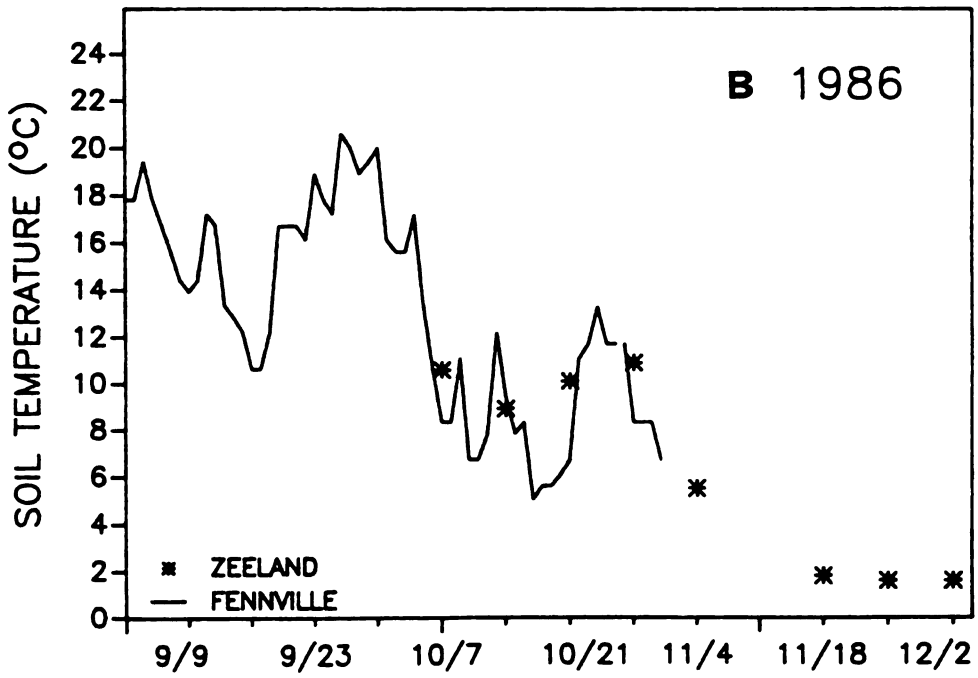
ZEELAND
FENNVILLE
9/12
9/26
10/10
10/24
11/7
11/21


B 1986
SOIL TEMPERATURE (°C)
24
22
20
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10
8
6
4
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ZEELAND
FENNVILLE
9/9
9/23
10/7
10/21
11/4
11/18
12/2

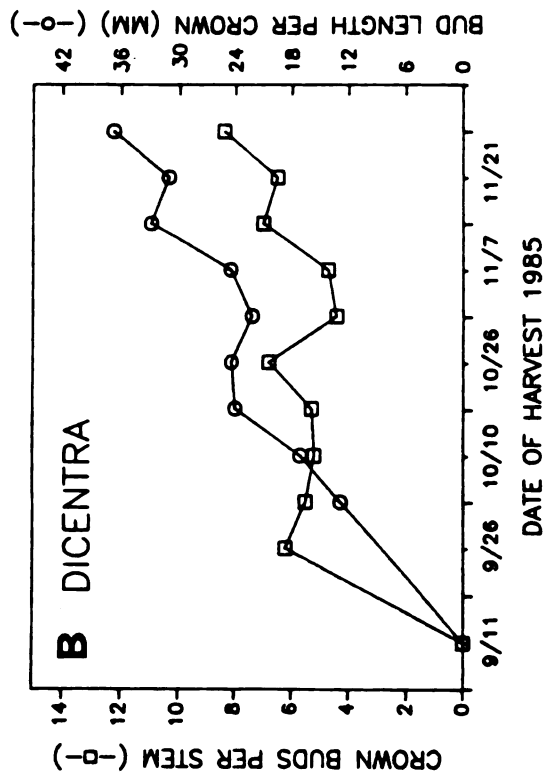
Figure 1.2 Number and average length of crown buds per plant at weekly harvests from 9/26/85 to 11/28/85. At least 30 plants sampled per mean.

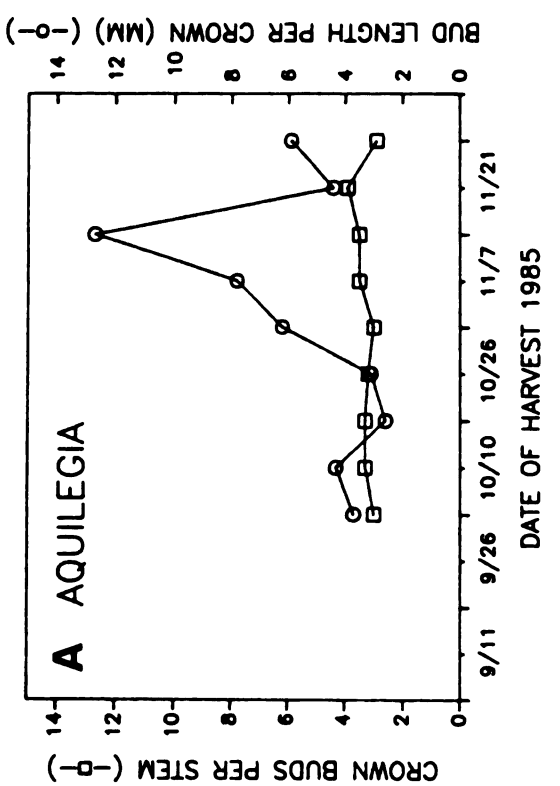
A. *Aquilegia* 'Biedermeier'; $LSD_{.05}$ (number)=0.1, $LSD_{.05}$ (length)=0.3.

B. *Dicentra spectabilis*; $LSD_{.05}$ (number)=0.1, $LSD_{.05}$ (length)=0.4.

C. *Gypsophila paniculata* 'Snowflake'; $LSD_{.05}$ (number)=0.1, $LSD_{.05}$ (length)=0.5.

D. *Lupinus* 'Russell Hybrids'; $LSD_{.05}$ (number)=7.5, $LSD_{.05}$ (length)=2.3.


A AQUILEGIA
CROWN BUDS PER STEM (-□-)
BUD LENGTH PER CROWN (MM) (-○-)
DATE OF HARVEST 1985
9/11
9/26
10/10
10/26
11/7
11/21


B DICENTRA
CROWN BUDS PER STEM (-□-)
BUD LENGTH PER CROWN (MM) (-○-)
DATE OF HARVEST 1985
9/11
9/26
10/10
10/26
11/7
11/21

C GYPSOPHILA
CROWN BUDS PER STEM (-□-)
BUD LENGTH PER CROWN (MM) (-○-)
DATE OF HARVEST 1985
9/11
9/26
10/10
10/26
11/7
11/21

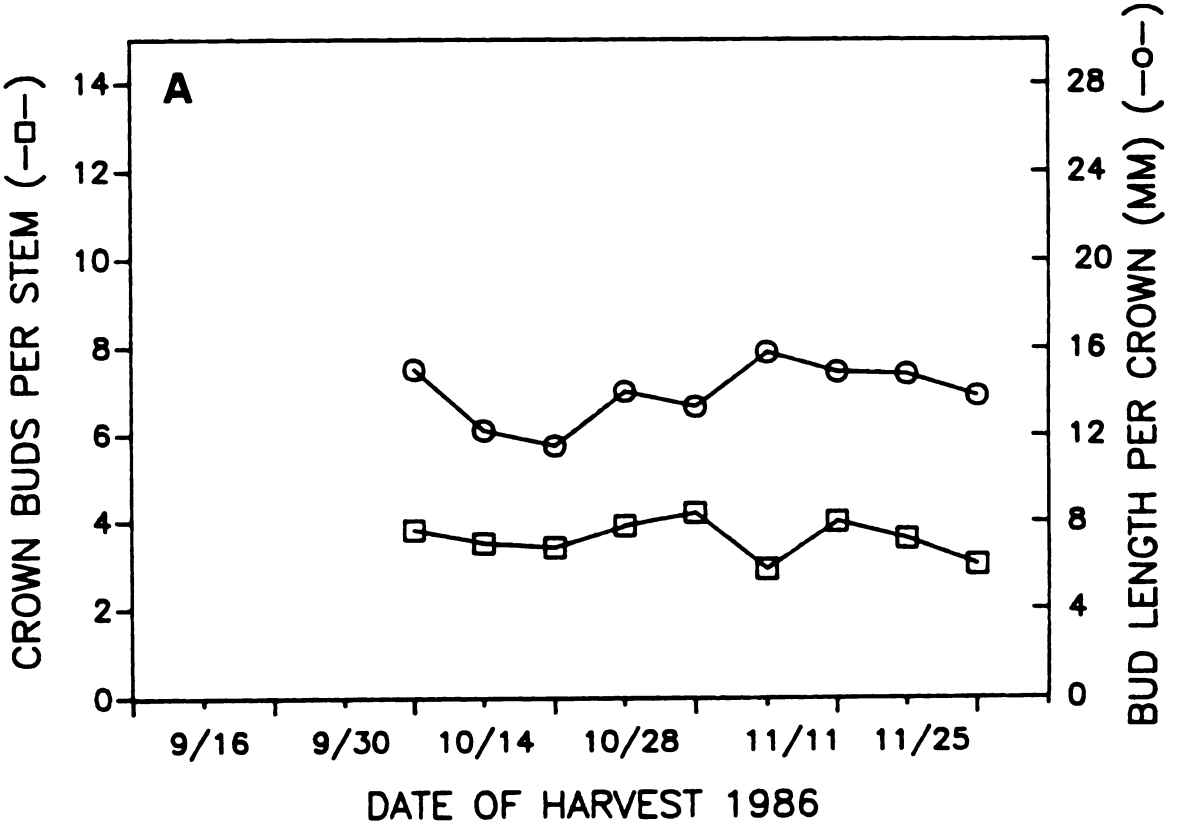
D LUPINUS
CROWN BUDS PER STEM (-□-)
BUD LENGTH PER CROWN (MM) (-○-)
DATE OF HARVEST 1985
9/11
9/26
10/10
10/26
11/7
11/21

Figure 1.3 Crown bud development of Dicentra spectabilis at weekly harvests from 10/7/86 to 12/2/86. At least 30 plants sampled per mean.

A. Mean number per plant and mean length of crown buds;no significant differences between means.

B. Mean dry weight in mg per eye; $LSD_{.05}$=20.5.

DICENTRA 1986



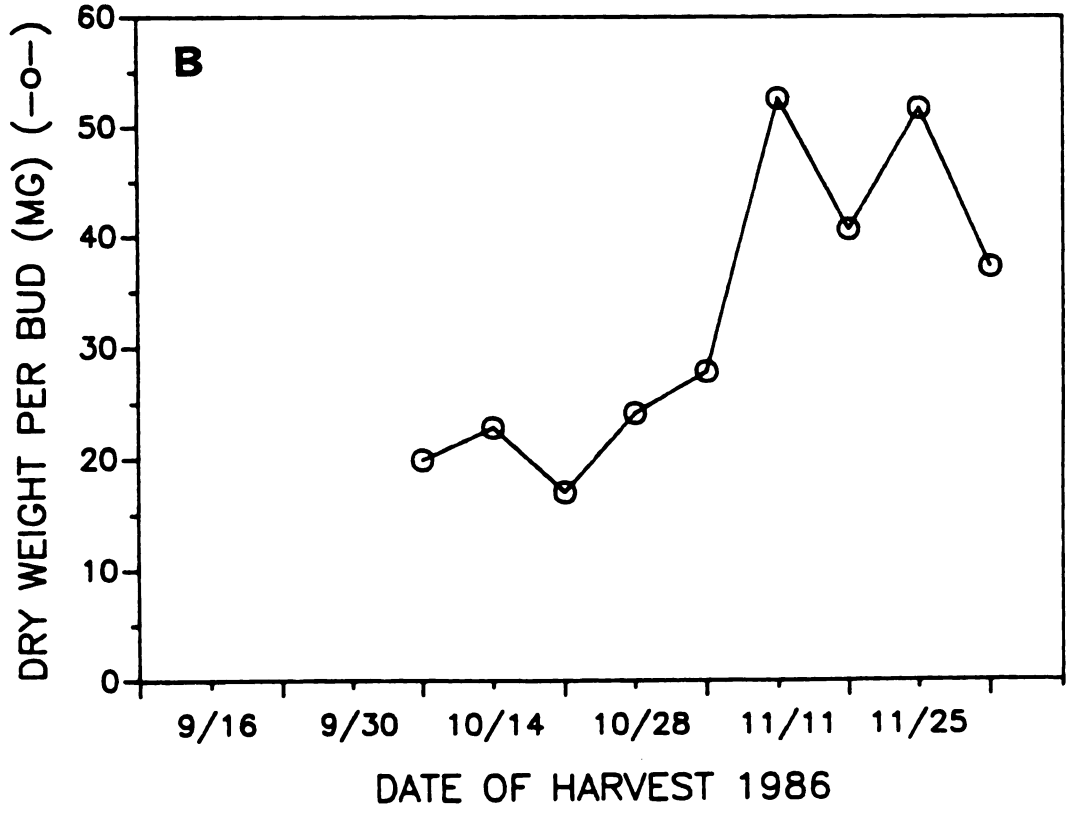


Figure 1.4 Effect of harvest date and length of storage at 0C on condition and regrowth of Aquilegia 'Beidermeier'.

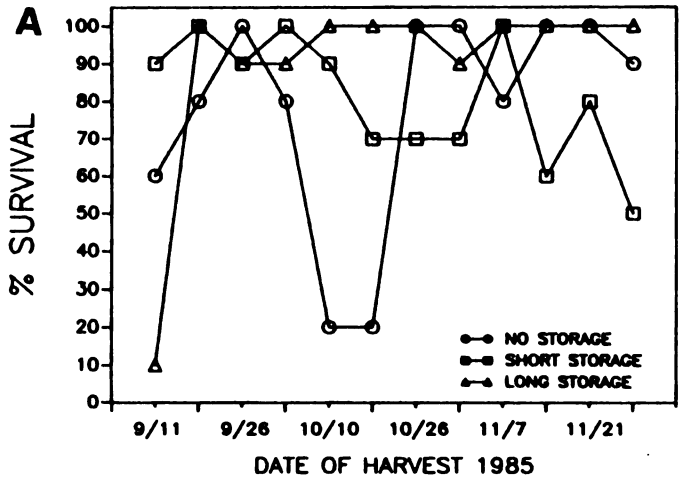
A. Percent survival.

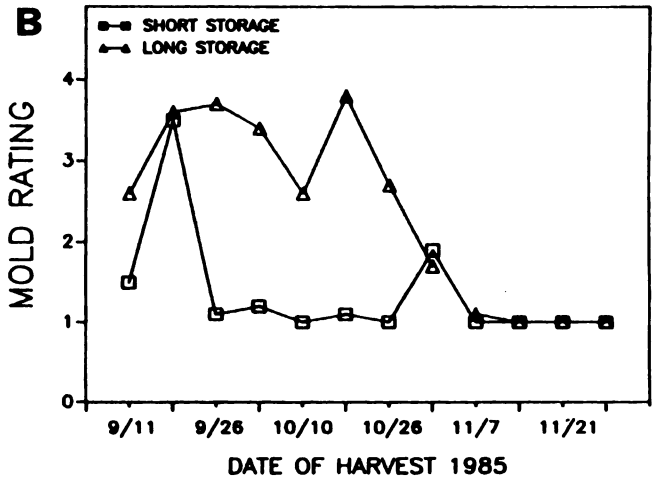
B. Mean mold rating at potting where 1=0-25% surface molded, ...4=76-100% surface molded; $LSD_{.05}$=0.7.

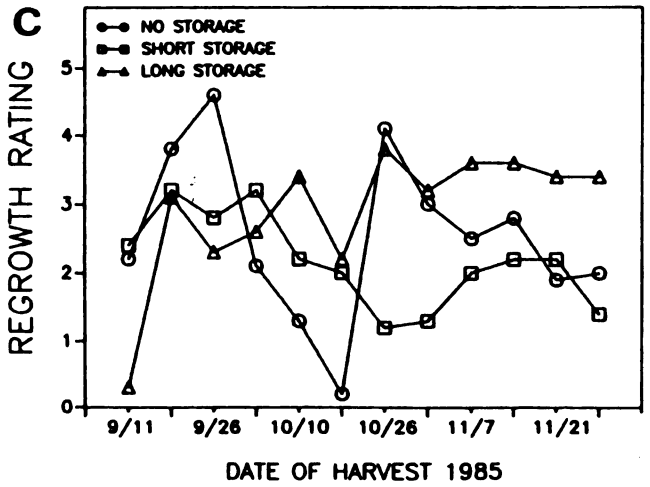
C. Mean regrowth quality at 3-4 weeks after potting where 0=dead, 0.5=dormant buds, 1=emergent growth, ...5=vigorous growth; $LSD_{.05}$ (no storage)=1.4, $LSD_{.05}$ (with storage)=1.0.

D. Percent plants flowering within 4 weeks after potting.

AQUILEGIA


A
% SURVIVAL
100
90
80
70
60
50
40
30
20
10
0
NO STORAGE
SHORT STORAGE
LONG STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985


B
MOLD RATING
4
3
2
1
0
SHORT STORAGE
LONG STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985


C
REGROWTH RATING
5
4
3
2
1
0
NO STORAGE
SHORT STORAGE
LONG STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985

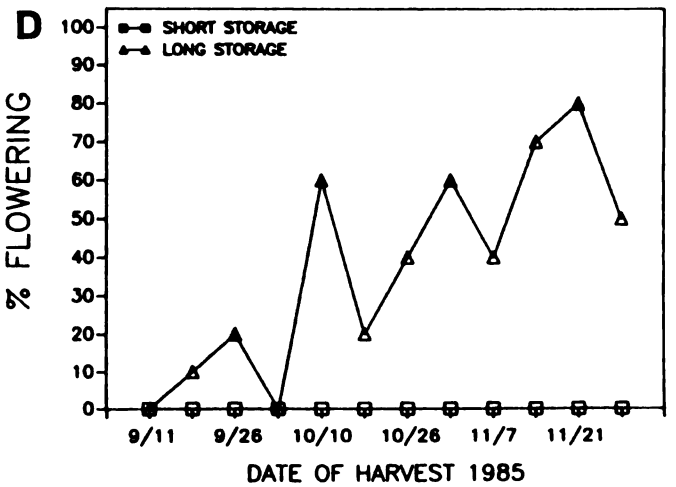

D
% FLOWERING
100
90
80
70
60
50
40
30
20
10
0
SHORT STORAGE
LONG STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985

Figure 1.5. Effect of harvest date and length of storage at 0C on condition and regrowth of Coreopsis lanceolata 'Sunburst' (1985) or Coreopsis grandiflora 'Sunray' (1986).

A. Percent survival in 1985.

B. Mean mold rating at potting in 1985 where 1=0-25% surface molded, ...4=76-100% surface molded; $LSD_{.05}=0.5$.

C. Mean regrowth quality at 3-4 weeks after potting in 1985 where 0=dead, 0.5=dormant buds, 1=emergent growth, ...5=vigorous growth; $LSD_{.05}$ (no storage)=1.0, $LSD_{.05}$ (with storage)=0.9.

D. Mean regrowth quality at 3-4 weeks after potting in 1986 where 0=dead, 0.5=dormant buds, 1=emergent growth, ...5=vigorous growth; $LSD_{.05}=0.5$.

COREOPSIS

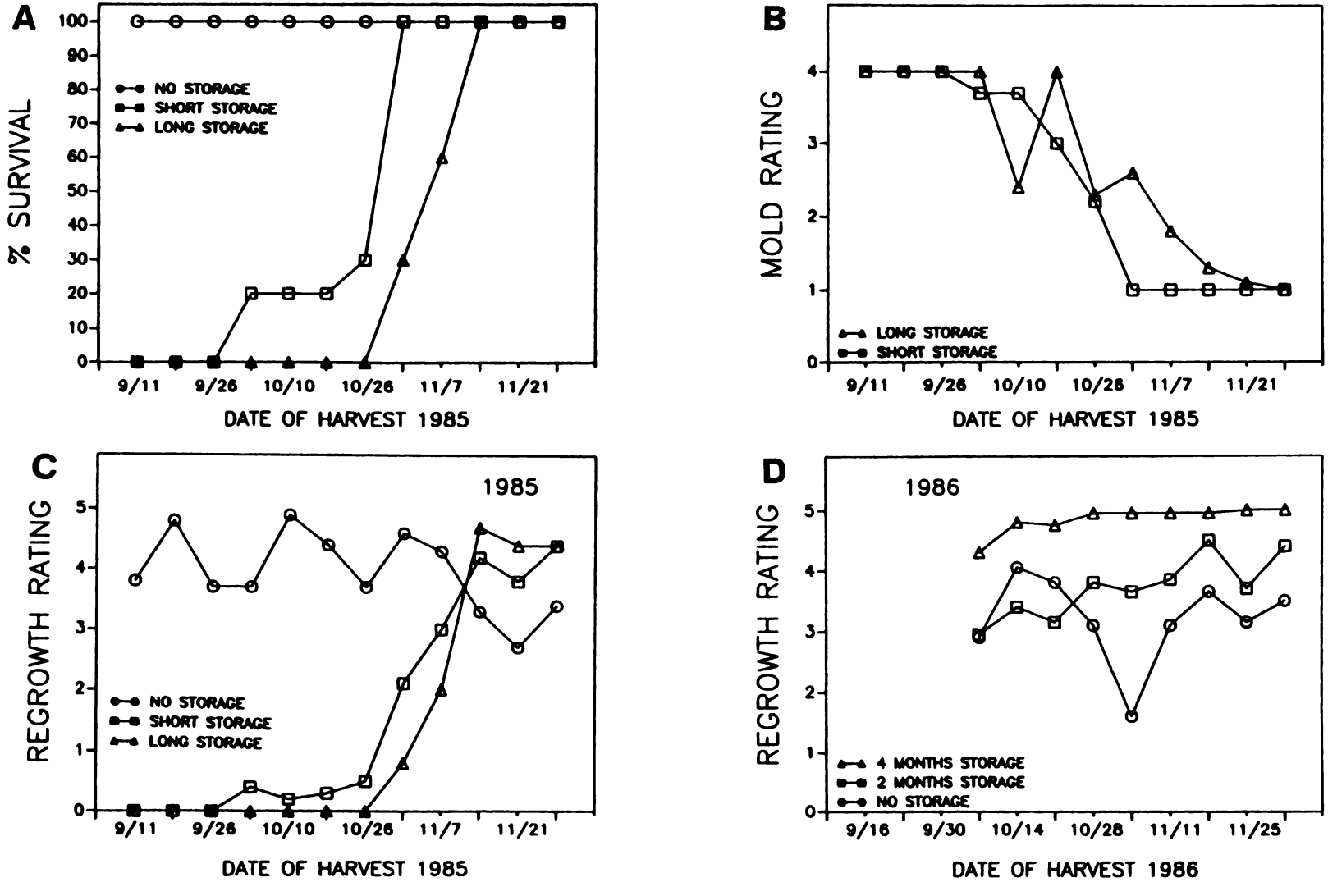

A
% SURVIVAL
100
90
80
70
60
50
40
30
20
10
0
NO STORAGE
SHORT STORAGE
LONG STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985
B
MOLD RATING
4
3
2
1
0
LONG STORAGE
SHORT STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985
C
REGROWTH RATING
1985
5
4
3
2
1
0
NO STORAGE
SHORT STORAGE
LONG STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985
D
REGROWTH RATING
1986
5
4
3
2
1
0
4 MONTHS STORAGE
2 MONTHS STORAGE
NO STORAGE
9/16
9/30
10/14
10/28
11/11
11/25
DATE OF HARVEST 1986

Figure 1.6. Effect of harvest date and length of storage at 0C on condition and regrowth of Dicentra spectabilis in 1985.

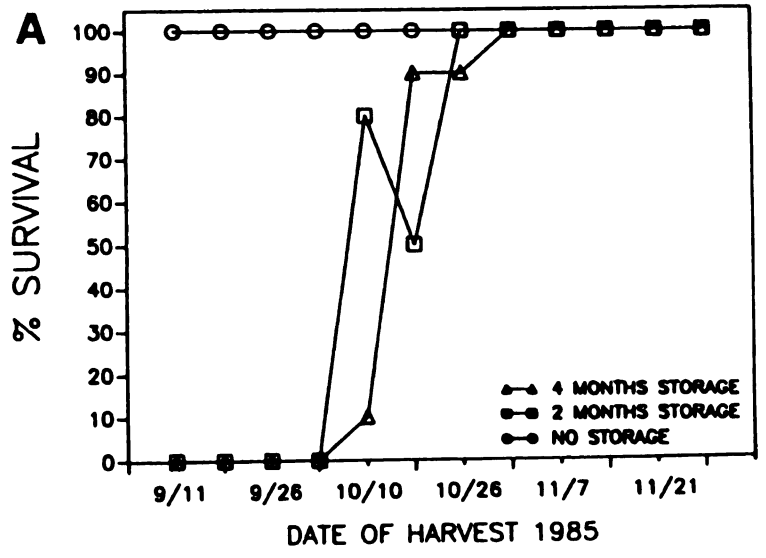
A. Percent survival.

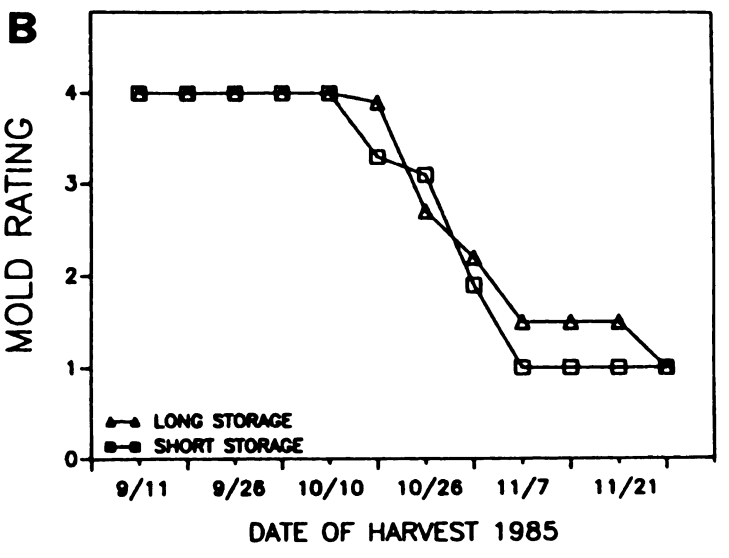
B. Mean mold rating at potting where 1=0-25% surface molded, ...4=76-100% surface molded; $LSD_{.05}$=0.5.

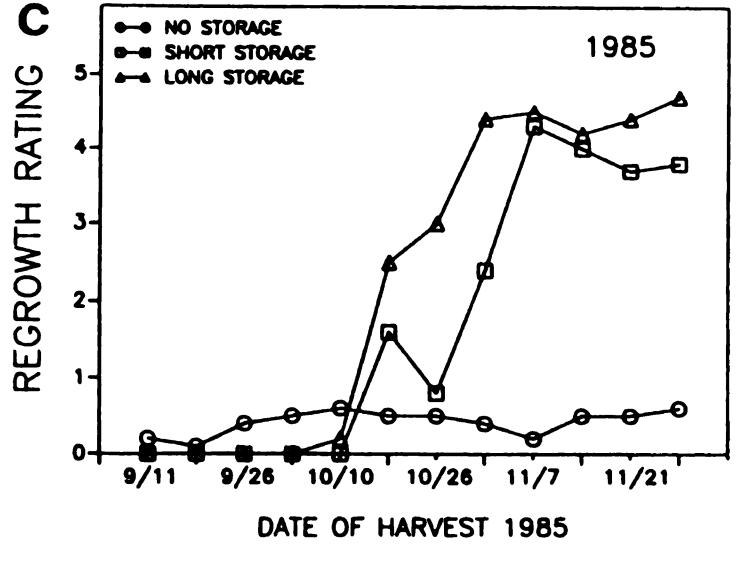
C. Mean regrowth quality at 3-4 weeks after potting where 0=dead, 0.5=dormant buds, 1=emergent growth, ...5=vigorous growth; no significant differences between no storage means, $LSD_{.05}$ (with storage)=0.9.

D. Percent crowns flowering within 4 weeks after potting.

DICENTRA 1985







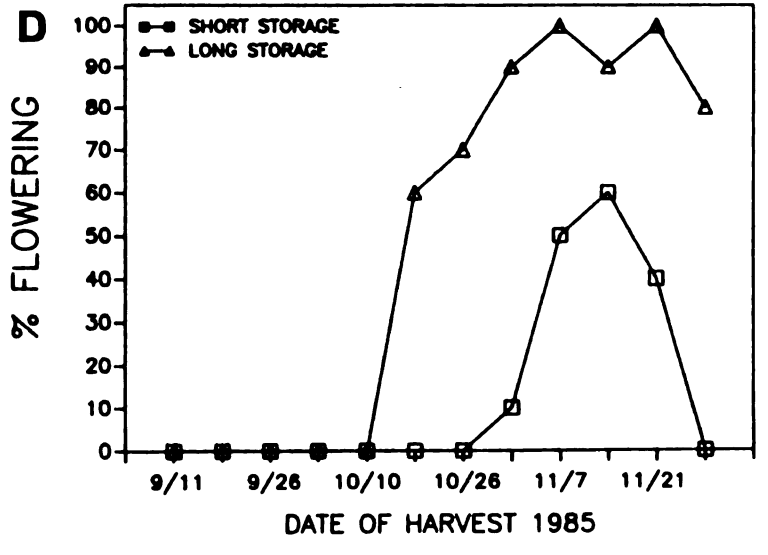
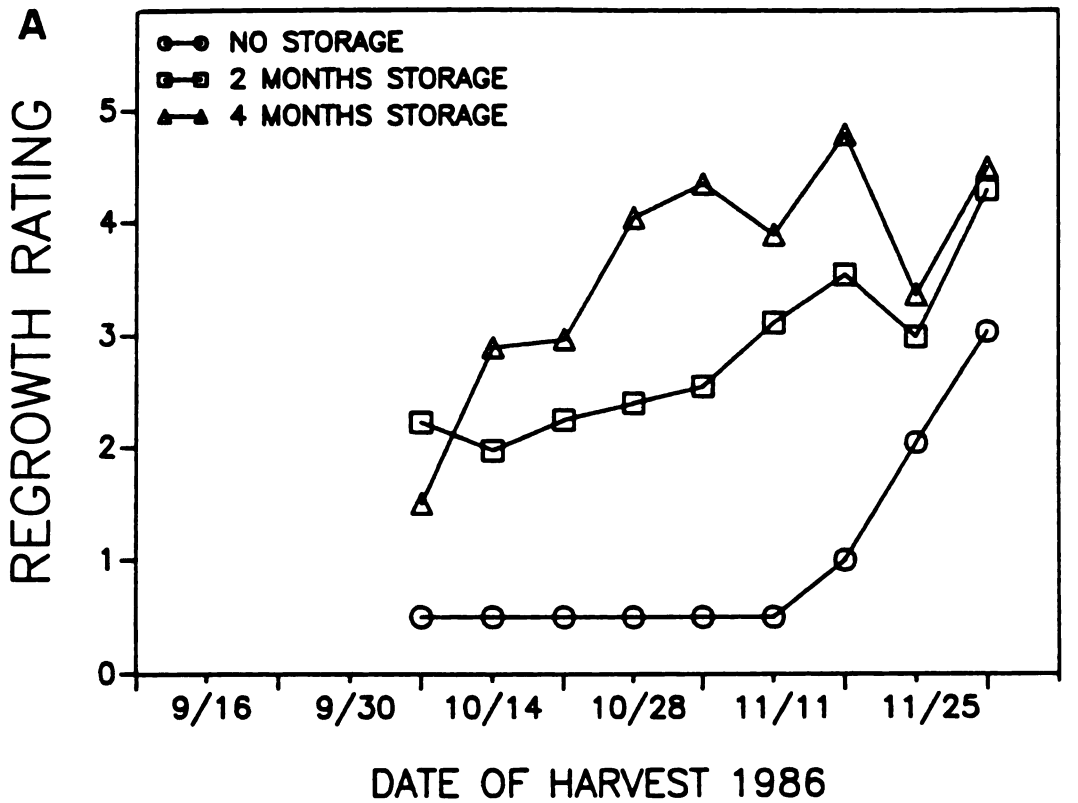


Figure 1.7. Effect of harvest date and length of storage at 0C on regrowth of Dicentra spectabilis in 1986.

A. Mean regrowth quality at 3-4 weeks after potting where 0=dead, 0.5=dormant buds, 1=emergent growth, ...5=vigorous growth; $LSD_{.05}$=1.0.

B. Percent crowns flowering within 4 weeks after potting.

DICENTRA 1986



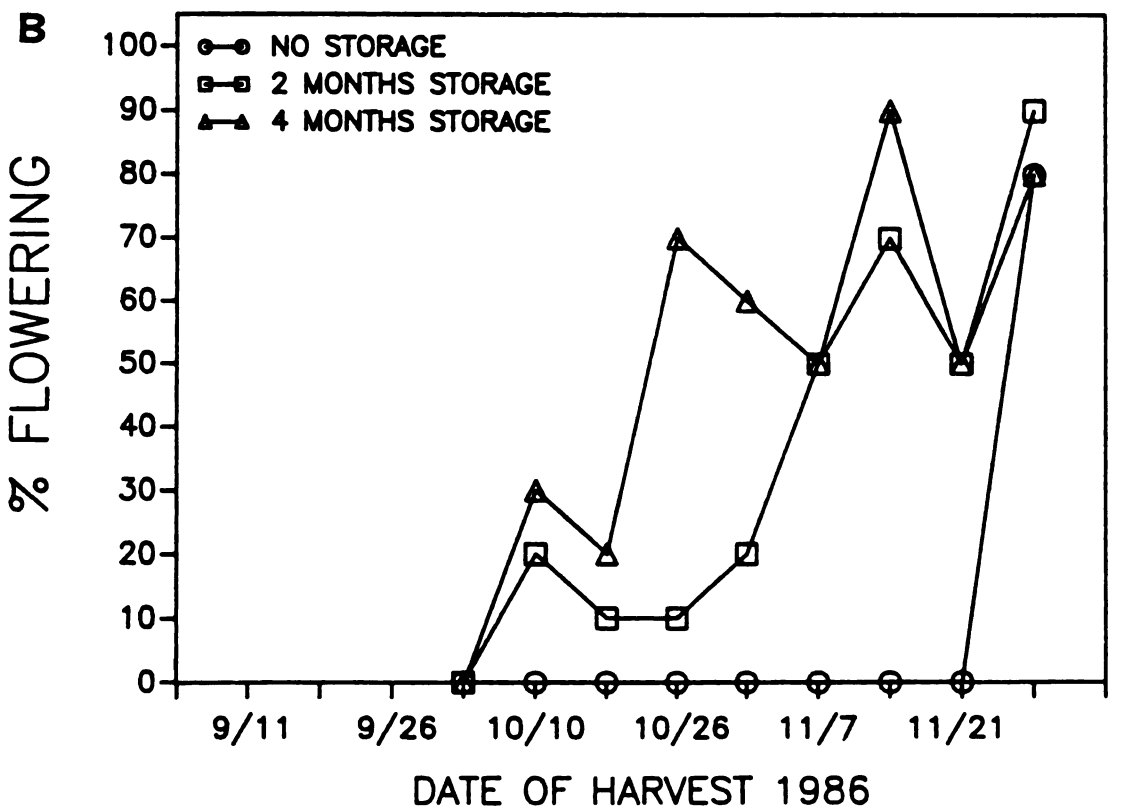


Figure 1.8. Effect of harvest date and length of storage at 0C on condition and regrowth of Geum quellyon 'Mrs. Bradshaw'.

A. Percent survival.

B. Mean mold rating at potting where 1=0-25% surface molded, ...4=76-100% surface molded; $LSD_{.05}$=0.4.

C. Mean regrowth quality at 3-4 weeks after potting where 0=dead, 0.5=dormant buds, 1=emergent growth, ...5=vigorous growth; no significant differences between no storage means, $LSD_{.05}$ (with storage)=0.7.

GEUM

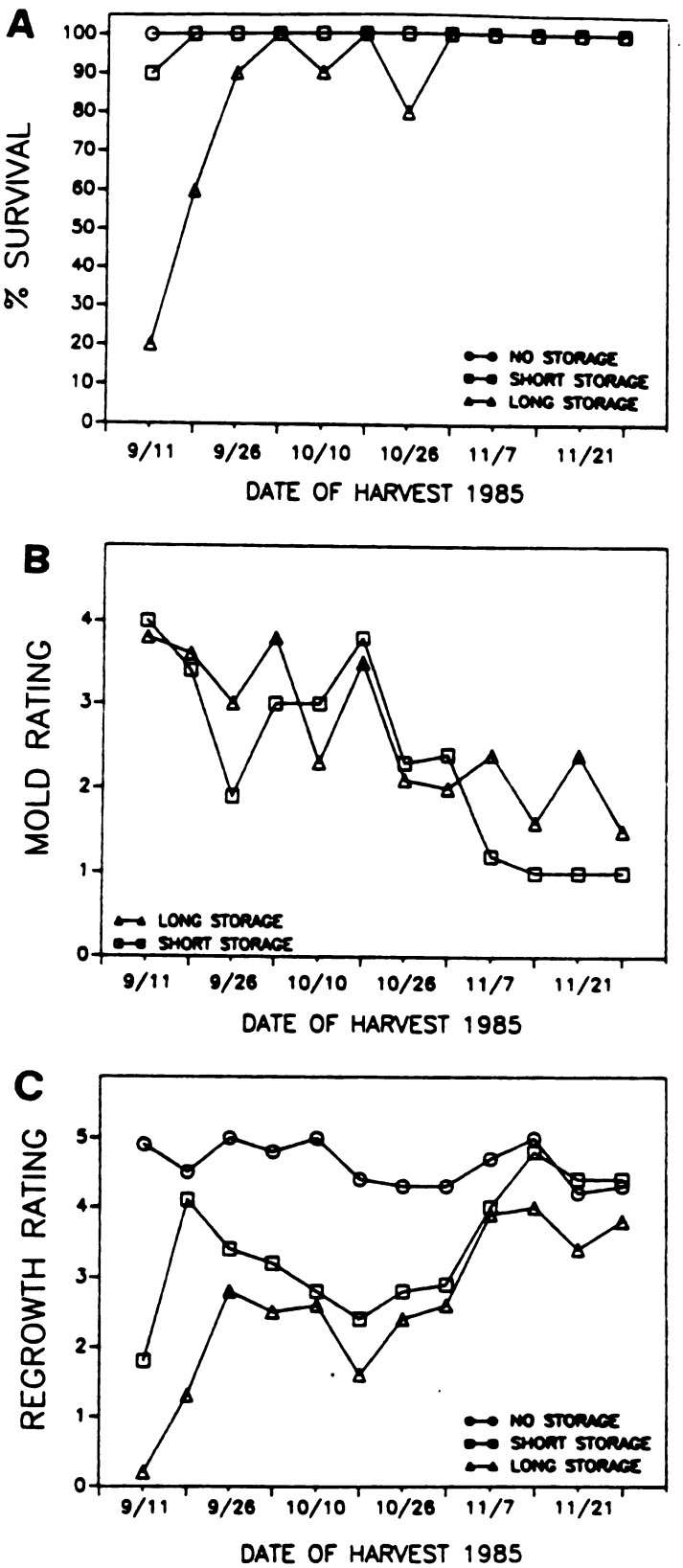

A
% SURVIVAL
100
90
80
70
60
50
40
30
20
10
0
NO STORAGE
SHORT STORAGE
LONG STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985
B
MOLD RATING
4
3
2
1
0
LONG STORAGE
SHORT STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985
C
REGROWTH RATING
5
4
3
2
1
0
NO STORAGE
SHORT STORAGE
LONG STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985

Figure 1.9. Effect of harvest date and length of storage at 0C on condition and regrowth of Gypsophila paniculata 'Snowflake'.

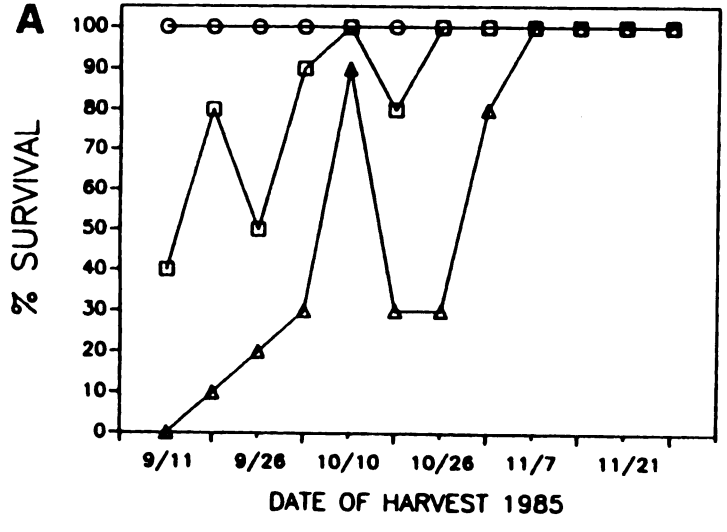
A. Percent survival in 1985.

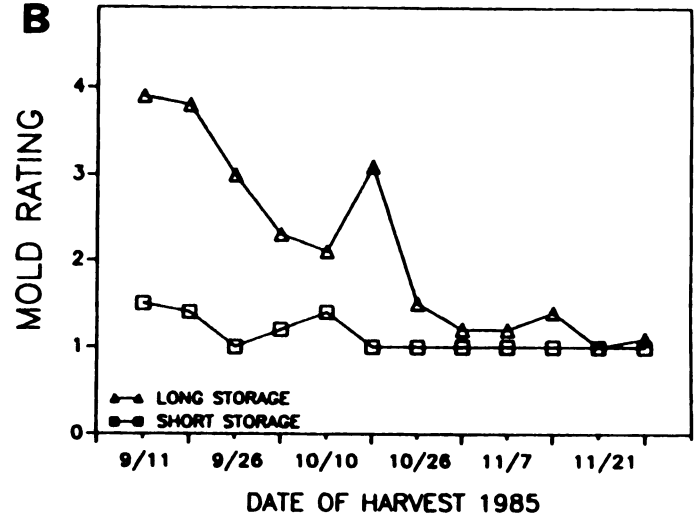
B. Mean mold rating at potting in 1985 where 1=0-25% surface molded, ...4=76-100% surface molded; $LSD_{.05}$=0.9.

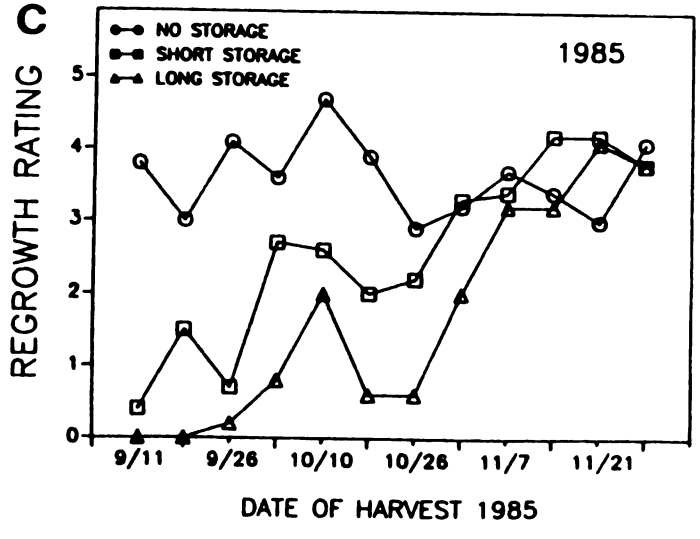
C. Mean regrowth quality at 3-4 weeks after potting in 1985 where 0=dead, 0.5=dormant buds, 1=emergent growth, ... 5=vigorous growth; no significant differences between no storage means, $LSD_{.05}$ (with storage)=0.9.

D. Mean regrowth quality at 3-4 weeks after potting in 1986 where 0=dead, 0.5=dormant buds, 1=emergent growth, ... 5=vigorous growth; $LSD_{.05}$=0.8.

GYPSOPHILA


A
% SURVIVAL
100
90
80
70
60
50
40
30
20
10
0
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985


B
MOLD RATING
4
3
2
1
0
LONG STORAGE
SHORT STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985


C
REGROWTH RATING
NO STORAGE
SHORT STORAGE
LONG STORAGE
1985
5
4
3
2
1
0
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985

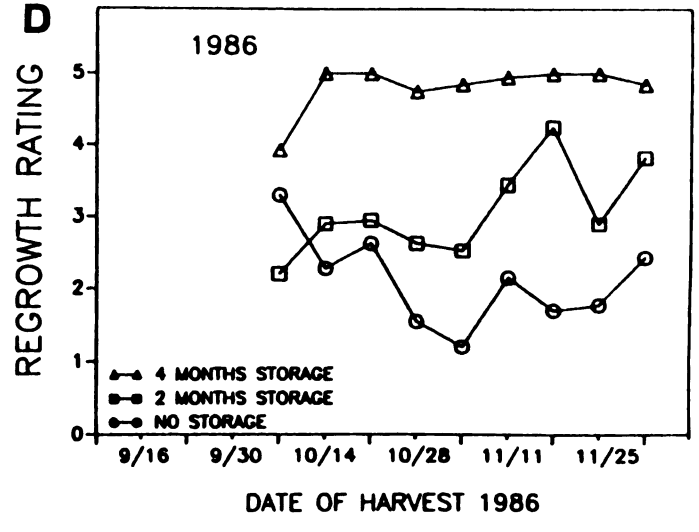

D
REGROWTH RATING
1986
5
4
3
2
1
0
4 MONTHS STORAGE
2 MONTHS STORAGE
NO STORAGE
9/16
9/30
10/14
10/28
11/11
11/25
DATE OF HARVEST 1986

Figure 1.10. Effect of harvest date and length of storage at 0C on condition and regrowth of Iberis sempervirens 'Snowflake'.

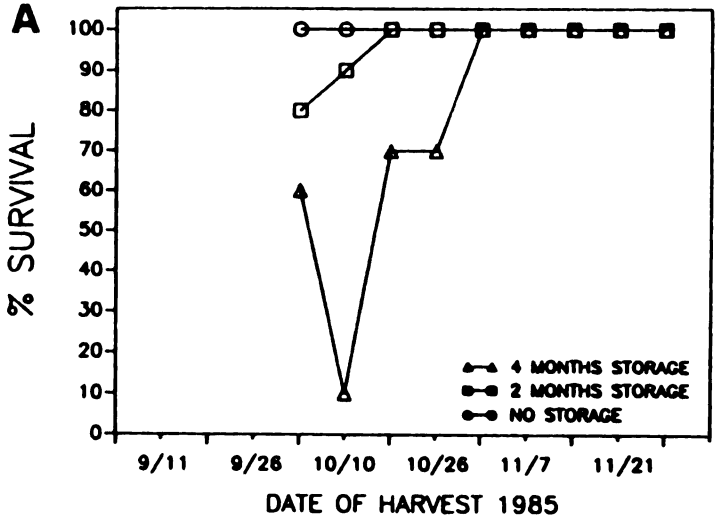
A. Percent survival.

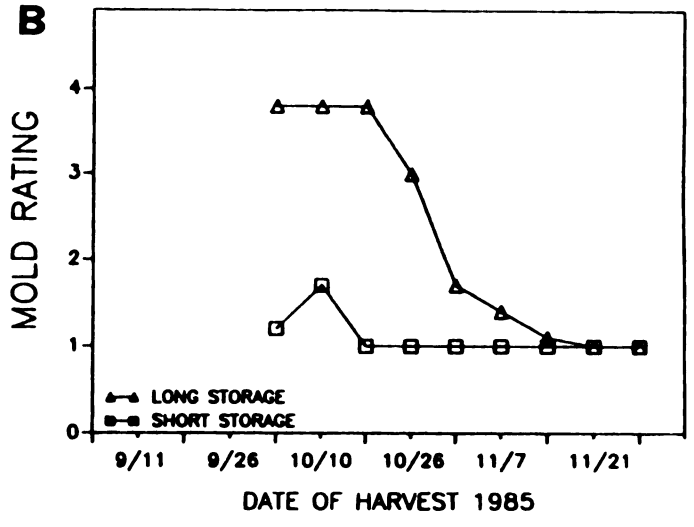
B. Mean mold rating at potting where 1=0-25% surface molded, ...4=76-100% surface molded; $LSD_{.05}$=0.5.

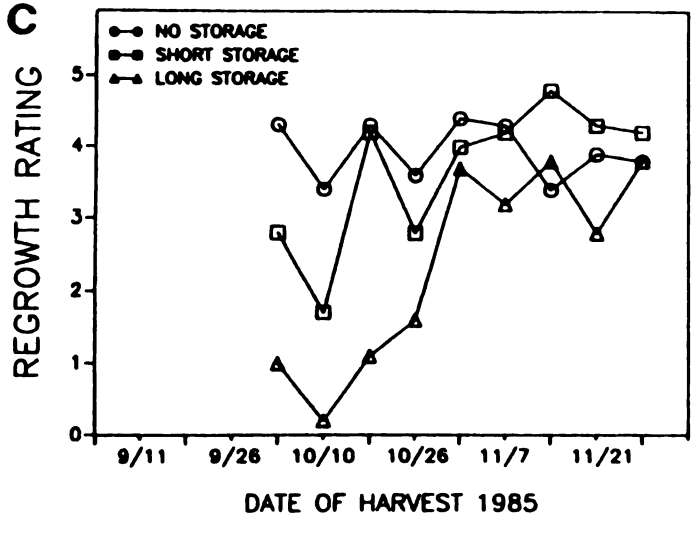
C. Mean regrowth quality at 3-4 weeks after potting where 0=dead, 0.5=dormant buds, 1=emergent growth, ...5=vigorous growth; $LSD_{.05}$ (no storage)=1.2, $LSD_{.05}$ (with storage)=0.9.

D. Percent plants flowering within 4 weeks after potting.

IBERIS


A
% SURVIVAL
100
90
80
70
60
50
40
30
20
10
0
4 MONTHS STORAGE
2 MONTHS STORAGE
NO STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985


B
MOLD RATING
4
3
2
1
0
LONG STORAGE
SHORT STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985


C
REGROWTH RATING
5
4
3
2
1
0
NO STORAGE
SHORT STORAGE
LONG STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985

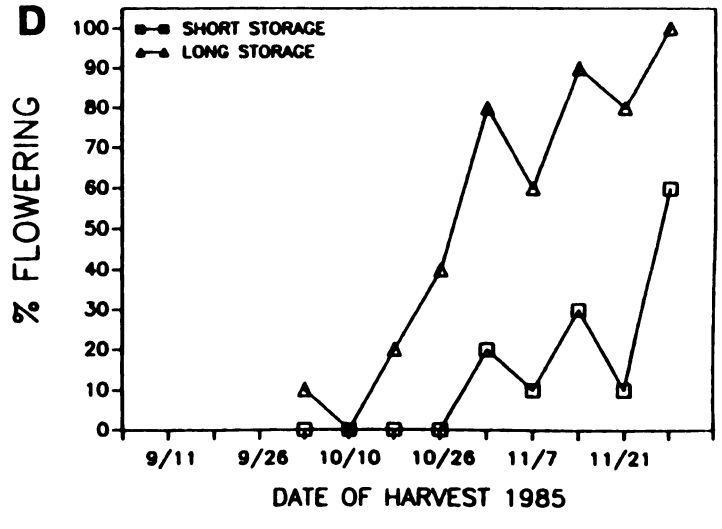

D
% FLOWERING
100
90
80
70
60
50
40
30
20
10
0
SHORT STORAGE
LONG STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985

Figure 1.11. Effect of harvest date and length of storage at 0C on condition and regrowth of Lupinus 'Russell Hybrids'.

A. Percent survival.

B. Mean mold rating at potting where 1=0-25% surface molded, ...4=76-100% surface molded; $LSD_{.05}$=0.7.

C. Mean regrowth quality at 3-4 weeks after potting where 0=dead, 0.5=dormant buds, 1=emergent growth, ...5=vigorous growth; no significant differences between no storage means, $LSD_{.05}$ (with storage)=1.0.

LUPINUS

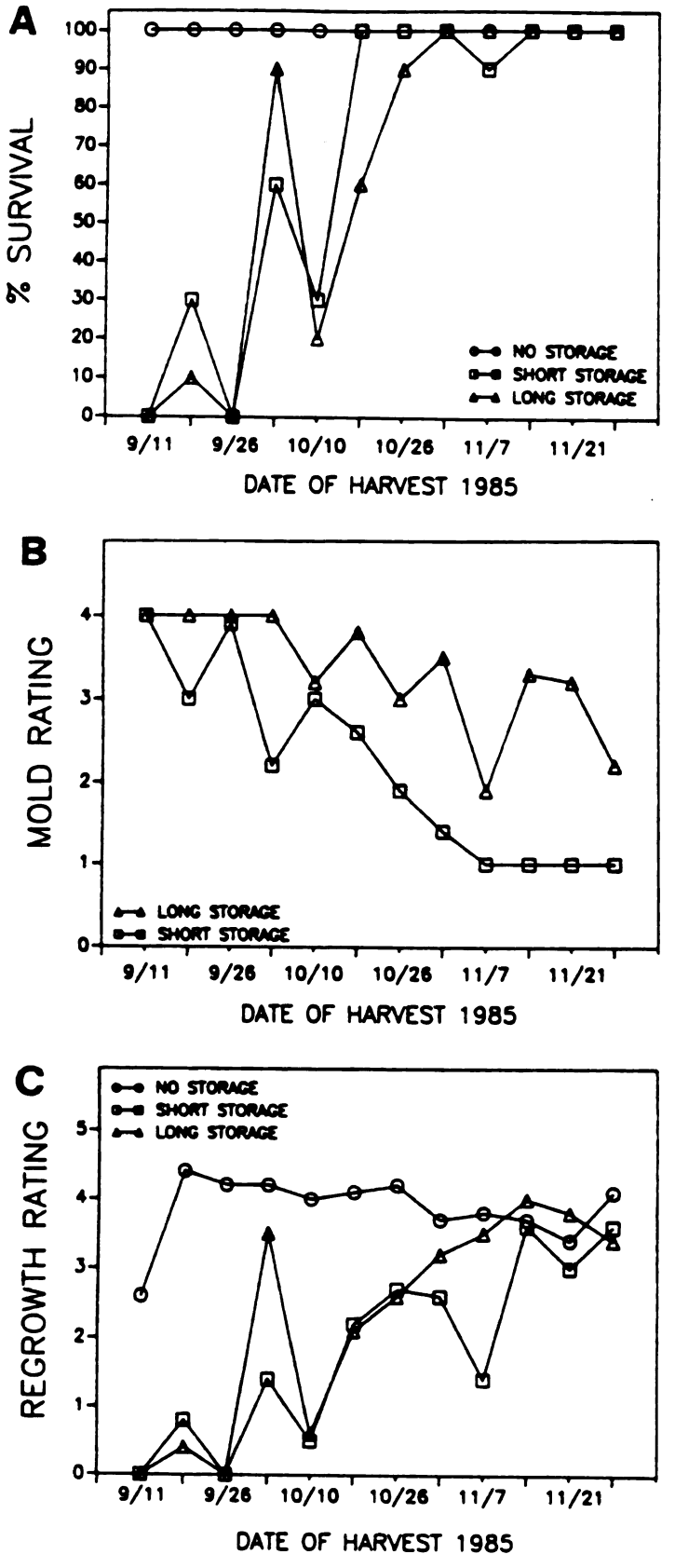
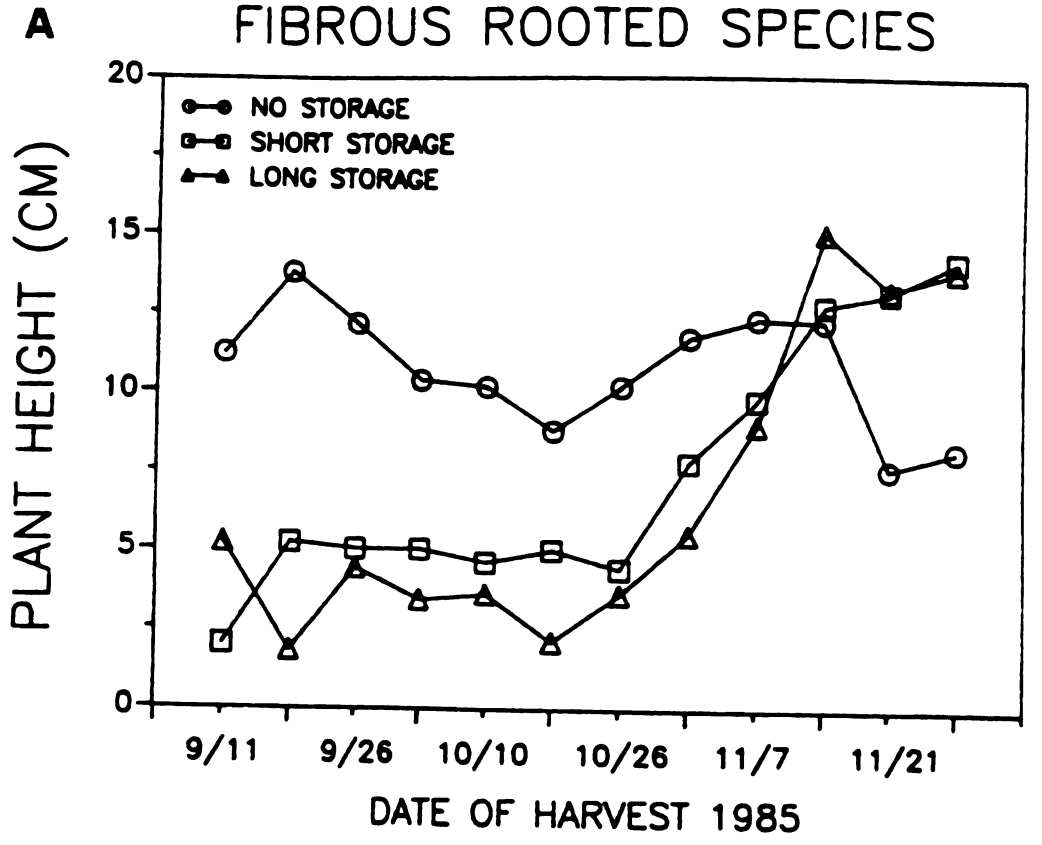

A
% SURVIVAL
100
90
80
70
60
50
40
30
20
10
0
NO STORAGE
SHORT STORAGE
LONG STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985
B
MOLD RATING
4
3
2
1
0
LONG STORAGE
SHORT STORAGE
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985
C
REGROWTH RATING
NO STORAGE
SHORT STORAGE
LONG STORAGE
5
4
3
2
1
0
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985

Figure 1.12. Effect of harvest date and length of storage at 0C on whole plant height of perennials at 3-4 weeks from potting. Data averaged over indicated cultivars.

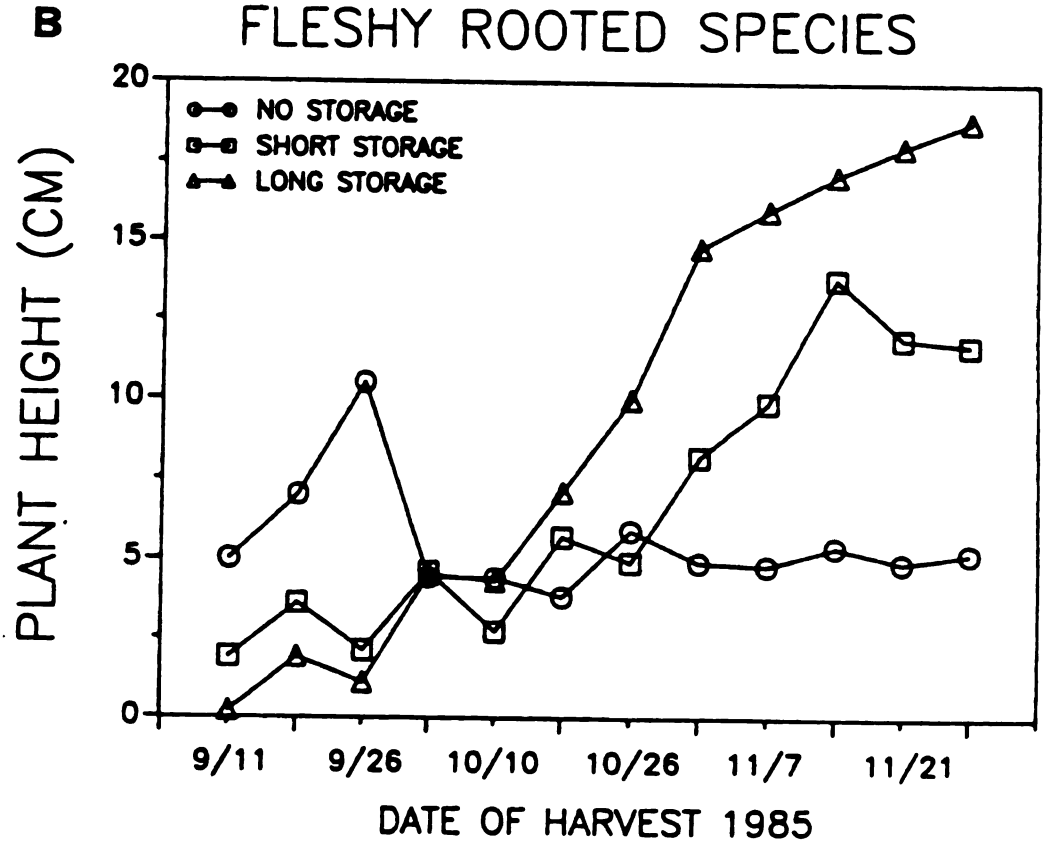
A. Fibrous rooted genera: Coreopsis and Geum.

B. Fleshy-rooted genera: Aquilegia, Dicentra, Gypsophila, and Lupinus.

A


FIBROUS ROOTED SPECIES
NO STORAGE
SHORT STORAGE
LONG STORAGE
PLANT HEIGHT (CM)
0
5
10
15
20
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985

B


FLESHY ROOTED SPECIES
NO STORAGE
SHORT STORAGE
LONG STORAGE
PLANT HEIGHT (CM)
0
5
10
15
20
9/11
9/26
10/10
10/26
11/7
11/21
DATE OF HARVEST 1985

LIST OF REFERENCES

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2. Bringhurst, R.S., V. Voth, and D. VanHook. 1960. Relationship of root starch content and chilling to performance of California strawberries. Proc. Amer. Soc. Hort. Sci. 75:373-381.

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CHAPTER 2

EFFECT OF HARVEST DATE ON GROWTH RESPONSES OF *DICENTRA SPECTABILIS* AFTER CHILLING

In earlier studies (Chapter 1), quality of stored herbaceous perennials increased with later harvests. *Dicentra spectabilis* in particular showed a marked change over the harvest season in its response to chilling. Quality was much higher for plants lifted in November than in September. At the whole plant level, storage quality is measured by overall vigor of subsequent regrowth, usually rated on a subjective, arbitrary scale. Although such a rating system is a valid and valuable means of assessment, it does not distinguish between the various components of successful regrowth after storage.

In forestry, the ability of a stored seedling to regenerate roots has been a useful tool in understanding establishment problems (17). The aboveground portion of a nursery transplant, however, has generally received greater attention. Days to budbreak as a measure of bud dormancy can be used very precisely (5,12,14), especially when stages of development are clearly defined (13) and the distinction is made between budbreak itself and subsequent growth of the bud (4). Overall height has also been widely used to quantify

regrowth (1,2,7) with the understanding that the results can be skewed by skinny, tall, low-quality plants (8).

Lopes and Weiler (7) used a variety of measurements to study the effect of growing conditions on Dicentra, including shoot number, node number, internode length, leaf area, plant height, and plant weight. In addition to examining post-storage growth responses in relation to date of harvest, this study was also an effort to identify specific parameters for assessing regrowth in Dicentra spectabilis.

MATERIALS AND METHODS

One year old Dicentra spectabilis (L.) Lem. crowns were harvested weekly in western Michigan fields (Walters Gardens, Zeeland) in 1986 for nine weeks from October 7 to December 2. Loose soil was removed by shaking and any green material was trimmed, leaving the eyes intact. At each harvest, ten soil temperatures at 10:00 a.m. at 10 cm depth in the field were measured. Soil temperature records were also obtained from the Trevor Nichols Experimental Farm, Fennville, MI (10). Crowns were stored in polyethylene-lined crates to avoid desiccation stress (3) and held at 0C for 0, 2, or 4 months, with ten plants per treatment. After treatment, the crowns were potted with eyes exposed and regrown in a cool greenhouse (19C day/12C night) under 16 hours of 8.5 mol/day-m2 supplemental light.

After potting, all plants were inspected daily for

budbreak, defined in this study as the opening of bud scales and appearance of floral parts or expanding leaf margins from within the eye. Time to first budbreak was recorded for each crown. If eyes had not broken after 180 days of growing conditions, crowns were discarded (Table 2.1). At time of break, eye length was measured. The eye was remeasured at 7 days post-break to determine the elongation rate of that individual eye during the first week post-break.

At 5 weeks post-break, the regrowth quality of the entire plant was rated on a 0 to 5 scale (0=dead, 0.5=dormant buds, 1=emergent growth, 2=minimal growth, 3=acceptable growth, 4=better growth, 5= vigorous growth) following Maqbool (8). Whole plant height to the highest leaf was measured at the same time. The date at which each crown first produced an expanded flower was also noted.

Treatment means were calculated on the basis of plants which survived to that point of development. The data were analyzed as a completely randomized design (9,11). Standard errors of interaction means were calculated with n=8 replicates per treatment cell, the smallest n in the analysis.

RESULTS

Soil temperatures at 10 cm below the surface dropped sharply in early November from 11C to 2C (Figure 2.1). Days from potting to budbreak of unstored *Dicentra* crowns also

decreased over the harvest season, with a sharp drop in mid-November (Figure 2.2). By the last harvest on December 2, unstored crowns broke in 10 days, essentially the same time as chilled crowns from earlier harvests.

Harvest date also affected time to budbreak following cold storage, decreasing it in general by 1 day for each extra week spent in the field. In addition, there was a small but significant decrease in days to budbreak with 4 months rather than 2 months exposure to 0C. For any given harvest date, the average difference after 2 or 4 months storage was 1.3 days. For some individual plants from November harvests, budbreak after 4 months of chilling was very rapid, taking place within the first day after potting. Overall, the difference between the two storage periods was greatly overshadowed by the difference between chilling for either duration and no chilling.

Longer chilling affected eye growth, however, in plants harvested in December. Length of the first eye to break was 18 mm with or without 2 months of chilling, but increased to 29 mm with 4 months of chilling. This growth occurred without budbreak and was termed "eye etiolation". The same eyes elongated rapidly after budbreak, up to 30 mm per day for some individuals. Initial growth rates increased with chilling duration in all cases (Figure 2.3). Although unchilled plants never grew quickly despite rapid budbreak, by late November they achieved a moderate growth rate and eventually moderate height. Chilled plants regrew well for

all harvest dates (Figure 2.4a). Regrowth ratings followed essentially the same pattern as height, with longer chilling consistently leading to higher quality plants (Figure 2.4b).

Flowering exceeded 80% in all 4 month treatments (Figure 2.5), while chilling for 2 months gave variable results. Among the unchilled plants, only those harvested on November 18 or later flowered to any extent, but late-harvest crowns flowered quite well. Time to flower from potting for chilled Dicentra decreased from nearly 50 days to 20 days or less over the harvest season (Figure 2.6). Time to bloom for unchilled plants also decreased with later harvests.

DISCUSSION

For Dicentra as for other nursery stock, chilling in storage did not completely replace hardening in the field (6,15,16). Harvest date still had an effect on chilled plants. There were significant interactions at the 0.05 level between date of harvest and length of chilling for all parameters tested. Although decreasing daylength has been shown to promote dormancy in Dicentra (18), the importance of diurnal temperature cycles in the hardening process is unknown.

In earlier studies (Chapter 1), overall plant quality increased as harvest was delayed. However, distinct events were obvious in the regrowth process. Budbreak was the first step, and in chilled plants, was followed by stem

elongation. Additional chilling in storage increased the rate of vegetative growth in the greenhouse. Early-harvest, non-chilled crowns eventually broke bud but did not grow in height. Such stunted individuals might even flower by pushing out a single floret from the open eye, but chilling improved both the ability and the time to flower.

As expected, since flowering could not occur until the eye opened, there was a strong overall correlation ($r=0.88$, $a=0.0001$) between days to budbreak and days to flower. Overall plant quality was closely related to plant height at 5 weeks post-break ($r^2=0.86$, $a=0.0001$), confirming earlier work (Chapter 1).

Based on these results, regrowth of Dicentra spectabilis after storage can be divided into four separate, albeit related responses: eye etiolation, budbreak, stem elongation, and flowering.

Table 2.1. Effect of harvest date and storage duration on number of *Dicentra spectabilis* crowns that broke bud within 180 days of growing conditions (19C day/12C night, 16 hrs 8.5 mol/day-m^2 supplemental light). Ten crowns per treatment.

HARVEST DATE 1986	LENGTH OF STORAGE AT 0C		
	0 MONTHS	2 MONTHS	4 MONTHS
October 7	10	10	8
October 14	8	10	8
October 21	9	10	10
October 28	8	9	10
November 4	9	9	10
November 11	10	9	9
November 18	10	10	10
November 25	10	10	8
December 2	10	10	10

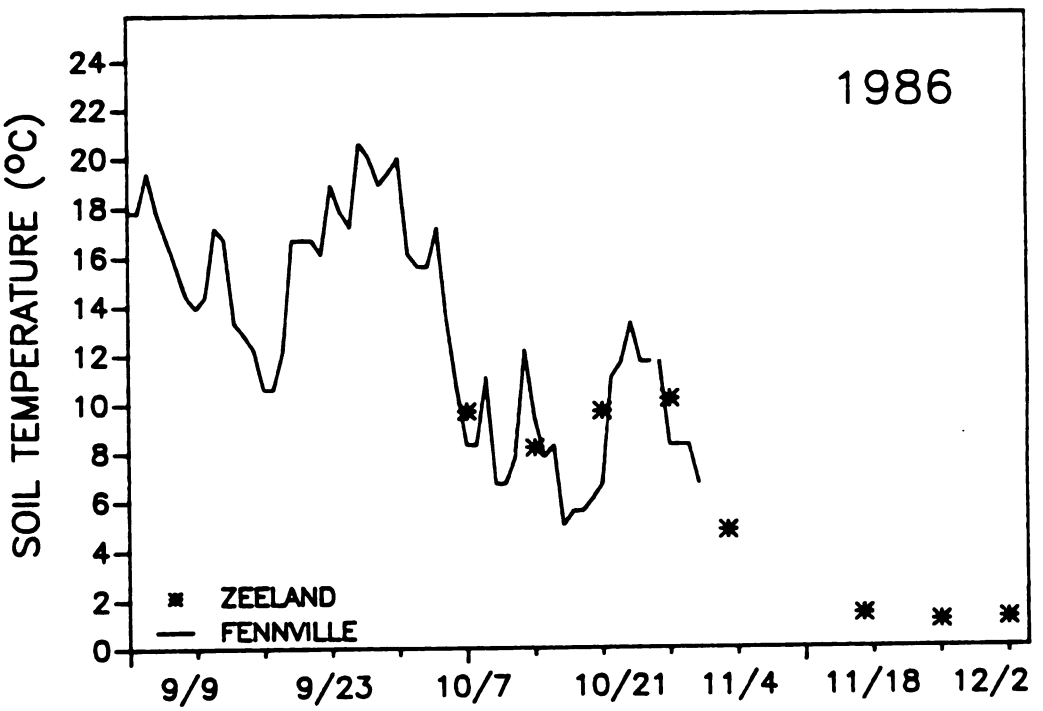


Figure 2.1. Minimum daily soil temperature at 10 cm depth at Trevor Nichols Experimental Farm, Fennville, MI, during the fall of 1986, and average soil temperature at 10cm depth at 10 am in Dicentra spectabilis field, Zeeland, MI. Zeeland standard error of means=0.7.

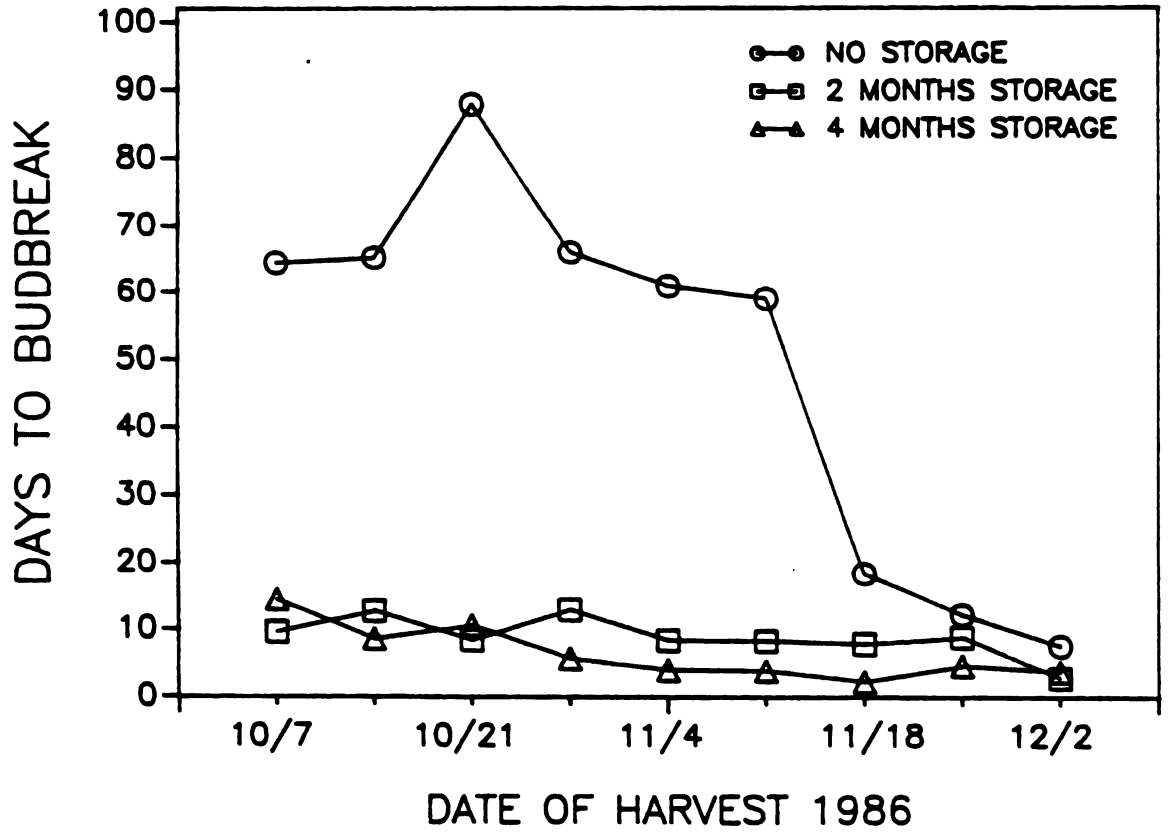


Figure 2.2. Effect of harvest date and length of storage at 0C on mean days from potting to budbreak of Dicentra spectabilis crowns. Means calculated for crowns with at least one broken bud; standard error of the interaction means=7.6.

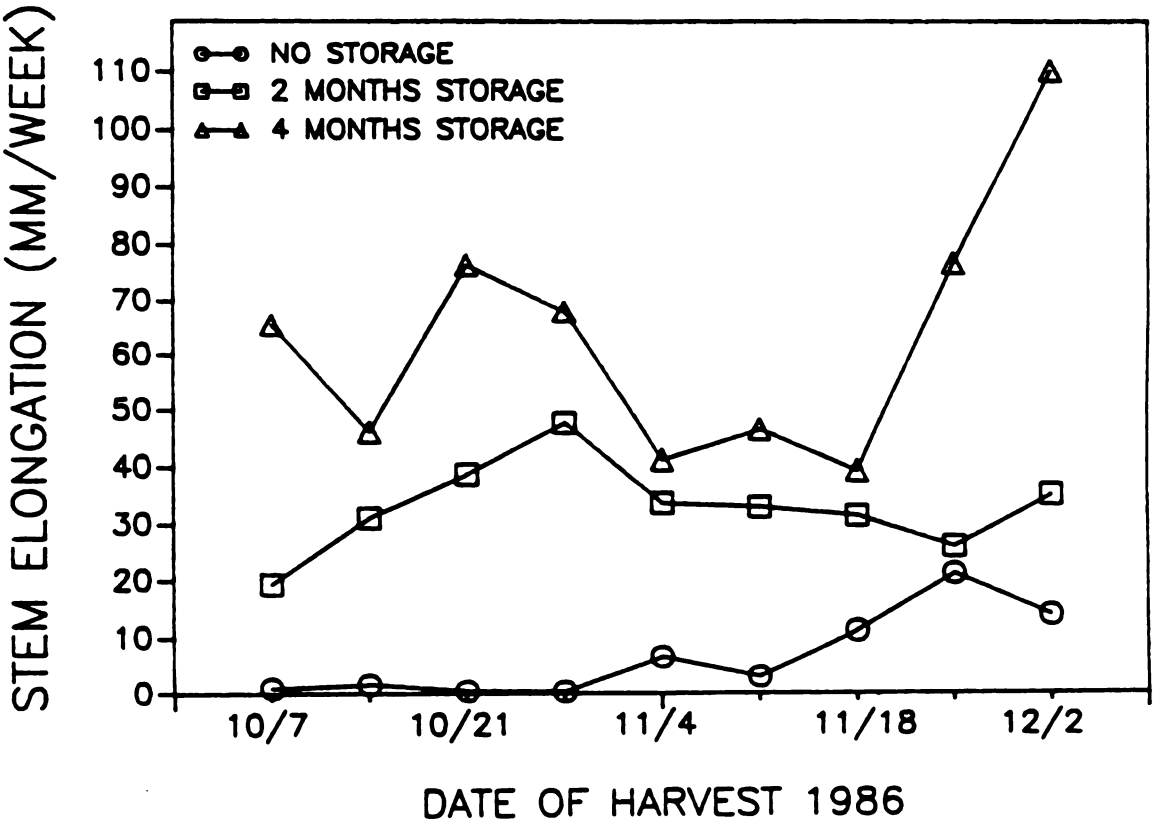
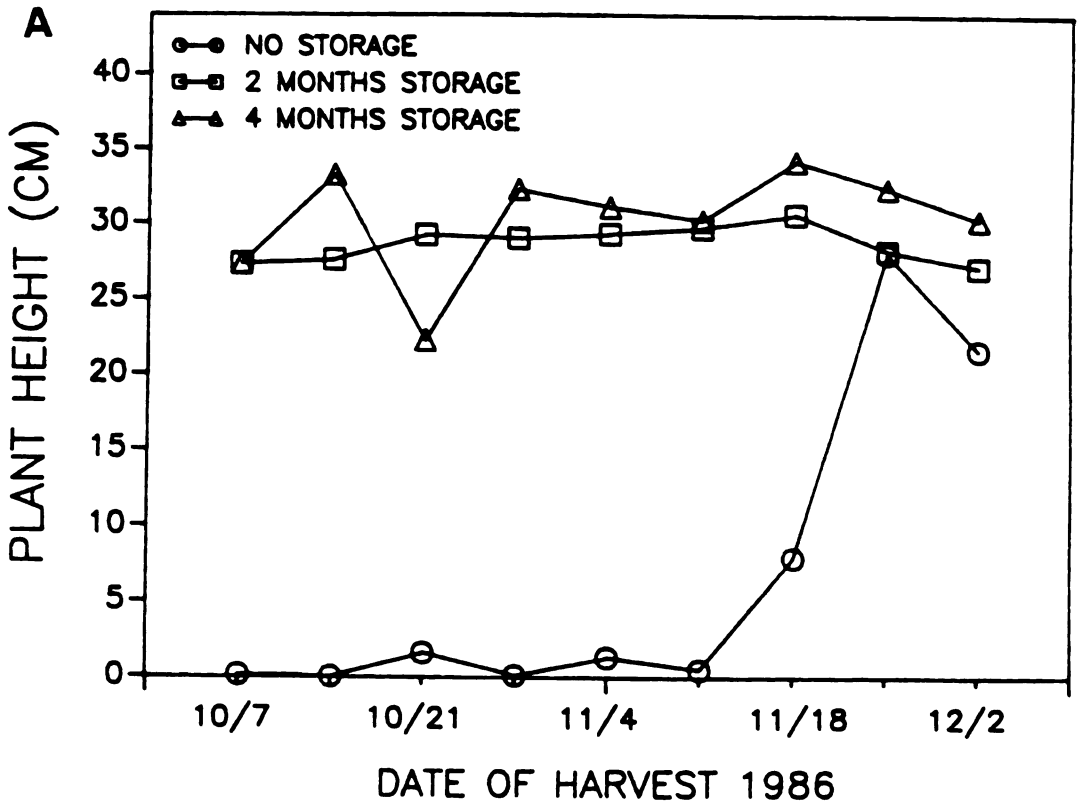


Figure 2.3. Effect of harvest date and length of storage at 0C on mean rate of stem elongation during first week of post-break growth of Dicentra spectabilis crowns. Means calculated for crowns with at least one broken bud; standard error of the interaction means=11.9.

Figure 2.4. Effect of harvest date and length of storage at 0C on regrowth at 5 weeks post-break of Dicentra spectabilis crowns. Means calculated for crowns with at least one broken bud.

A. Mean plant height; standard error of the interaction means=2.8.

B. Mean regrowth quality. Rating scale of 0 to 5 where 0=dead, 0.5=dormant buds, 1=emergent growth, ..5=vigorous growth); standard error of the interaction means=0.4.


A
NO STORAGE
2 MONTHS STORAGE
4 MONTHS STORAGE
PLANT HEIGHT (CM)
40
35
30
25
20
15
10
5
0
10/7
10/21
11/4
11/18
12/2
DATE OF HARVEST 1986

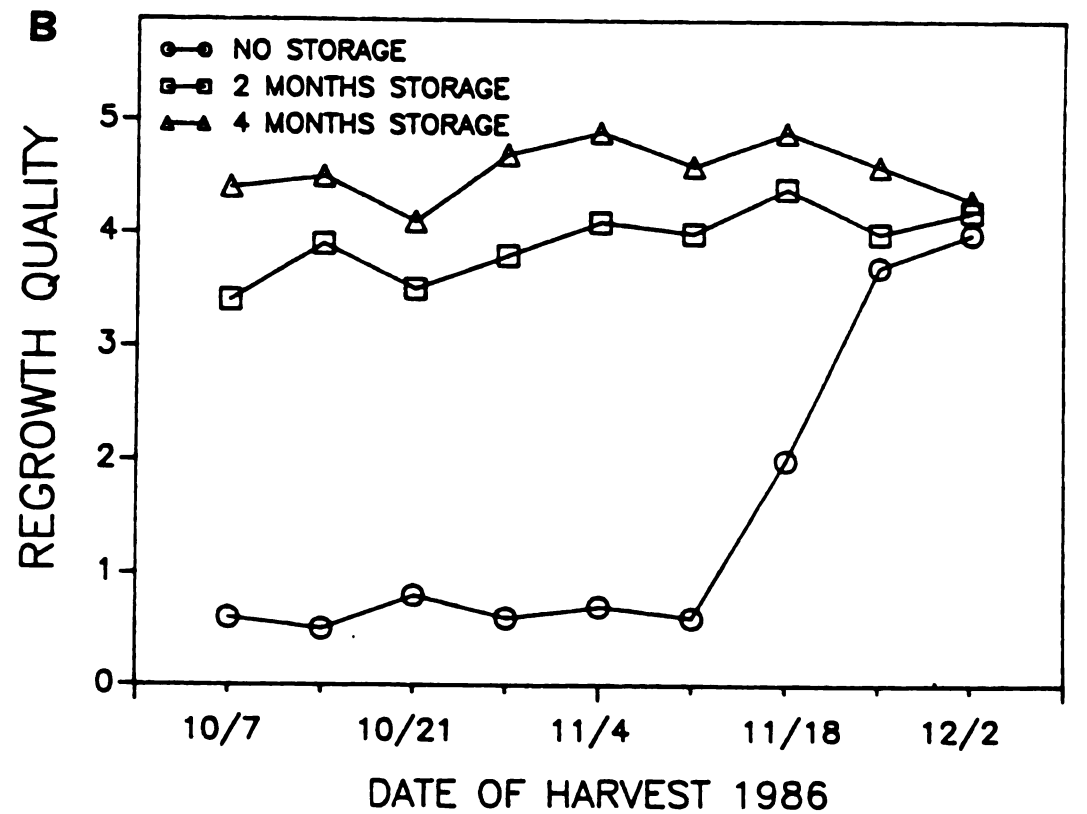
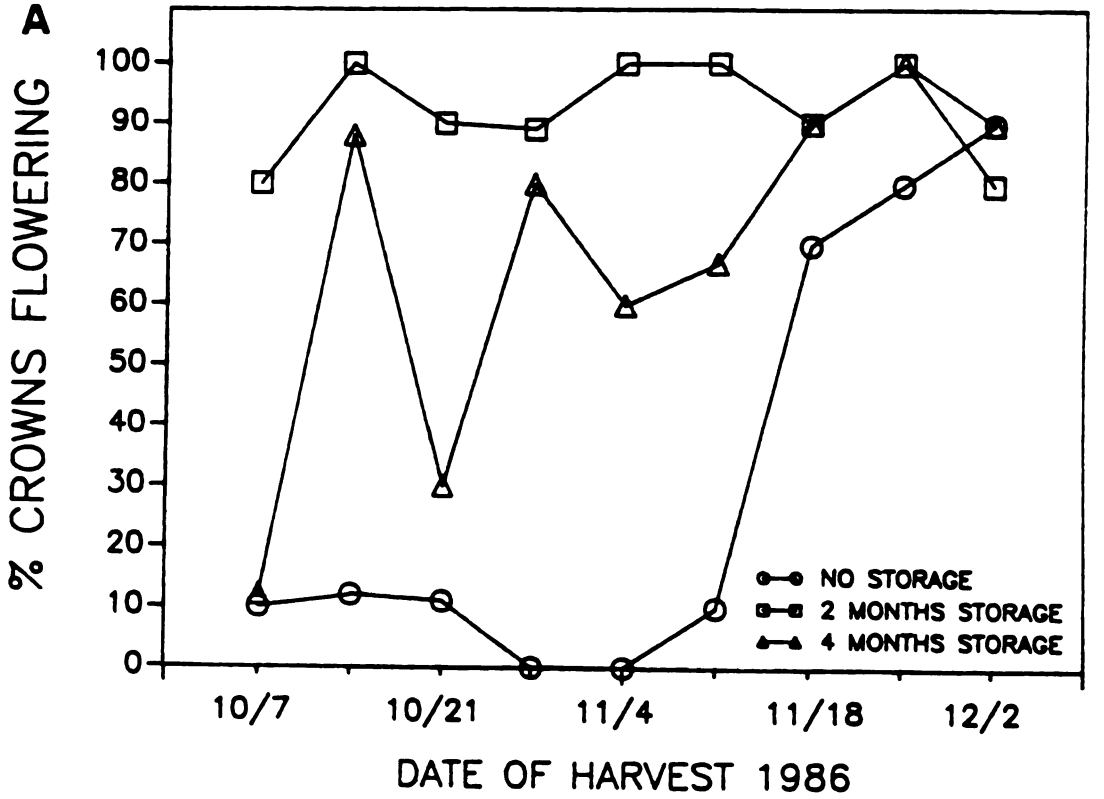
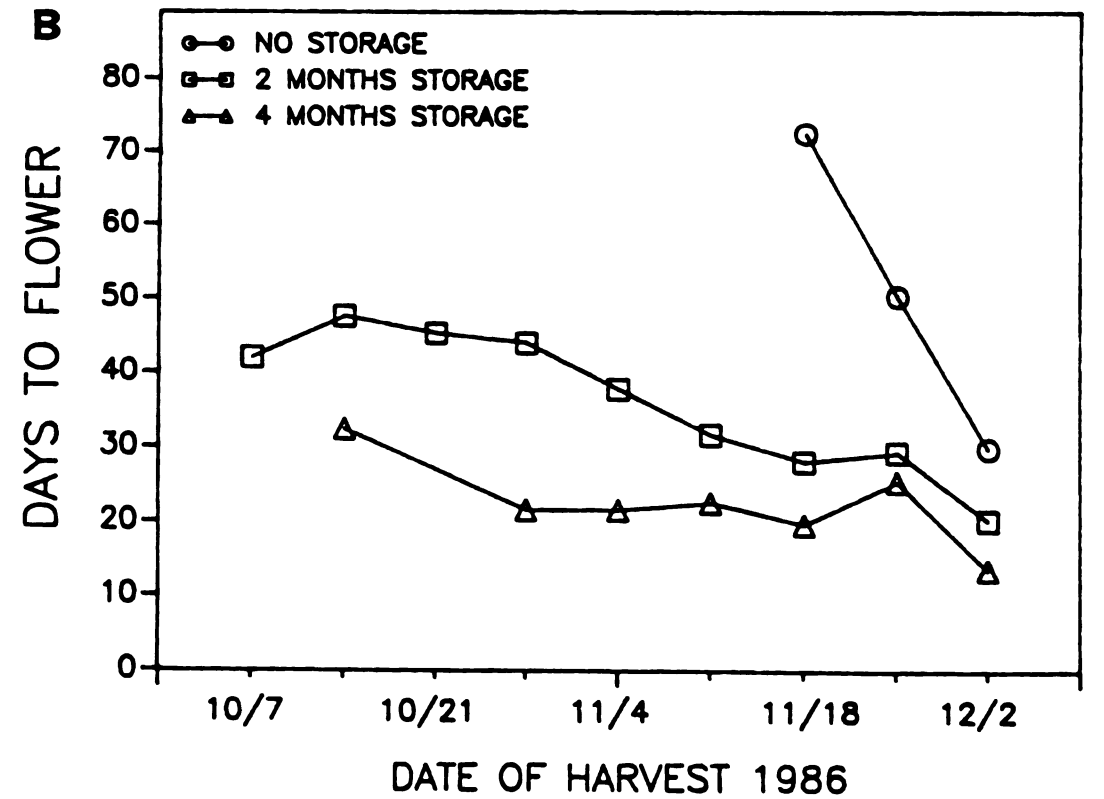

B
NO STORAGE
2 MONTHS STORAGE
4 MONTHS STORAGE
REGROWTH QUALITY
5
4
3
2
1
0
10/7
10/21
11/4
11/18
12/2
DATE OF HARVEST 1986

Figure 2.5. Effect of harvest date and length of storage at 0C on flowering of Dicentra spectabilis crowns.

A. Percent non-dormant crowns producing at least one expanded flower.

B. Mean days from potting to flowering. Means calculated for crowns with at least one expanded flower. Only treatments with ≥50% flowering shown.


A
% CROWNS FLOWERING
100
90
80
70
60
50
40
30
20
10
0
NO STORAGE
2 MONTHS STORAGE
4 MONTHS STORAGE
10/7
10/21
11/4
11/18
12/2
DATE OF HARVEST 1986


B
DAYS TO FLOWER
80
70
60
50
40
30
20
10
0
NO STORAGE
2 MONTHS STORAGE
4 MONTHS STORAGE
10/7
10/21
11/4
11/18
12/2
DATE OF HARVEST 1986

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CHAPTER 3

REVIEW OF BUD DORMANCY LITERATURE

In the past 50 years, there have been many extensive reviews of bud dormancy in the scientific literature (10,14,15,24,43,46,52,53,57,61,63). Despite research and discussion, dormancy remains an elusive phenomenon. Several current reviews have focussed on the search for a "universal terminology" that will resolve the semantic confusion in describing types of dormancy (30,31). The definition of dormancy itself is controversial (see Lang et al. (31) for an excellent comparison of published definitions). Lack of growth at the whole organ level, i.e. a bud, is quite different from the microscopic level, i.e. meristematic tissue. Due to this dependence on morphology, a definition of dormancy is often specific to one system.

The American Society for Horticultural Science at its 1988 annual meeting proposed this general definition: dormancy is "the suspension of (visible) growth of any plant structure(s) containing a meristem(s) in response to external or internal control" (3). Under the broad heading of dormancy, three physiological states are recognized. Ecodormant/quiescent structures resume growth in a favorable

environment. Paradormant/correlatively inhibited structures will not grow in a favorable environment due to the influence of other plant parts such as bud scales, an apical bud, leaves, or the seed coat. Endodormant/resting structures have an internal block which prevents growth, despite favorable conditions. The block is often overcome by chilling.

These terms refer to the status of the plant without reference to underlying mechanism. The lack of a physiological understanding of the basic processes of dormancy induction and release has contributed to the confusion in terminology. General hormonal models involving one to several plant growth regulators have been proposed but have done little to clarify real mechanisms of response based on experimental evidence (14,44,61). New work using single-gene ABA-deficient Arabidopsis mutants holds great promise for revealing mechanisms of genetic and hormonal regulation of dormancy in seeds (25).

Dormancy in perennating buds, however, may involve factors other than, or in addition to, those controlling growth of seeds. Like a seed, a bud contains a meristem within a durable outer covering (bud scales), but there are often several competing meristems in one structure. Unlike a seed, a bud is physically connected to stem and root with potential interaction between organs. Also, a dormant bud is usually well-hydrated in comparison to a seed.

Much of the research on bud dormancy has been based on

woody plant systems in which short days and subsequent cool temperatures promote dormancy and cold acclimation (20,43, 53,63). Endodormancy is broken by further chilling before environmental conditions actually allow growth. The optimum chilling temperature is usually given as 5 to 7C with temperatures at or below 0C considered ineffective (14,19,43,44). A number of fairly accurate empirical models predict the end of endodormancy based on "chilling units" accumulated during exposure to that temperature range (4,47,54). Foresters working with conifer seedlings, however, include temperatures $\leq$0C when assessing chilling history and optimum lift date (49,50,51).

Since the buds of woody plants are aerial, generally only air temperature is considered the driving factor. An unusual model by Mullin and Parker (41) uses soil temperature in the root zone at 15 cm depth to calculate "degree hardening days" for best nursery storage of seedlings. Root growth potential is strongly correlated with shoot survival and extension (50), but a direct causal link is hard to demonstrate (11,22) despite evidence that hormone synthesis/conversion in roots may promote budbreak and growth in Douglas-fir (34) and perhaps apple (65). The role of roots in bud dormancy remains largely unexplored.

A basic problem in the study of dormancy is knowing the physiological state of the plant at a given time (16). The same plant may respond differently to chilling at different seasons, but this inherent dynamic quality is often

overlooked in applying treatments. A recent approach to bud dormancy of woody plants based on physiological status is the degree growth stage (^{o}gs) model of Fuchigami et al. (20). Like some earlier phenological descriptions (42), the ^{o}gs model orders growth cycle events, but with precise definitions and without reference to calendar time. Point events in the cycle can be determined by tests. For example, vegetative maturity is reached when leaf removal no longer stimulates regrowth. A plant moves continuously through the cycle from maximum growth to maximum rest to maximum growth.

The model contains some interesting points: 1) The growth cycle is continuous, implying that growth and dormancy are quantitative states. 2) Processes such as development of dormancy and cold acclimation can be separated physiologically (27,43). 3) Although the model itself seems applicable to all temperate woody plants, its relation to real time varies with year, location, species, and plant age, deriving specific models from the general one (26,42). In many ways, the ^{o}gs model resembles the cellular life cycle model presented in biology textbooks and provides a valuable context in which to study dormancy phenomena.

An entirely different reductionist approach to growth has been used with bulbs and corms, highly specialized herbaceous perennials of the Liliaceae and Iridaceae. Growth and flowering of these small, self-contained units

can be precisely controlled by applied temperature treatments. Bulbs are environmentally programmed or "forced" to flower at a specific time (12,17,23). Usually a stepped series of temperatures are applied, with different levels promoting different processes such as flower formation or stem elongation. The treatments have been established through years of trial and error and are designed for specific cultivars grown under specific conditions. The goal is flower production, however, so less attention has been paid to release from vegetative dormancy than to phenology of floral development (45).

Rapid flowering of tulip, hyacinth, and narcissus depends on completion of organogenesis at warm temperatures (20C), promotion of stem elongation by cool temperatures (8C), and modification of growth rate by greenhouse conditions (12,13,23). The effect of cold on days to budbreak has been largely ignored in the literature. However, in tulip, rate of stem elongation is greater after storage at 5C than at 21C and after 12 weeks of 5C than after 2-10 weeks (39,40). Some additional effect was seen with -1C in short-term storage.

Unlike tulip and most bulbs and corms, lily requires vernalization (32). Chilling at 0.5 to 9C induces floral initiation to occur after storage (12,17,23). For lily, as for woody plants, chilling hours can be calculated to predict regrowth responses. Cold treatment also promotes vegetative growth. Long periods of chilling shorten time to

budbreak for lily but reduce flowering (55,60). However, as in tulip, some vegetative growth can occur without chilling; stems simply do not elongate (33). The work of Wang and Roberts (60) suggests that the primary daughter axis in lily is paradormant in early spring and summer due to inhibitors in daughter scales, then becomes ecodormant under cool temperatures and short days as the mother axis senesces.

Not all bulbs need a cold treatment. Bulbous iris and Zephyranthes are two examples of strictly ecodormant bulbs, growing whenever temperature and moisture permit (23,24). In contrast, bulbs which evolved under a mediterrannean climate, such as tulip, require cold to stimulate stem elongation, while lily, a temperate native, requires cold to induce flowering as well (24,45). The relative effects of chilling on time to budbreak vs. rate of stem elongation need to be studied separately.

Forcing schedules for bulbs incorporate many of the same concepts used in dormancy models for woody plants. Perhaps the distinction between bud and bulb is not as great as has been thought, despite obvious physical differences (32,46). Bulbs and corms in nature respond to the soil environment; like seeds they can be independent of a root system during dormancy; and the meristem is deeply embedded in dense, protective tissue. Non-bulbous herbaceous perennials combine characteristics of both woody perennials and bulbs. They carry perennating buds at or below the soil surface, but not within a bulb or corm. They maintain a

full root system during dormancy--in fact, a dormant herbaceous perennial is often little more than roots and buds, with highly reduced stems. The physical arrangement of these organs varies greatly among temperate zone plants with the herbaceous perennial habit (29).

As small, easily handled plants with exposed buds and distinct growth cycles, it is surprising that few herbaceous perennials have been the subject of dormancy studies. The exception is strawberry, an important semi-evergreen small fruit. Short days in the fall promote dormancy in strawberry (8), as in trees, with maximum rest assumed to develop in mid-November (5). Survival and regrowth after storage depend greatly upon harvest date and chilling history (1,5,8,18,58,64). Without sufficient chilling, leaf initiation proceeds slowly (2) and plants are stunted (21). After storage at -1 to 7C, vegetative regrowth is vigorous (5,21,28,59). Longer chilling stimulates runner production (5) but reduces flowering (8,58).

Chilling requirements for vegetative regrowth after harvest of dormant crowns have been demonstrated for a number of herbaceous perennials. Rhubarb, a plant with underground buds, shows release of dormancy in late November to early December in the northern temperate zone (7,38,56). Before that time, harvested crowns will not grow under forcing conditions. By mid-November, forced growth is quite vigorous. According to Loughton (38) and Tompkins (56), chilling units accumulate below 10C as in woody systems, and

soil temperatures at 10 cm depth can be used to predict the end of rest and best lift date for forcing (Loug, Tomp) as in woody plant systems.

Astilbe requires 9-12 weeks at 5C for vigorous growth (6), peony 9 weeks at 6C (9), American ginseng 50-100 days at 5C (35), and Dicentra cucullaria 120 days at 0C (48). These conditions in general have not been optimized for harvest date and storage temperature, but requirements tend to decrease with later harvest (9,35). Near 0C or long-term chilling results in taller plants in many cases (6,9,48).

Dicentra spectabilis also requires chilling to overcome dormancy developed in the field (Chapters 1 and 2) or induced by short days under greenhouse conditions (36,37). Fully dormant crowns of greenhouse provenance regrew well after 8-12 weeks at 5C (37; Hanchek, unpub. data). Field-harvested crowns required less chilling but were highly variable in response (62). The following study attempts to explore dormancy of Dicentra spectabilis in greater detail.

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CHAPTER 4

EFFECT OF TEMPERATURE AND DURATION OF TEMPERATURE EXPOSURE ON REGROWTH OF *DICENTRA SPECTABILIS* AFTER STORAGE

Earlier studies (Chapters 1,2) made it clear that *Dicentra spectabilis* changed physiologically as the harvest season proceeded, and the evidence pointed to temperature, both in the field and in storage, as a major factor controlling subsequent growth. Four separate responses can be distinguished in the regrowth of *Dicentra* after storage: eye etiolation, budbreak, stem elongation, and flowering. This study was begun to explore the relationship between these growth responses and storage temperature, and to examine the chilling requirement in detail.

MATERIALS AND METHODS

Full temperature series-1986. One-year-old *Dicentra spectabilis* (L.) Lam. crowns were harvested from commercial fields in western Michigan (Walters Gardens, Zeeland) on October 7 and November 18 of 1986. Loose soil was removed by shaking and any green material was trimmed, leaving the eyes intact. At each harvest, ten soil temperatures at 10 cm depth in the field were measured. Records of soil

temperatures were also obtained from the Trevor Nichols Experimental Farm, Fennville, MI (25). The crowns were packed in a moistened 1:1 peat:perlite mixture in polyethylene-lined crates to avoid desiccation stress (6) and simulate *in situ* chilling, and stored at -2.5, 0, 2.5, 5, 10, 15, or 20C for 0, 2, 4, 6, 8, or 10 weeks. Each treatment was applied to twenty plants. After treatment, the crowns were potted with eyes exposed and held in a cool greenhouse (19C day/12C night) under 16 hours of 8.5 mol/day-m^2 supplemental light. At one week after break, they were moved to benches under natural lighting.

Those crowns which were removed after 0, 4, and 10 weeks were first closely examined and the length of every visible eye was measured. All plants were inspected daily after potting for budbreak, defined in this study as the opening of bud scales and appearance of floral parts or expanding leaf margins from within the eye. Days to first budbreak was recorded for each crown. If eyes had not broken after 180 days in the greenhouse, the crowns were discarded. At time of break, eye length was measured. It was remeasured at 7 days post-break to determine the elongation rate of that individual eye during the first week post-break.

At 5 weeks post-break, the regrowth quality of the entire plant was rated on a 0 to 5 scale (0=dead, 0.5=dormant buds, 1=emergent growth, ... 5=vigorous growth) after Maqbool (23). Whole plant height to the highest leaf

was measured at the same time. The date at which each crown first produced an expanded flower was also noted. An expanded flower was defined as a well-colored floret with sepals detached (34). If flowers were not produced, presence or absence of aborted flower buds was noted.

Intermediate temperature series-1987. Crowns were harvested from southwestern Michigan fields (DeGroot Nurseries, Coloma) on October 9, 1987. At harvest, ten field soil temperatures at 10 cm depth were measured. Records of soil temperatures were also obtained from the Trevor Nichols Experimental Farm, Fennville, MI (25). The plants were processed and packed as in 1986, and stored at 5, 7.5, or 10C for 0, 4, 8, or 12 weeks with twenty plants per treatment.

They were then potted and regrown under 18 hours of 8.3 mol/day-m^2 supplemental light, and the same parameters were measured as in the 1986 temperature series experiments. The plants were held under lights until flowering peaked with a maximum number of fully developed, apically reflexed flowers (34). The inflorescences were then removed. Since the flowers of D. spectabilis are essentially 2-dimensional, floral production was measured in mm^2 by a Delta-T area measurement system, just as leaf area is measured. All floral parts contributed to the surface area measurement, including flowers, axes, and aborted flower buds, but no subtending leaves.

Treatment means were calculated on the basis of plants

which survived to that point of development. Data were analyzed as a completely randomized design (24,28). Standard errors of the interaction means were calculated based on the smallest n (replicates per treatment cell) in that analysis.

RESULTS

Soil Conditions. Minimum soil temperatures at 10 cm depth had not dropped below 10C before the October 7 harvest in 1986 (Figure 4.1a). By the late harvest on November 18, temperatures below 10C had been common during the previous six weeks. In the week preceding harvest in October of 1987, soil temperatures often fell below 10C (Figure 4.1b).

Full temperature series-1986. When October crowns were held at -2.5C, many had frozen, blackened, or rotted eyes after even 2 weeks. Much less damage was observed on November plants. Death of apparent growing points at -2.5C may have been responsible for the high number of crowns which failed to break bud following that temperature treatment (Table 4.1). Cold hardiness, however, was apparently an all-or-nothing situation since plants which survived -2.5C grew quite vigorously after potting. Due to overall lower survival and visibly damaged eyes, the -2.5C treatment was analyzed separately from other data (Table 4.2).

The change in eye length due to chilling was striking, especially for the early harvest. After 10 weeks in storage at 10 and 15C, October crowns had eyes whose average length

was more than double the length at harvest (Figure 4.2). Dicentra harvested in late November showed less etiolation at 10 or 15C but had more eyes that opened in storage by separation of bud scales without the appearance of expanding leaf margins (Figure 4.3). The distinction between eye etiolation and stem elongation is important: the former occurred in dark storage without or without opening of eyes; the latter took place in the greenhouse after budbreak and consisted of elongation of the bud axis from within and protruding out of the eye.

The time from potting to budbreak declined from 77 days for control plants harvested in early October to 29 days for November controls (Table 4.3). Time to budbreak decreased as temperature decreased from 20 to 0C (Figure 4.4). 0 and 2.5C were the most effective treatments at 2 and 4 weeks, but after 8 weeks, all temperatures of 5C and lower caused eyes on October crowns to break in 10 to 20 days. Crowns harvested in mid-November broke in 5 to 15 days from potting after 2 weeks at 15C or lower. Further chilling did not consistently hasten budbreak, and constant exposure to 20C delayed it.

Although days to budbreak from potting decreased with chilling, it is important to distinguish between the effects of simple aging and true chilling effect. Plotting days to budbreak from harvest against temperature shows that exposure to 0C-5C actually did induce earlier budbreak, especially for the October harvest (Figure 4.5). At 10C or

higher, time to budbreak was not reduced even after 10 weeks of storage. After exposure to low temperatures for about 4 weeks, dormancy release was practically complete, and further chilling had diminishing promotive effects. This was even more obvious for the November harvest which received field chilling.

Highly etiolated eyes on October crowns from 10 and 15C treatments generally did not break upon transfer to the greenhouse. The eyes shrivelled and died, while smaller eyes broke first (Figure 4.2). Moderately etiolated eyes on November crowns did break but often died later. For both harvest dates, average eye length upon breaking was greater after 6 weeks of higher temperatures.

After 1 week in growing conditions, however, crowns exposed to 5C or less in storage showed rapid rates of stem elongation, as much as 10 mm per day for some individuals (Figure 4.6). Growth rate was not substantially affected until 4 weeks of chilling, although budbreak was promoted after 2 weeks (Table 4.2). Once again, there was a clear distinction between the growth responses of budbreak and stem elongation. For both the October and November-harvested crowns, 8 weeks of exposure to constant temperatures depressed the subsequent initial growth rate. At 10C to 20C, growth in the first week was negligible. In the case of the mid-November harvest, after 15C or 20C the rate was even less than for the unstored control.

At 5 weeks post-break, plant height still reflected the

initial rate of stem elongation (Figure 4.7). Plants held at non-chilling temperatures, or for insufficient time at chilling temperatures, never made up the difference. Either they continued to grow slowly or they experienced arrested growth soon after break. Some eyes, particularily etiolated ones, died in the second or third week post-break.

Regrowth quality of Dicentra crowns closely matched height measurements, except that shorter, bushier individuals received high ratings (data not shown). Plants harvested in mid-November were of better quality overall than October plants. In general, 5C or lower was required to produce a vigorous, attractive plant.

In 1986, the only flowering data taken were percent crowns flowering per treatment and days from potting to first flower. Many crowns did not successfully expand a single floret (Figure 4.8), although many produced aborted flower buds. From the October harvest, 41% of all surviving crowns flowered, while 25% more showed evidence of aborted flowering. From the November group, 55% of survivors flowered while an additional 22% had aborted buds.

Chilling at 0C to 5C for 6 or more weeks produced more flowering plants from the October harvest than other treatments, while 10C and below encouraged flowering in the November harvest (Figure 4.8). But even after storage at 10C or warmer, a few October crowns managed to push expanded flowers from the eyes, often without any accompanying foliage. In plants that received insufficient chilling, the

flowering axis simply did not elongate. The effect of temperature on days to flower is hard to assess statistically since so many plants failed to bloom, but it appears that longer periods at chilling temperatures hastened flowering for plants from both harvest dates (Figure 4.9).

Intermediate temperature series-1987. Eye etiolation in storage was again measured in 1987, and was definitely promoted by 10C in darkness (Figure 4.10). Highly etiolated eyes from 10C storage were less likely to break than moderately etiolated ones.

As in 1986, eyes broke quickly after chilling at 5C (Figure 4.11), and growth due to stem elongation was correspondingly rapid (Figure 4.12). After 10C, budbreak was much slower and growth rate during the first week did not change from the control. The "intermediate" temperature of 7.5C promoted budbreak and growth to about the same extent as 10C.

The same relationship between the three temperatures held true in regard to plant height and regrowth quality at 5 weeks post-break (Figure 4.13). Height and overall quality were best expressed after 8 weeks of exposure to 5C. The warmer temperatures of 7.5C and 10C were both ineffective in stimulating regrowth.

After 5 weeks of regrowth, most crowns held for 8 weeks at any of the temperatures showed some evidence of floral development (Figure 4.14a). However, only plants held at 5C

produced expanded flowers with any success, even after 90 days in the greenhouse (Figure 4.14b). Days to flower from potting appeared to decrease with longer exposure to 5C (Figure 4.15), but the limited number of plants flowering prevented statistical comparison of means. Most crowns exposed to 5C for 8 weeks flowered in 40 days.

A single normal Dicentra floret has an average area of about 40 mm^2. Only 9% of all the unchilled crowns in this experiment flowered, and the average inflorescence area per plant was about 50 mm^2, hardly more than one blossom. After chilling at 5C, crowns produced large racemes of 140-200 mm^2 average area (Figure 4.16).

DISCUSSION

Four separate growth responses were observed in D. spectabilis during the course of this study, each with a different time/temperature requirement. Eye etiolation, unaccompanied by meristematic growth of the primary bud within the eye, was promoted by warm temperatures (10 to 20C). Budbreak, stem elongation, and flowering were promoted by cold temperatures (-2.5 to 5C). The "intermediate" temperature of 7.5C did not act as a promoting temperature for any of these responses.

After chilling at 0 to 2.5C, early-harvest Dicentra required only 2 weeks of exposure to break bud quickly, but 4 weeks were required to induce stem elongation, and 8 weeks to hasten flowering. As the harvest season progressed and

soil temperatures dropped in the field, chilling in storage had much less effect. However, storage at warm temperatures late in the season seriously reduced regrowth.

Optimum temperatures for dormancy release in Dicentra were lower than the 4 to 7C range cited for woody plants (10,13,29,30), but were similar to those given for greatest stem elongation in tulip (9,26,27), lily (8,11,15), and strawberry (3,14,17,35). Increased elongation with longer periods of chilling was also reported for tulip (26) and Dicentra cucullaria (33).

Stunted growth of incompletely chilled plants has been reported for peach seedlings (12), strawberry (14), lily (19), Dicentra spectabilis (22), and Dicentra cucullaria (33), indicating quanitatively different requirements for budbreak and elongation of the meristematic axis. One physiological explanation for a differential response was put forward by Zigas and Coombe (36) who suggested that cold promotes germination of peach seedlings by reducing ABA levels, and elongation by increasing GA levels. This hormonal model for the breaking of dormancy could possibly be extended to buds. Exogenous GA has been shown to partially substitute for the cold requirement for elongation in many plants (7) including Dicentra spectabilis (21).

Flowering is a complex response incorporating several steps: initiation of floral buds, differentiation of the flowering axis, and maturation and expansion of florets (18). Since storage temperature affects bud axis

elongation, it was not surprising that days to flower decreased with chilling of crowns while incidence of flowering increased. However, production of visible flower buds was much less affected by temperature. Expanded flowers were occasionally produced even by stunted crowns from 20C treatments (Figure 4.7).

A causal relationship between temperature and flowering in Dicentra remains to be seen. Many spring-flowering perennials such as tulip, iris, and strawberry do not require vernalization (1,15,17) although chilling may enhance organogenesis (2,4,8,26,27,31,32). Buds on Dicentra crowns may have aborted due to storage conditions (16) or, as Lopes and Weiler (22) observed, to low light in growing conditions. There was complete loss of flower buds with 6.9 mol/day-m2 total light. In these present studies, expansion of florets and number per panicle was always greater on Dicentra flowered under supplemental light, indicating the importance of total light in the growing environment on floral production.

Response of Dicentra spectabilis to storage temperature seems consistent with dormancy patterns observed in woody plants and bulbs, with optimum chilling for dormancy release at 0 to 2.5C. Growth responses are distinct and easily observed. In addition, D. spectabilis can be readily propagated by tissue culture (20) or stem cuttings and is easily handled in the field, the storage room, and the greenhouse, allowing statistically valid numbers of

replicates. Dicentra seems an excellent system for the further study of bud dormancy and the effects of storage environment on vegetative regrowth.

Table 4.1. Effect of storage duration and temperature on number of Dicentra spectabilis crowns that broke bud within 180 days of growing conditions (19C day/12C night, 16 hrs 8.5 mol/day-m^2 supplemental light). Twenty crowns per treatment.

OCTOBER 7, 1986 HARVEST

STORAGE TEMPERATURE	STORAGE DURATION IN WEEKS 2	4	6	8	10
-2.5 C	11	7	12	18	13
0	19	15	17	20	13
2.5	20	15	20	20	16
5	17	19	20	20	20
10	20	19	18	20	19
15	18	20	19	20	19
20	19	18	15	19	17
CONTROL: 20					

NOVEMBER 18, 1986 HARVEST

STORAGE TEMPERATURE	STORAGE DURATION IN WEEKS 2	4	6	8	10
-2.5 C	20	15	18	18	18
0	20	20	20	20	19
2.5	20	20	20	20	19
5	20	19	19	20	18
10	20	18	19	20	20
15	20	20	20	20	20
20	20	20	19	16	19
CONTROL: 18					

Table 4.2. Effect of storage at -2.5C on condition and regrowth of *Dicentra spectabilis* crowns. Twenty crowns per treatment. Means calculated for plants with at least one broken eye. SEM: standard error of the treatment means.

OCTOBER 7, 1986 HARVEST

WEEKS	% SURVIVAL	DAYS TO BUDBREAK	GROWTH RATE (mm/week)	PLANT HEIGHT AT 5 WEEKS (cm)	% CROWNS FLOWERING	DAYS TO FLOWER
0	100	77	0.7	0.0	5	139
2	55	56	1.4	0.1	5	117
4	35	51	1.4	1.0	5	207
6	60	27	15.4	11.6	15	73
8	90	11	23.1	22.4	65	50
10	65	13	30.8	25.8	10	48
SEM (n=7)	---	9	4.9	3.2	---	---

NOVEMBER 18, 1986 HARVEST

WEEKS	% SURVIVAL	DAYS TO BUDBREAK	GROWTH RATE (mm/week)	PLANT HEIGHT AT 5 WEEKS (cm)	% CROWNS FLOWERING	DAYS TO FLOWER
0	90	29	18.2	8.9	79	35
2	100	12	29.4	29.9	44	90
4	75	14	44.8	21.8	50	55
6	90	10	35.0	24.9	37	65
8	90	9	29.4	25.0	38	70
10	90	10	44.9	30.5	34	75
SEM (n=15)	---	3	4.9	2.0	---	---

Table 4.3. Effect of storage duration and temperature on mean days from potting to budbreak of Dicentra spectabilis crowns. Means calculated for crowns with at least one broken eye; SEM = standard error of the interaction means.

OCTOBER 7, 1986 HARVEST

STORAGE TEMPERATURE	STORAGE DURATION IN WEEKS 2	4	6	8	10
0 C	48	27	19	10	24
2.5	47	29	15	16	23
5	63	36	27	12	9
10	73	82	46	47	50
15	68	68	72	58	75
20	74	83	66	68	75

CONTROL: 77 days $SEM_{n=13}=9.4$

NOVEMBER 18, 1986 HARVEST

STORAGE TEMPERATURE	STORAGE DURATION IN WEEKS 2	4	6	8	10
0	9	8	7	6	6
2.5	10	10	10	5	8
5	11	10	9	6	4
10	16	12	5	6	4
15	15	16	12	9	6
20	18	37	26	34	41

CONTROL: 29 days $SEM_{n=16}=3.5$

Table 4.4. Effect of storage duration and temperature on mean rate of stem elongation in mm/week during the first week of post-break growth of Dicentra spectabilis crowns. Means calculated for crowns with at least one broken eye; SEM = standard error of the interaction means.

OCTOBER 7, 1986 HARVEST

STORAGE TEMPERATURE	STORAGE DURATION IN WEEKS 2	4	6	8	10
0 C	0.6	37.1	34.7	28.8	49.6
2.5	1.0	26.9	35.7	25.3	43.9
5	1.2	8.8	28.8	24.2	20.2
10	0.9	1.3	1.1	1.1	2.3
15	0.9	1.4	1.1	0.9	2.7
20	1.3	0.3	1.7	0.8	0.8

CONTROL: 0.6 mm/week $SEM_{n=13}$=3.8

NOVEMBER 18, 1986 HARVEST

STORAGE TEMPERATURE	STORAGE DURATION IN WEEKS 2	4	6	8	10
0	20.3	23.8	33.6	18.9	42.7
2.5	21.7	33.6	37.1	15.4	44.8
5	18.2	28.0	35.7	19.6	46.2
10	15.4	17.5	18.2	16.1	37.1
15	7.7	9.8	7.0	4.2	19.6
20	2.8	4.2	5.6	1.4	1.4

CONTROL: 18.2 mm/week $SEM_{n=16}$=4.7

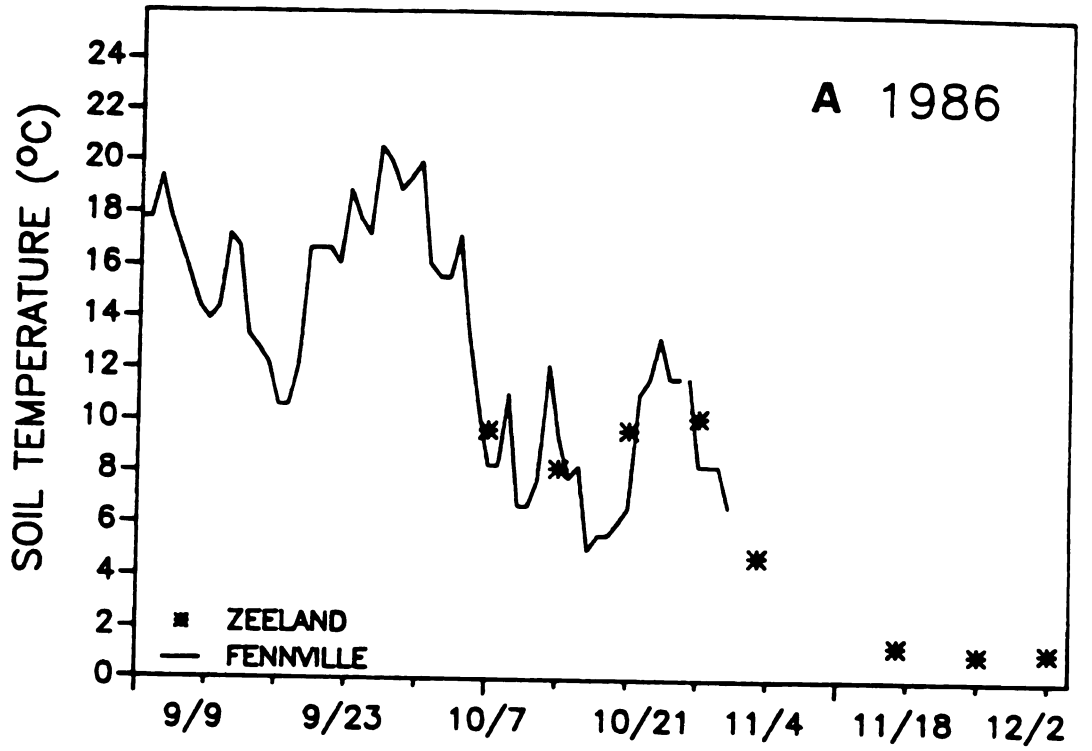
Table 4.5. Effect of storage duration and temperature on number of *Dicentra spectabilis* crowns harvested on 10/9/87 that broke bud within 120 days of growing conditions (19C day/12C night, 16 hrs 8.3 mol/day-m^2 supplemental light). Twenty crowns per treatment.

STORAGE TEMPERATURE	STORAGE DURATION IN WEEKS 0	4	8	12
5 C	16	19	20	20
7.5	19	20	18	20
10	14	17	20	18

Figure 4.1 Minimum daily soil temperatures at 10 cm depth at Trevor Nichols Experimental Farm, Fennville, MI, and average soil temperature at 10 cm depth at 10:00 am in *Dicentra spectabilis* fields.

A. 1986; Zeeland, MI. Zeeland standard error of means=0.7.

B. 1987; Coloma, MI. Coloma standard error=0.1.


A 1986
SOIL TEMPERATURE (°C)
24
22
20
18
16
14
12
10
8
6
4
2
0
ZEELAND
FENNVILLE
9/9
9/23
10/7
10/21
11/4
11/18
12/2

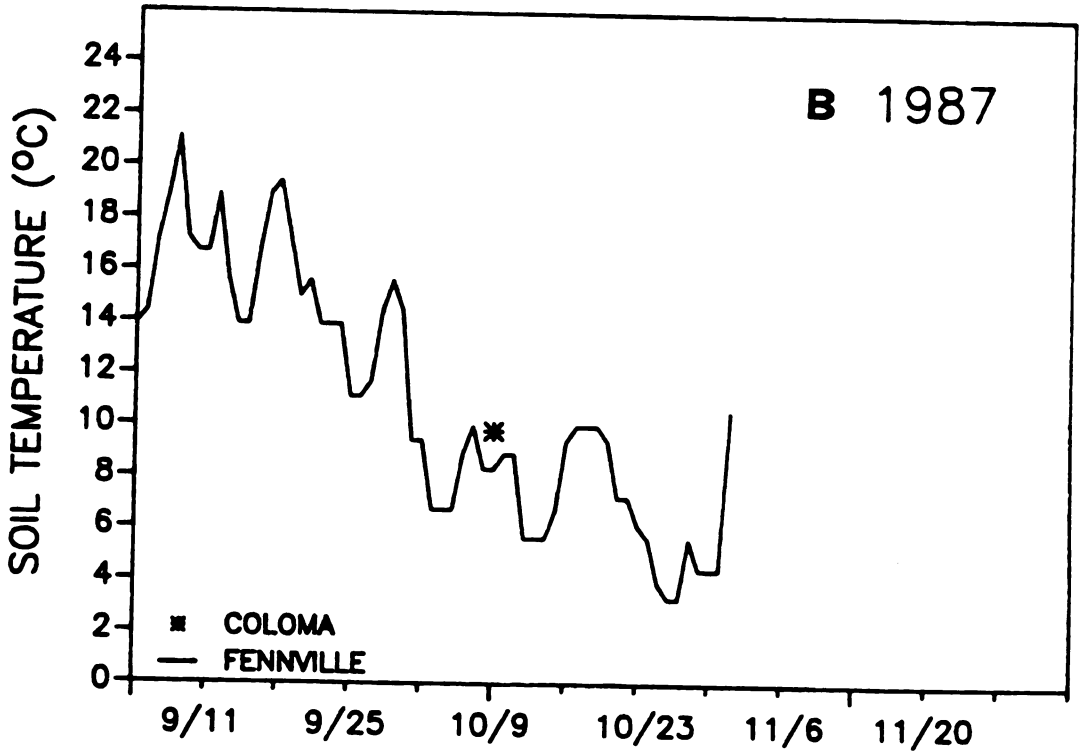

B 1987
SOIL TEMPERATURE (°C)
24
22
20
18
16
14
12
10
8
6
4
2
0
COLOMA
FENNVILLE
9/11
9/25
10/9
10/23
11/6
11/20

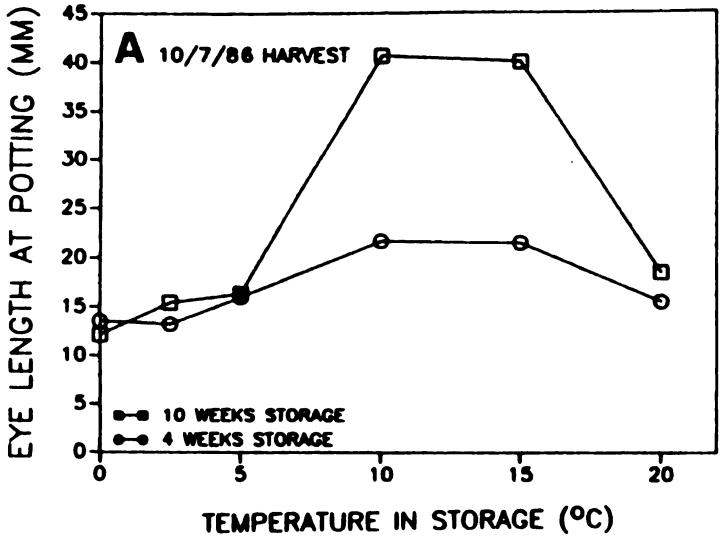
Figure 4.2. Effect of storage for 4 or 10 weeks at 0, 2.5, 5, 10, 15 or 20C on mean length of Dicentra spectabilis eyes.

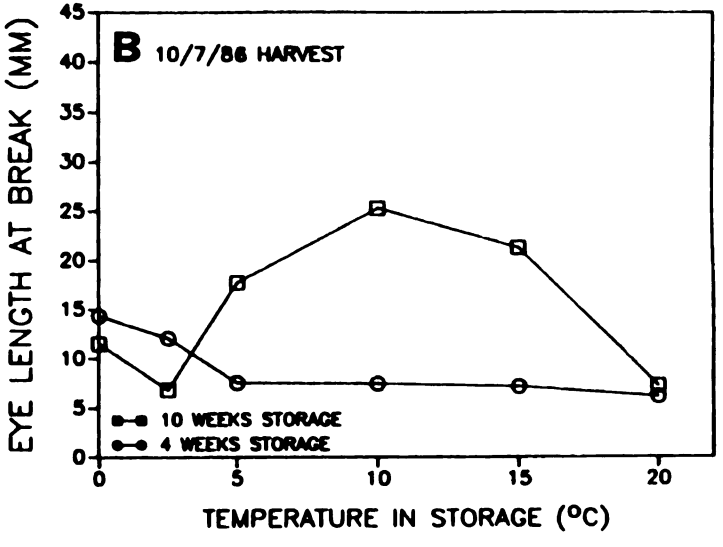
A. Mean eye length at potting for crowns harvested on October 7, 1986; standard error of the interaction means (n=62) = 2.5 mm.

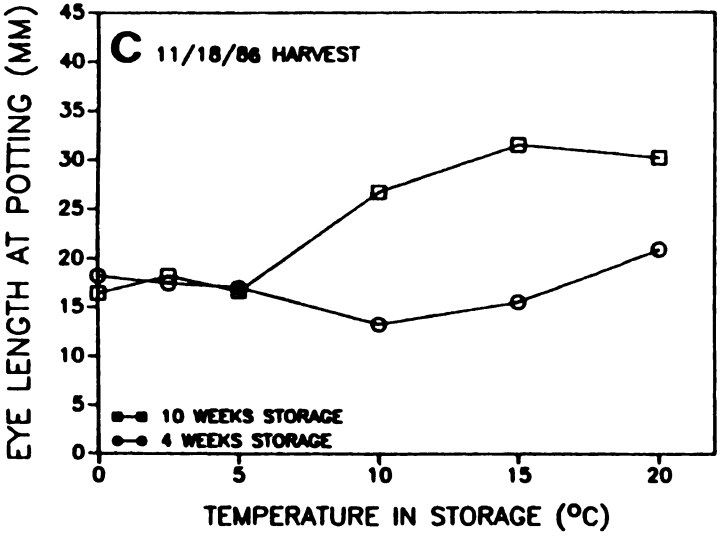
B. Mean length at budbreak of first eye to break on crowns harvested on October 7, 1986; standard error of the interaction means (n=13) = 4.7 mm.

C. Mean eye length at potting for crowns harvested on November 18, 1986; standard error of the interaction means (n=63) = 2.5 mm.

D. Mean length at budbreak of first eye to break on crowns harvested on November 18, 1986; standard error of the interaction means (n=18) = 3.5 mm.


A 10/7/86 HARVEST
EYE LENGTH AT POTTING (MM)
TEMPERATURE IN STORAGE (°C)
10 WEEKS STORAGE
4 WEEKS STORAGE


B 10/7/86 HARVEST
EYE LENGTH AT BREAK (MM)
TEMPERATURE IN STORAGE (°C)
10 WEEKS STORAGE
4 WEEKS STORAGE


C 11/18/86 HARVEST
EYE LENGTH AT POTTING (MM)
TEMPERATURE IN STORAGE (°C)
10 WEEKS STORAGE
4 WEEKS STORAGE

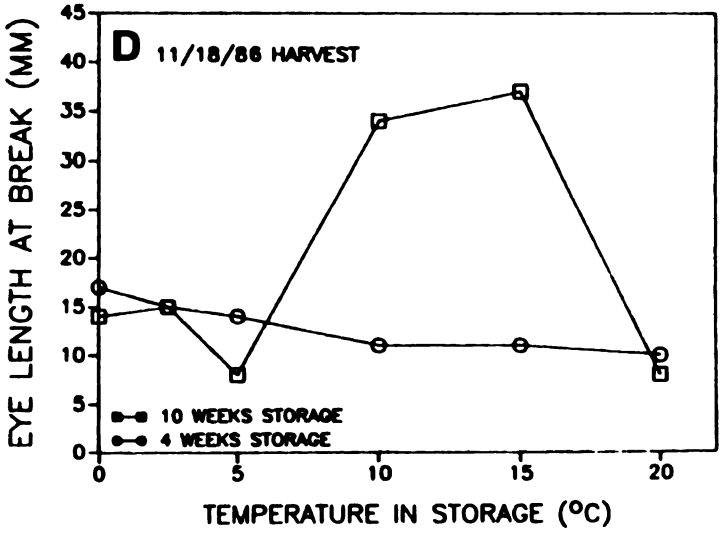
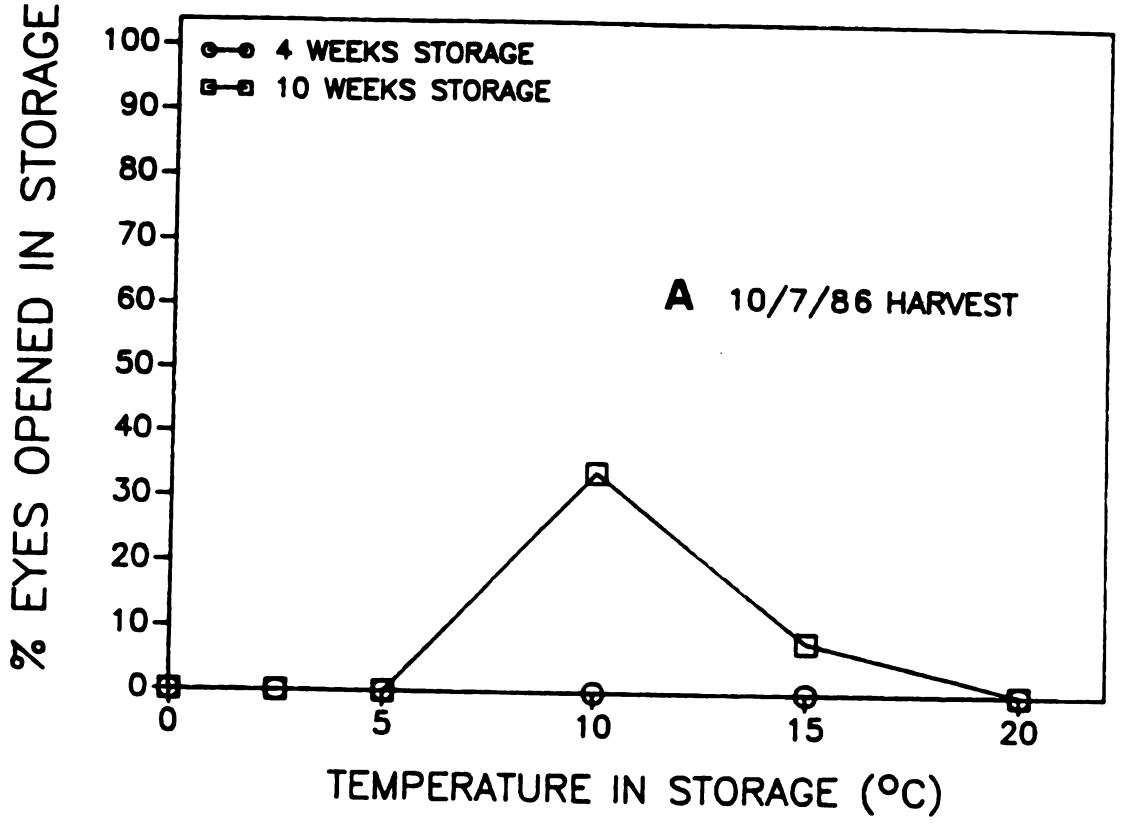

D 11/18/86 HARVEST
EYE LENGTH AT BREAK (MM)
TEMPERATURE IN STORAGE (°C)
10 WEEKS STORAGE
4 WEEKS STORAGE

Figure 4.3. Effect of storage for 4 or 10 weeks at 0, 2.5, 5, 10, 15 or 20C on percent of Dicentra spectabilis eyes open in storage.

A. Crowns harvested October 7, 1986.

B. Crowns harvested November 18, 1986.


% EYES OPENED IN STORAGE
100
90
80
70
60
50
40
30
20
10
0
4 WEEKS STORAGE
10 WEEKS STORAGE
A 10/7/86 HARVEST
0
5
10
15
20
TEMPERATURE IN STORAGE (°C)

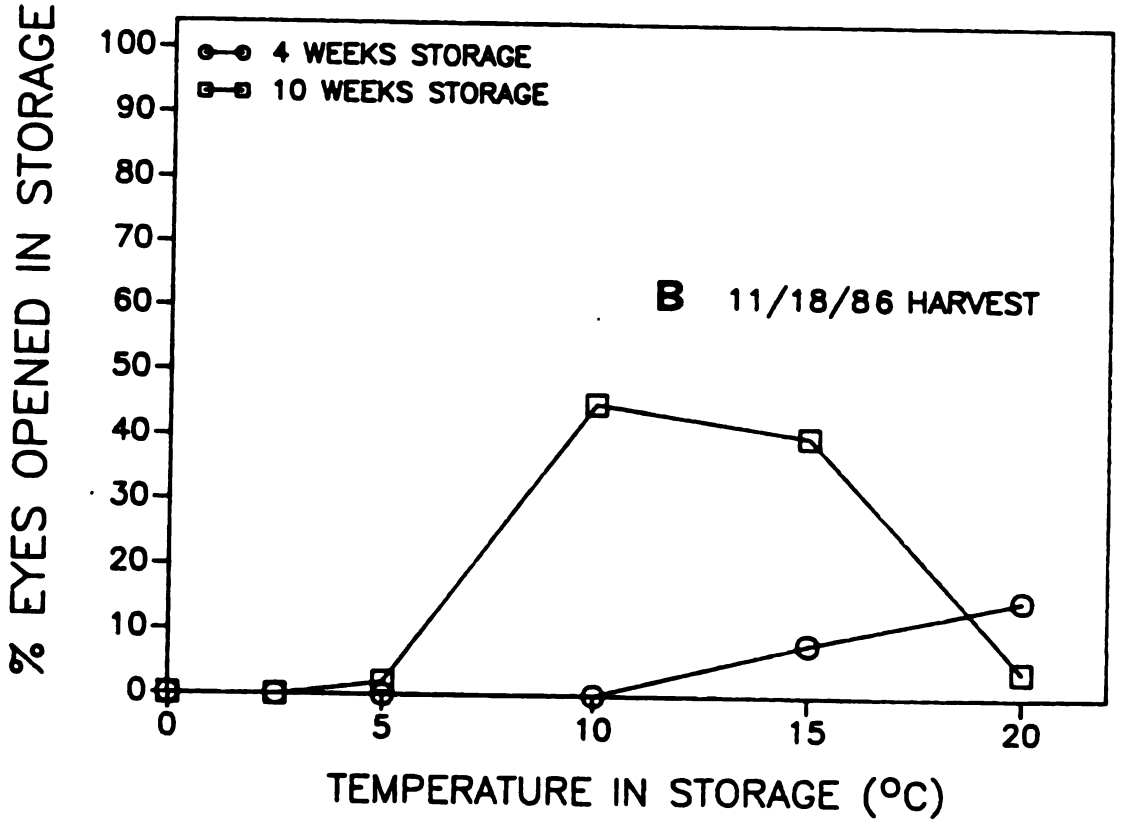
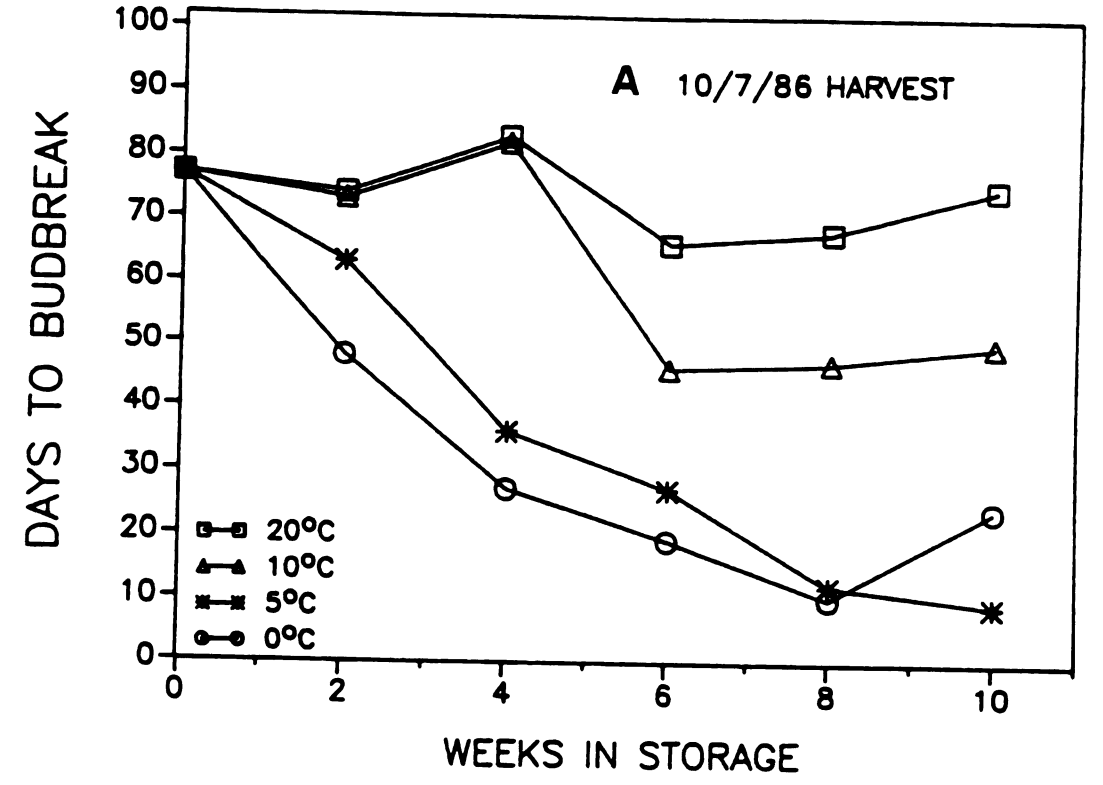

% EYES OPENED IN STORAGE
100
90
80
70
60
50
40
30
20
10
0
4 WEEKS STORAGE
10 WEEKS STORAGE
B 11/18/86 HARVEST
0
5
10
15
20
TEMPERATURE IN STORAGE (°C)

Figure 4.4. Effect of storage temperature and duration on mean days from potting to budbreak of Dicentra spectabilis crowns. Means calculated for crowns with at least one broken eye.

A. Crowns harvested October 7, 1986; standard error of the interactions means (n=13) = 9.4 days.

B. Crowns harvested November 18, 1986; standard error of the interaction means (n=16) = 3.5 days.


A 10/7/86 HARVEST
DAYS TO BUDBREAK
WEEKS IN STORAGE
20°C
10°C
5°C
0°C
0
10
20
30
40
50
60
70
80
90
100
0
2
4
6
8
10

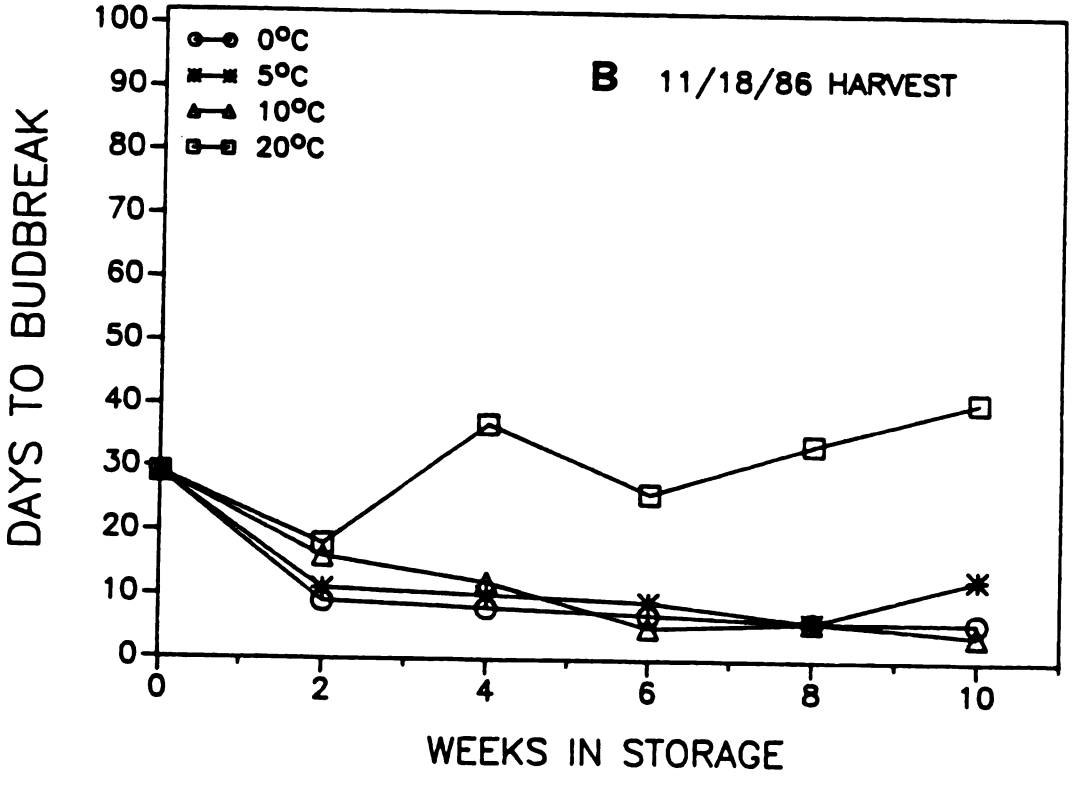
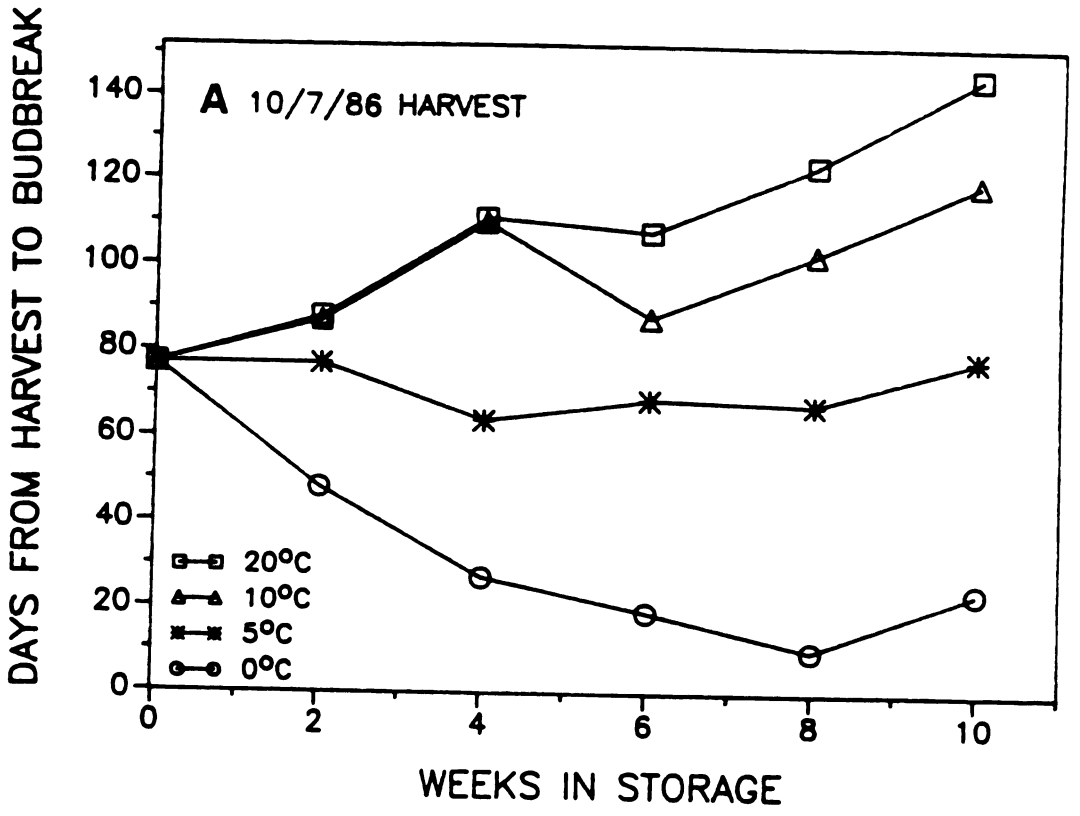

B 11/18/86 HARVEST
DAYS TO BUDBREAK
WEEKS IN STORAGE
0°C
5°C
10°C
20°C
0
10
20
30
40
50
60
70
80
90
100
0
2
4
6
8
10

Figure 4.5. Effect of storage temperature and duration on mean days from harvest to budbreak of Dicentra spectabilis crowns. Means calculated for crowns with at least one broken eye.

A. Crowns harvested October 7, 1986; standard error of the interactions means (n=13) = 9.6 days.

B. Crowns harvested November 18, 1986; standard error of the interaction means (n=16) = 3.4 days.


A 10/7/86 HARVEST
DAYS FROM HARVEST TO BUDBREAK
WEEKS IN STORAGE
20°C
10°C
5°C
0°C
0
20
40
60
80
100
120
140
0
2
4
6
8
10

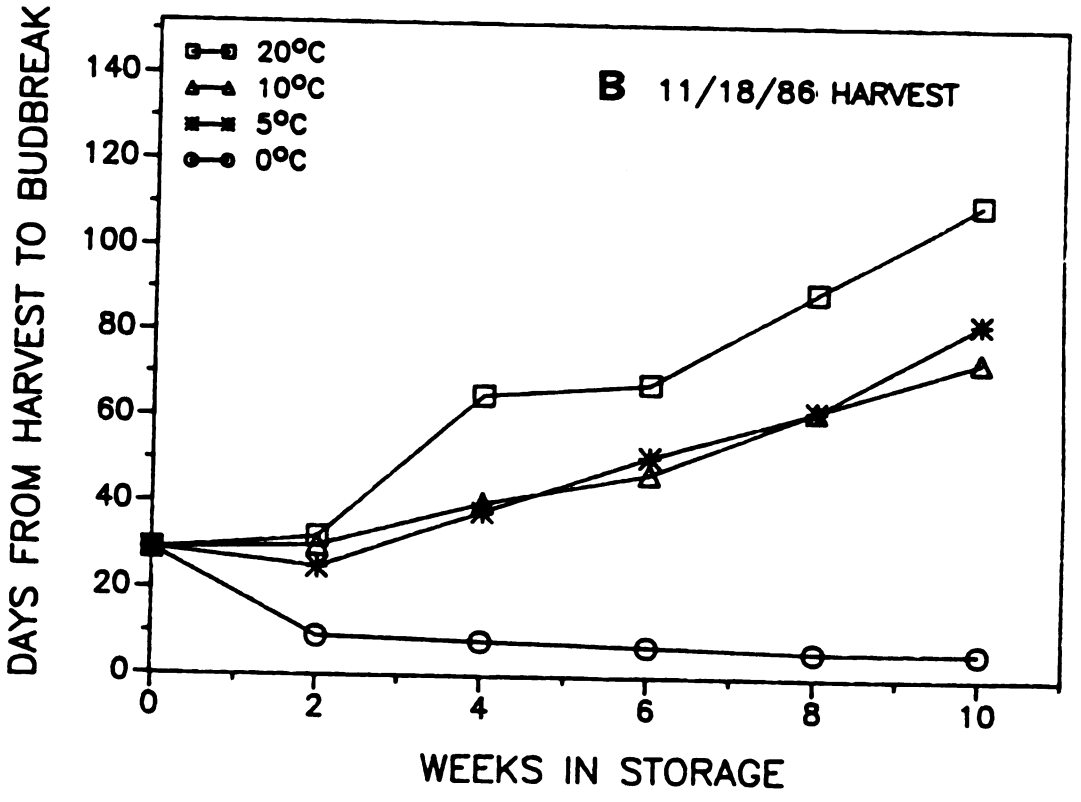
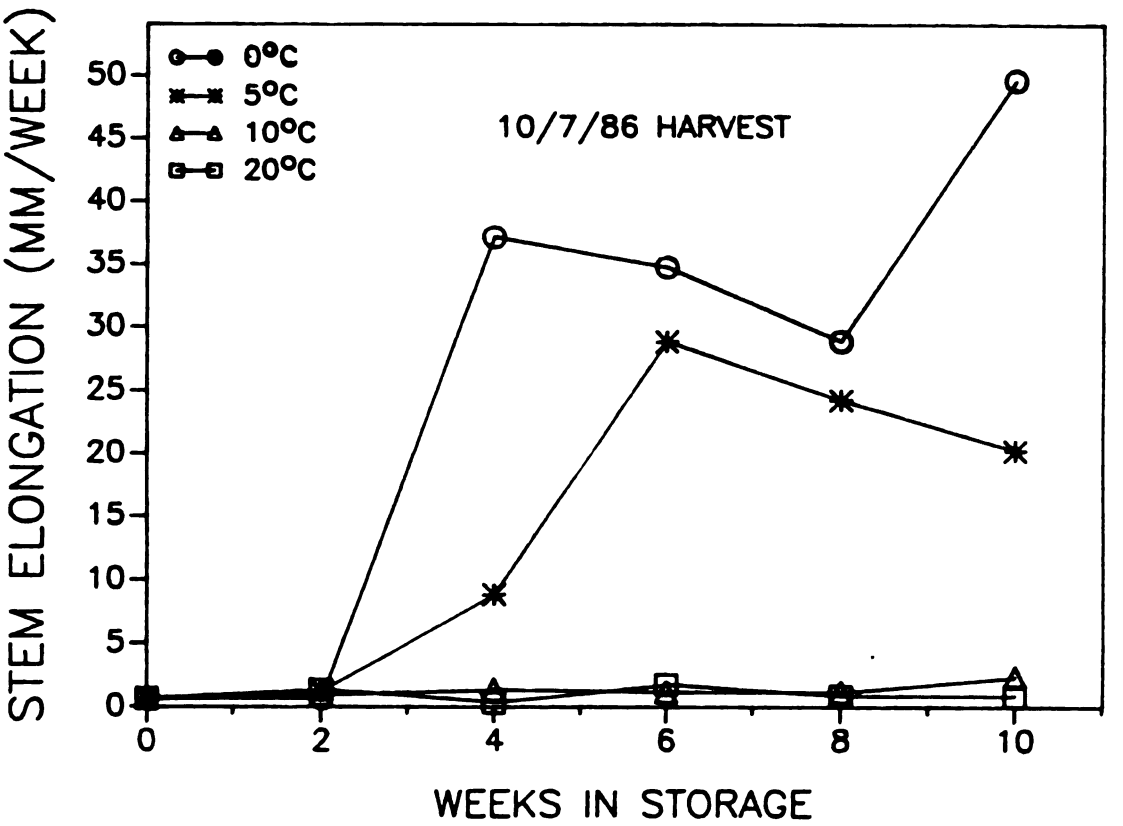

B 11/18/86 HARVEST
DAYS FROM HARVEST TO BUDBREAK
WEEKS IN STORAGE
20°C
10°C
5°C
0°C
0
20
40
60
80
100
120
140
0
2
4
6
8
10

Figure 4.6. Effect of storage temperature and duration on mean rate of stem elongation during the first week of post-break growth of Dicentra spectabilis crowns. Means calculated for crowns with at least one broken eye.

A. Crowns harvested October 7, 1986; standard error of the interactions means (n=13) = 3.8 mm/week.

B. Crowns harvested November 18, 1986; standard error of the interaction means (n=16) = 4.7 mm/week.


0°C
5°C
10°C
20°C
10/7/86 HARVEST
STEM ELONGATION (MM/WEEK)
WEEKS IN STORAGE
0
5
10
15
20
25
30
35
40
45
50
0
2
4
6
8
10

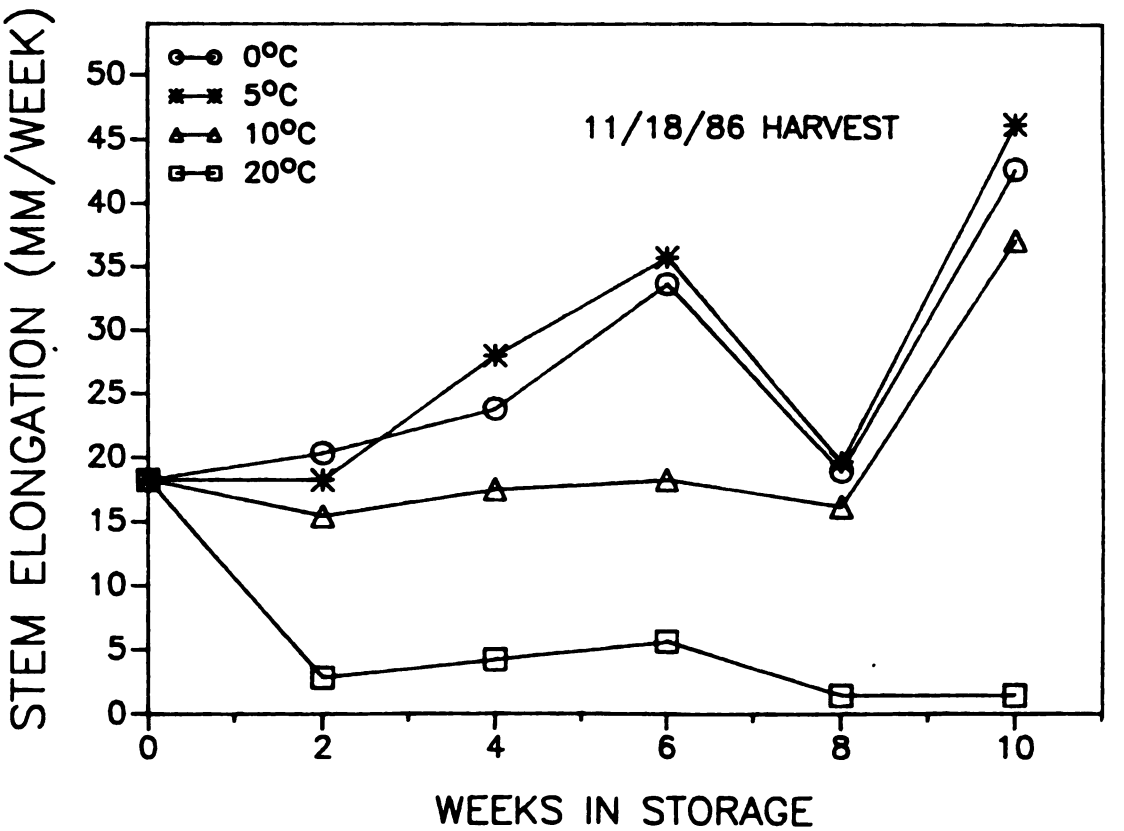
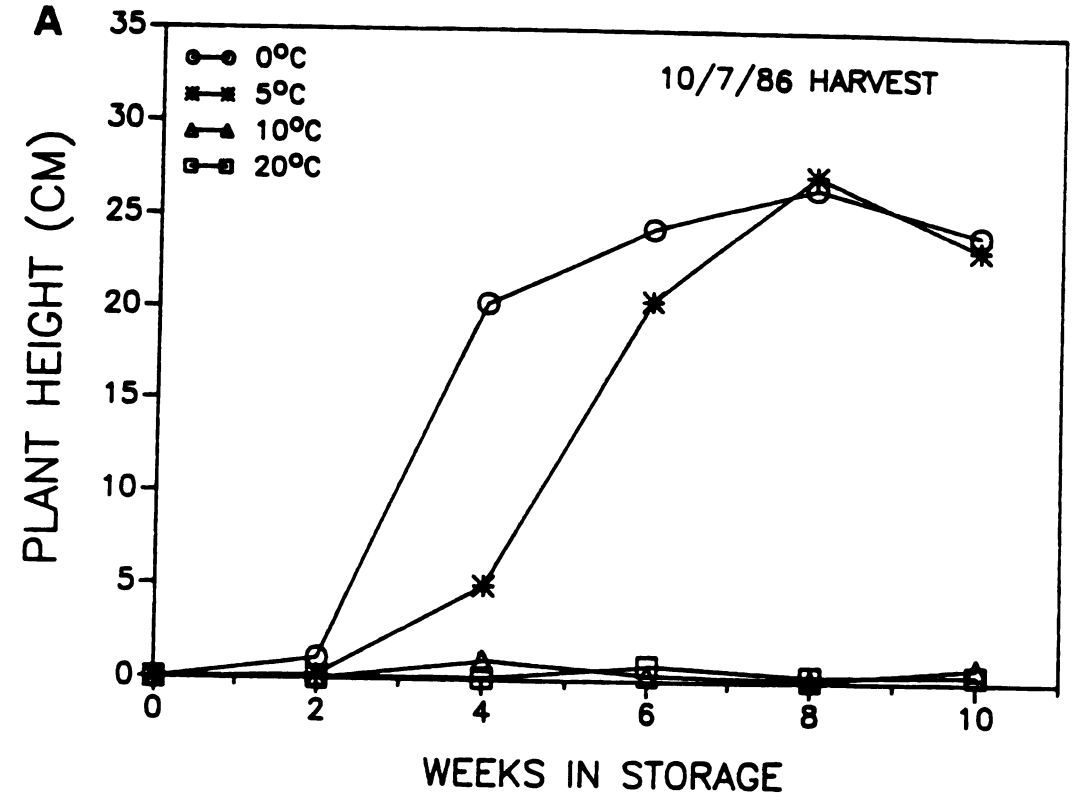

0°C
5°C
10°C
20°C
11/18/86 HARVEST
STEM ELONGATION (MM/WEEK)
WEEKS IN STORAGE
0
5
10
15
20
25
30
35
40
45
50
0
2
4
6
8
10

Figure 4.7. Effect of storage temperature and duration on mean height at 5 weeks post-break of Dicentra spectabilis plants. Means calculated for crowns with at least one broken eye.

A. Crowns harvested October 7, 1986; standard error of the interactions means (n=13) = 1.4 cm.

B. Crowns harvested November 18, 1986; standard error of the interaction means (n=16) = 1.6 cm.


A
0°C
5°C
10°C
20°C
10/7/86 HARVEST
PLANT HEIGHT (CM)
35
30
25
20
15
10
5
0
0
2
4
6
8
10
WEEKS IN STORAGE

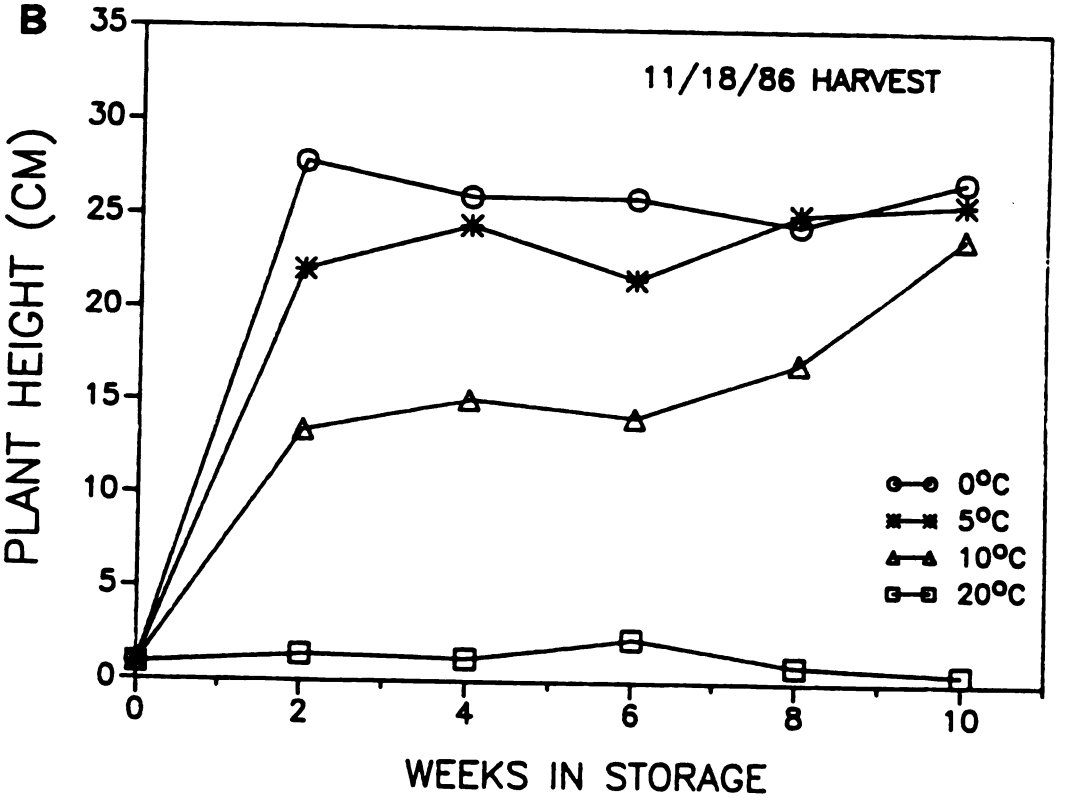
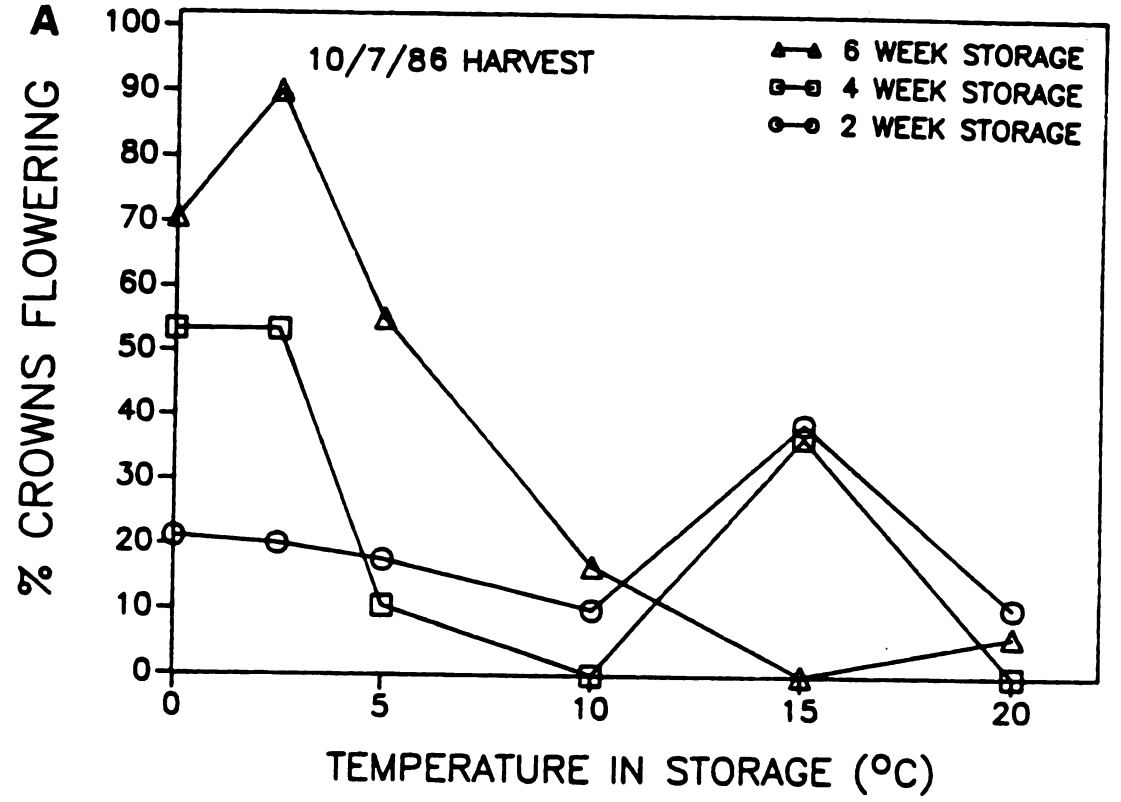

B
11/18/86 HARVEST
PLANT HEIGHT (CM)
35
30
25
20
15
10
5
0
0°C
5°C
10°C
20°C
0
2
4
6
8
10
WEEKS IN STORAGE

Figure 4.8. Effect of storage temperature and duration on flowering of Dicentra spectabilis: percent non-dormant crowns producing at least one expanded flower within 220 days after potting.

A. Crowns harvested October 7, 1986; 20% flowering without storage.

B. Crowns harvested November 18, 1986; 39% flowering without storage.


A
10/7/86 HARVEST
6 WEEK STORAGE
4 WEEK STORAGE
2 WEEK STORAGE
% CROWNS FLOWERING
100
90
80
70
60
50
40
30
20
10
0
0
5
10
15
20
TEMPERATURE IN STORAGE (°C)

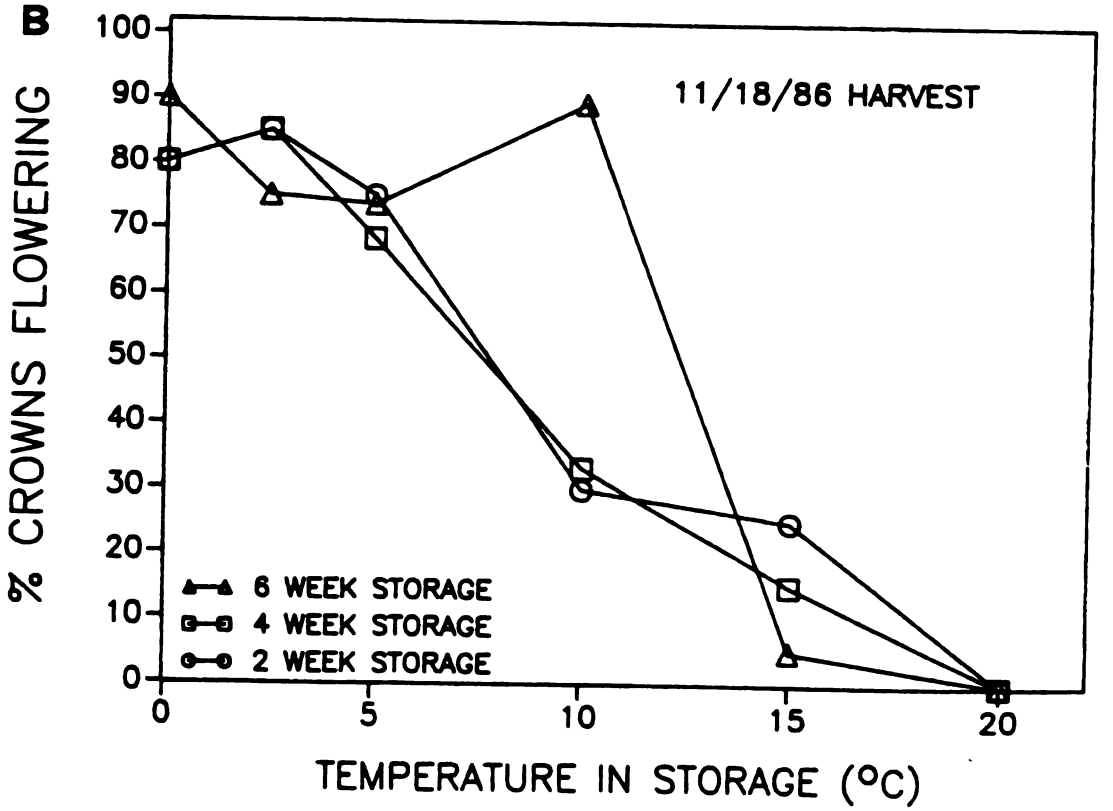
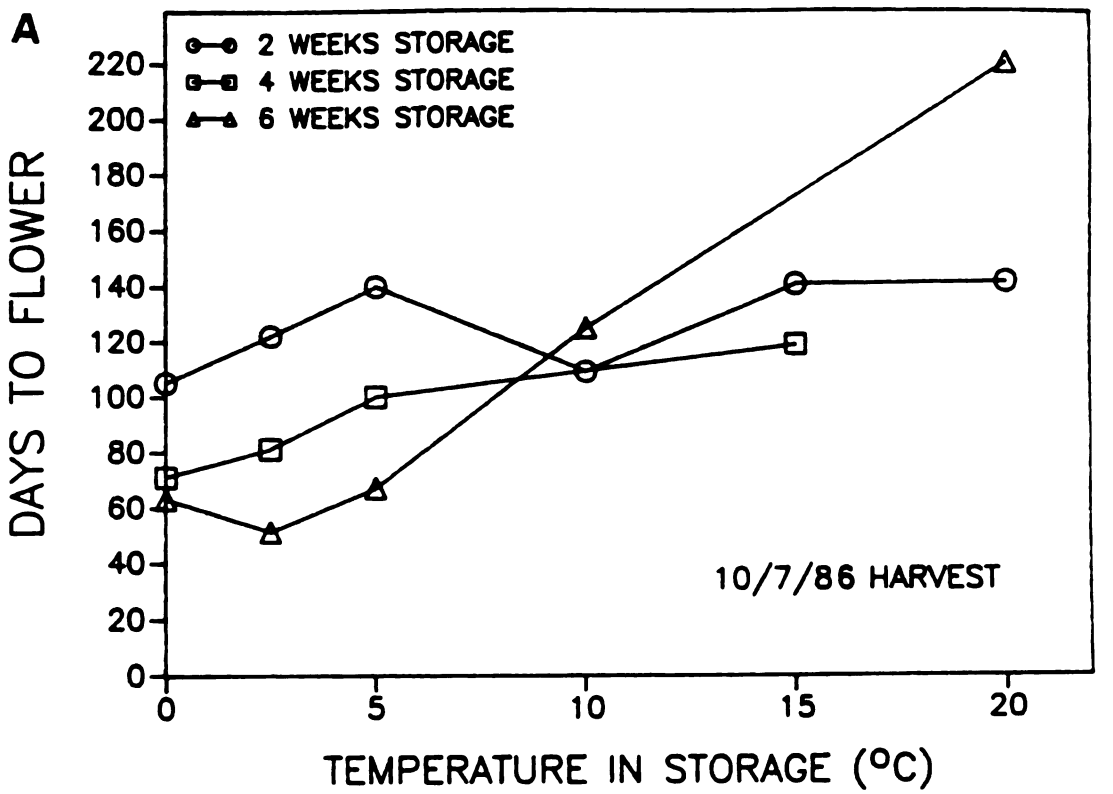

B
11/18/86 HARVEST
6 WEEK STORAGE
4 WEEK STORAGE
2 WEEK STORAGE
% CROWNS FLOWERING
100
90
80
70
60
50
40
30
20
10
0
0
5
10
15
20
TEMPERATURE IN STORAGE (°C)

Figure 4.9. Effect of storage temperature and duration on mean days to flower for Dicentra spectabilis: means calculated for non-dormant crowns producing at least one expanded flower.

A. Crowns harvested October 7, 1986; 139 days to flower without storage.

B. Crowns harvested November 18, 1986; 79 days to flower without storage.


A
2 WEEKS STORAGE
4 WEEKS STORAGE
6 WEEKS STORAGE
DAYS TO FLOWER
0
20
40
60
80
100
120
140
160
180
200
220
10/7/86 HARVEST
0
5
10
15
20
TEMPERATURE IN STORAGE (°C)

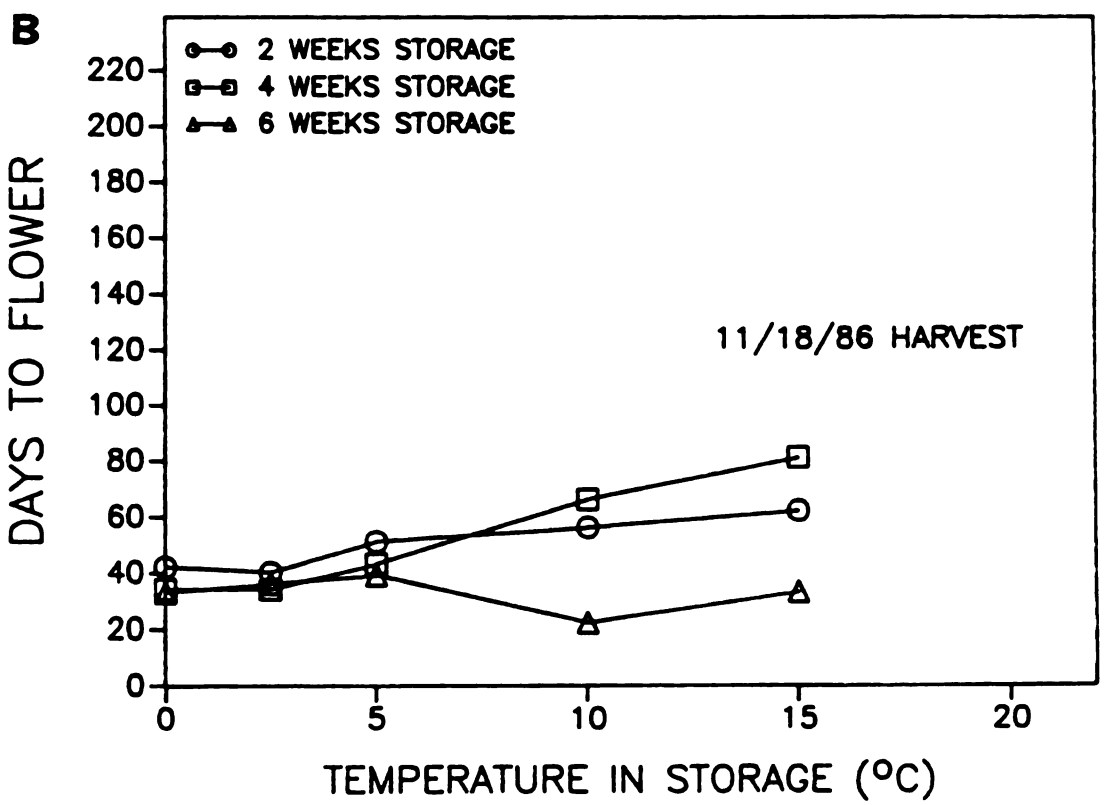
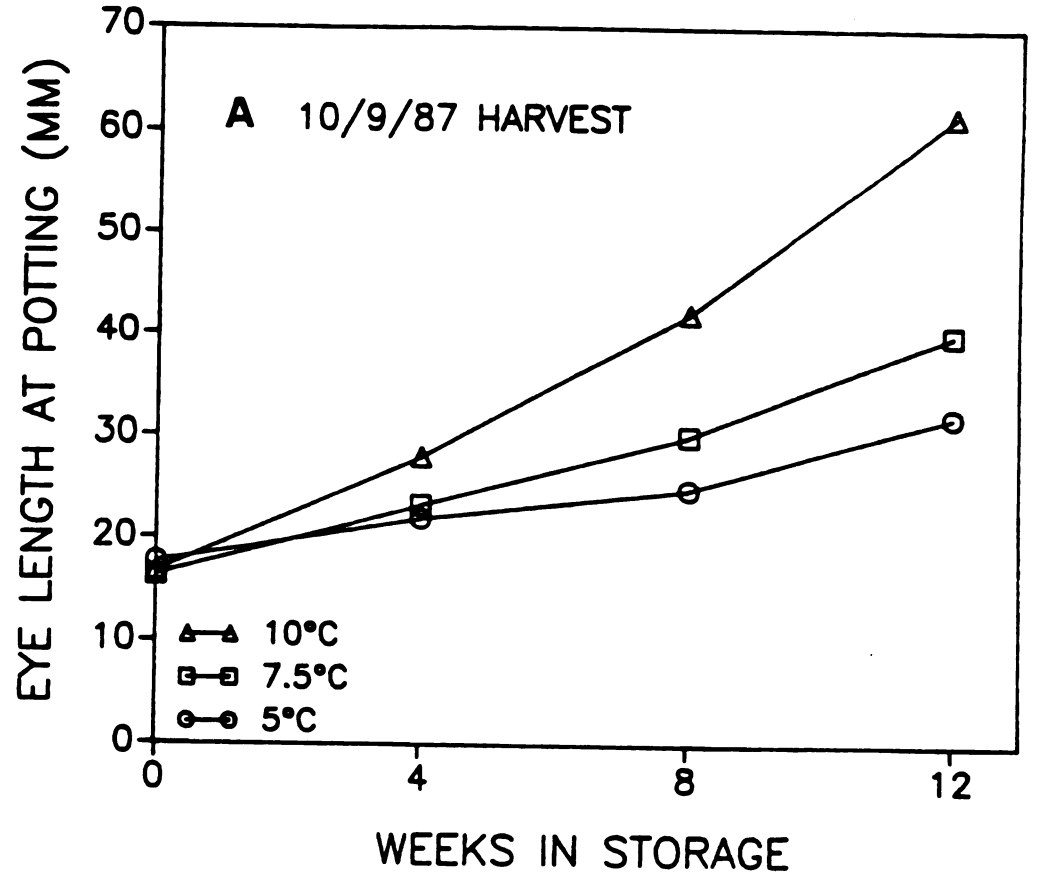
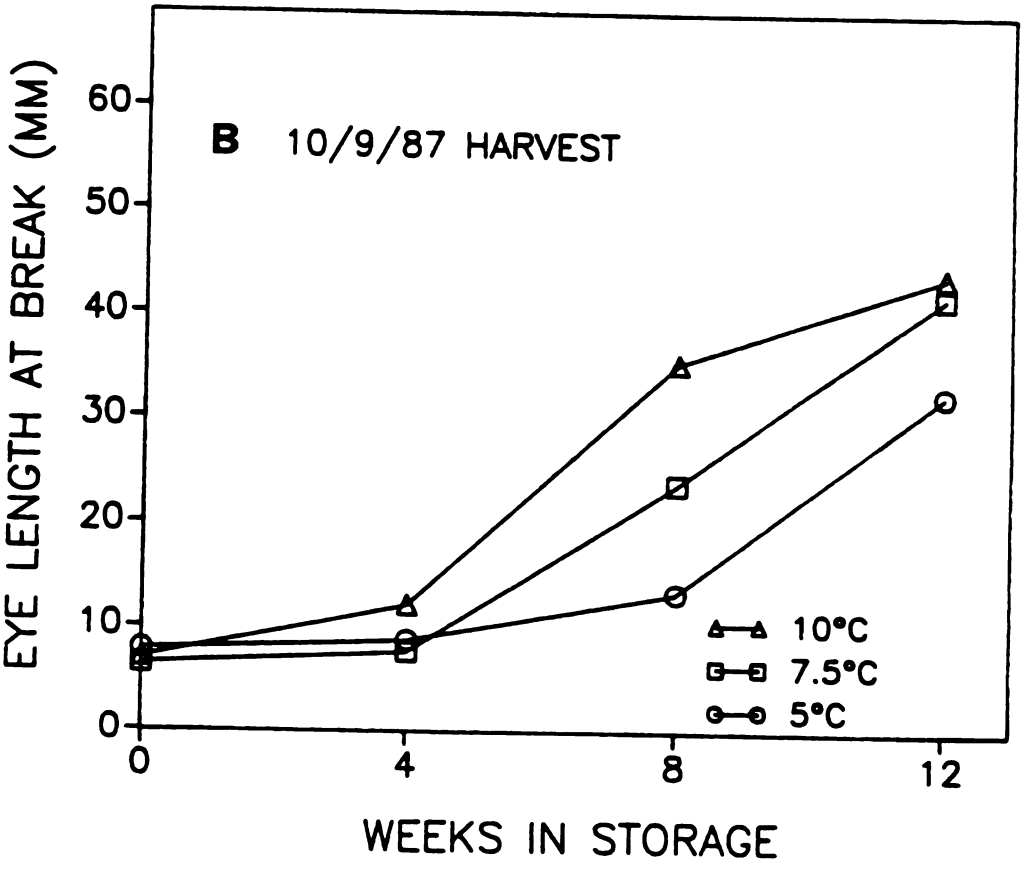

B
2 WEEKS STORAGE
4 WEEKS STORAGE
6 WEEKS STORAGE
DAYS TO FLOWER
0
20
40
60
80
100
120
140
160
180
200
220
11/18/86 HARVEST
0
5
10
15
20
TEMPERATURE IN STORAGE (°C)

Figure 4.10. Effect of storage temperature and duration on mean length of Dicentra spectabilis eyes. Crowns harvested October 9, 1987.

A. Mean eye length at potting; standard error of the interaction means (n=58)=2.1 mm.

B. Mean length at budbreak of first eye to break; standard error of the interaction means (n=14)= 4.3 mm.


A 10/9/87 HARVEST
EYE LENGTH AT POTTING (MM)
70
60
50
40
30
20
10
0
0
4
8
12
WEEKS IN STORAGE
10°C
7.5°C
5°C


B 10/9/87 HARVEST
EYE LENGTH AT BREAK (MM)
60
50
40
30
20
10
0
0
4
8
12
WEEKS IN STORAGE
10°C
7.5°C
5°C

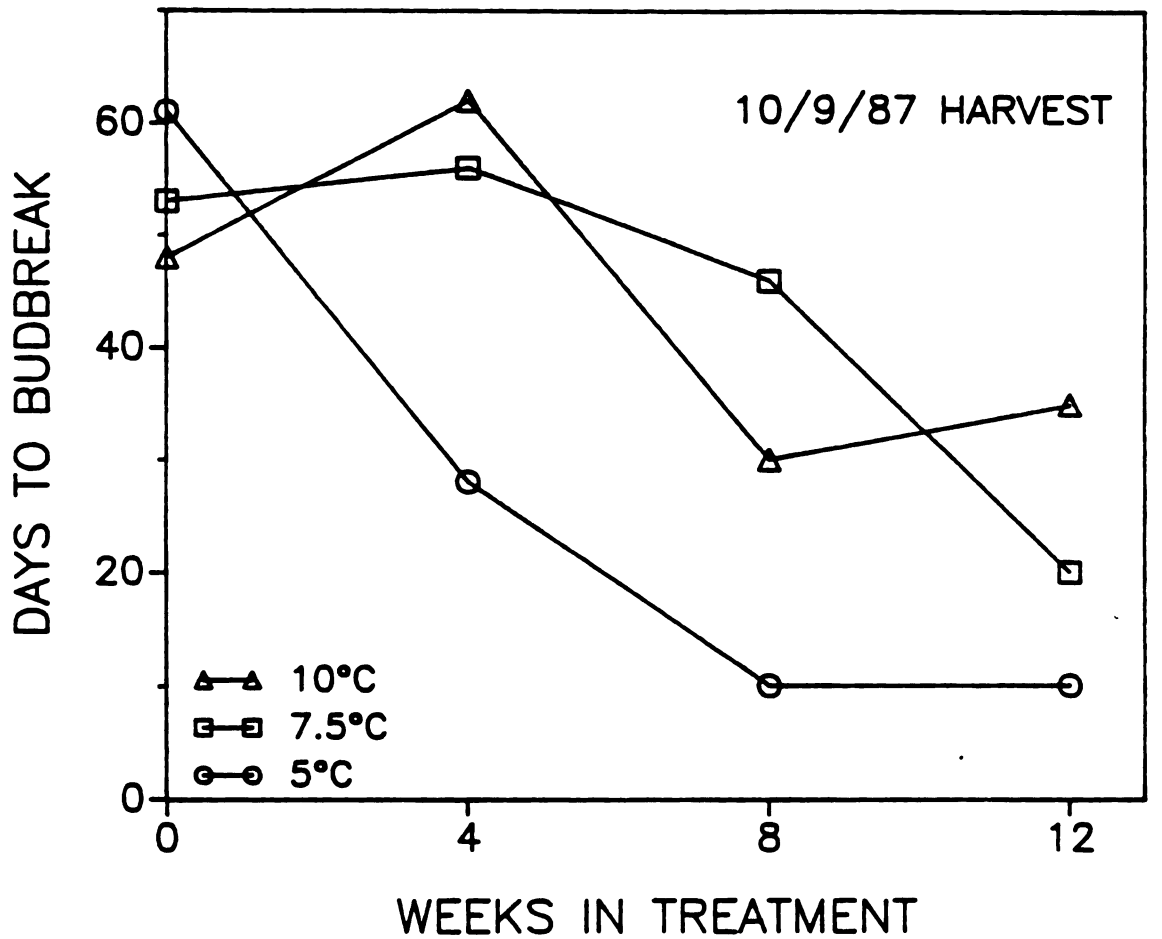


Figure 4.11. Effect of storage temperature and duration on mean days to budbreak for Dicentra spectabilis crowns harvested October 9, 1987. Means calculated for crowns with at least one broken eye; standard error of the interaction means (n=14) = 7.3 days.

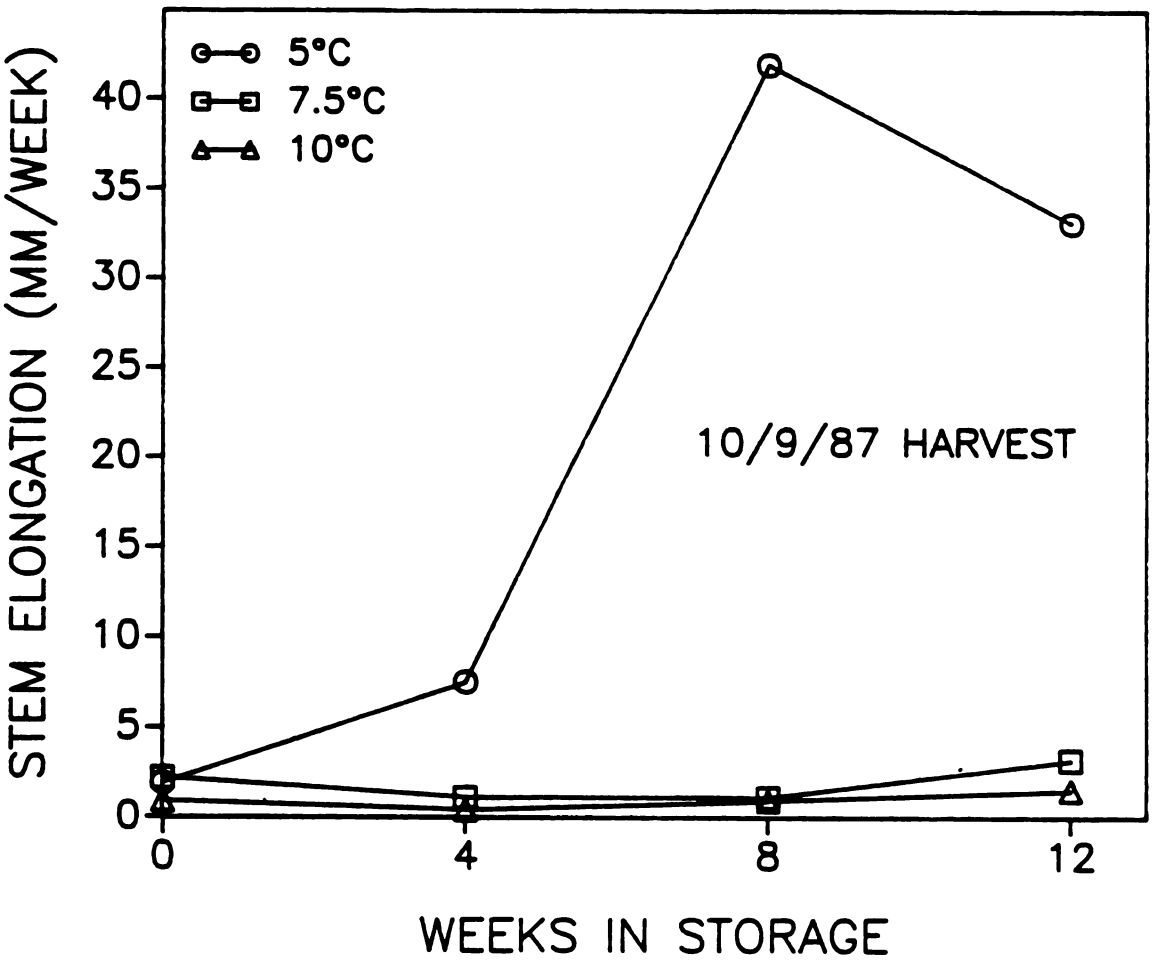
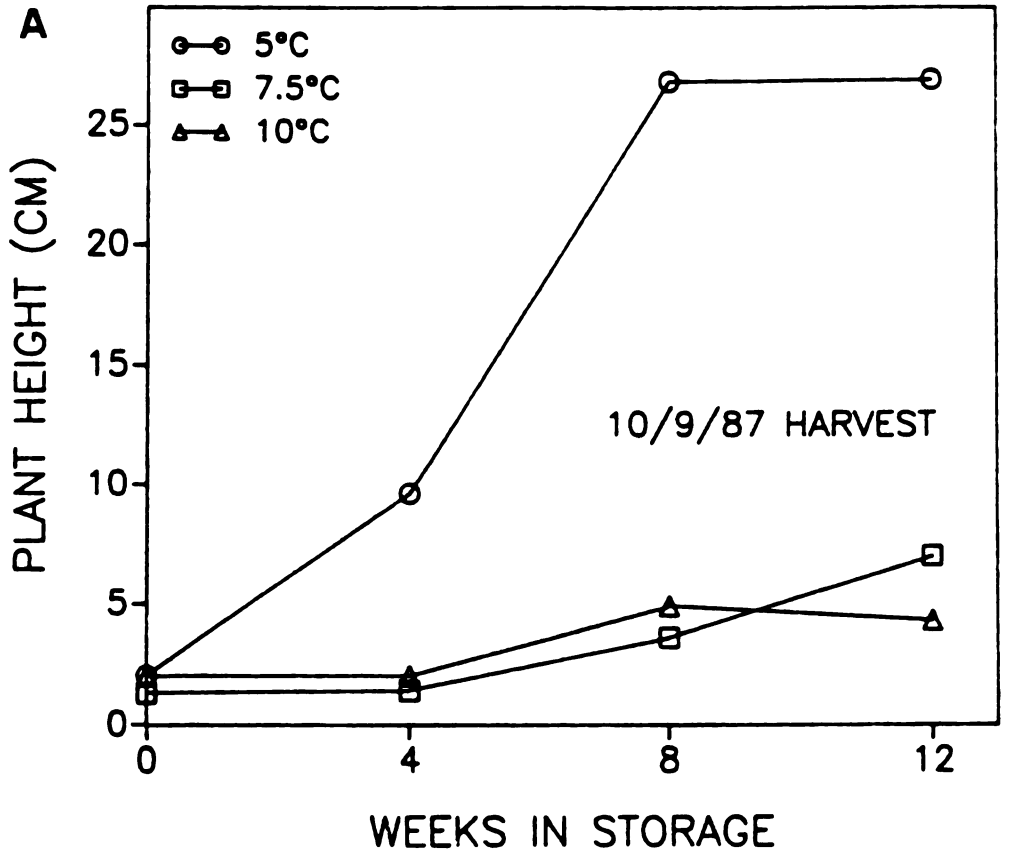


Figure 4.12. Effect of storage temperature and duration on mean rate of stem elongation during the first week of post-break growth of Dicentra spectabilis crowns harvested October 9, 1987. Means calculated for crowns with at least one broken eye; standard error of the interaction means (n=14) = 3.3 mm/week.

Figure 4.13. Effect of storage temperature and duration on regrowth of Dicentra spectabilis crowns harvested October 9, 1987. Means calculated for crowns with at least one broken eye.

A. Mean plant height at 5 weeks post-break; standard error of the interaction means (n=14) = 1.9 cm.

B. Mean regrowth quality at 5 weeks post-break where 0=dead, 0.5=dormant buds, 1=emergent growth, ..5=vigorous growth; standard error of the interaction means (n=14)=0.1.


A
5°C
7.5°C
10°C
PLANT HEIGHT (CM)
25
20
15
10
5
0
10/9/87 HARVEST
0
4
8
12
WEEKS IN STORAGE

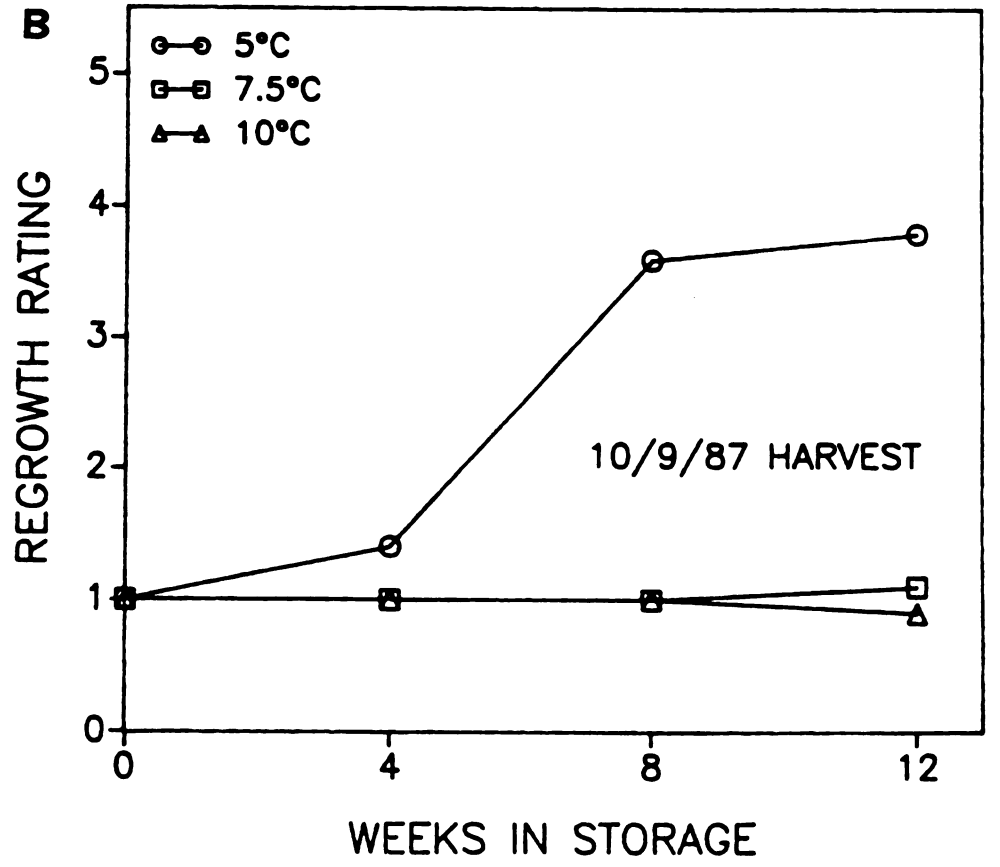
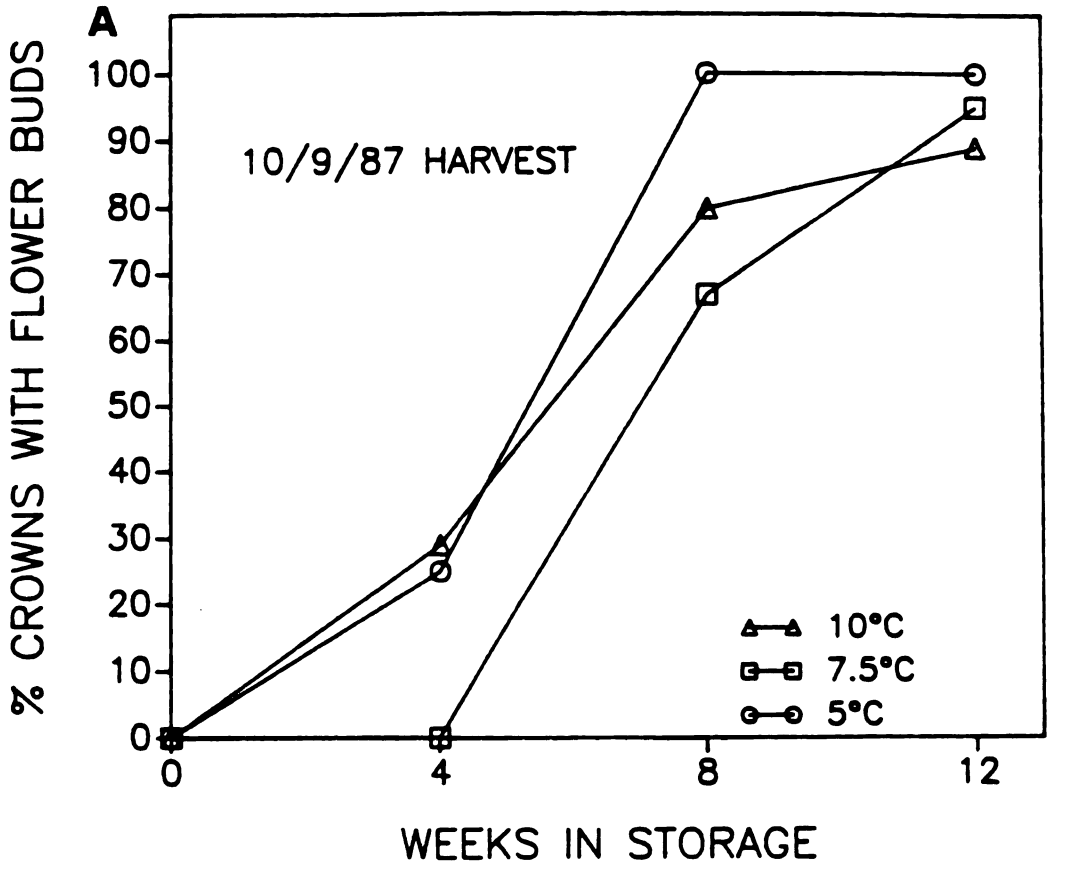
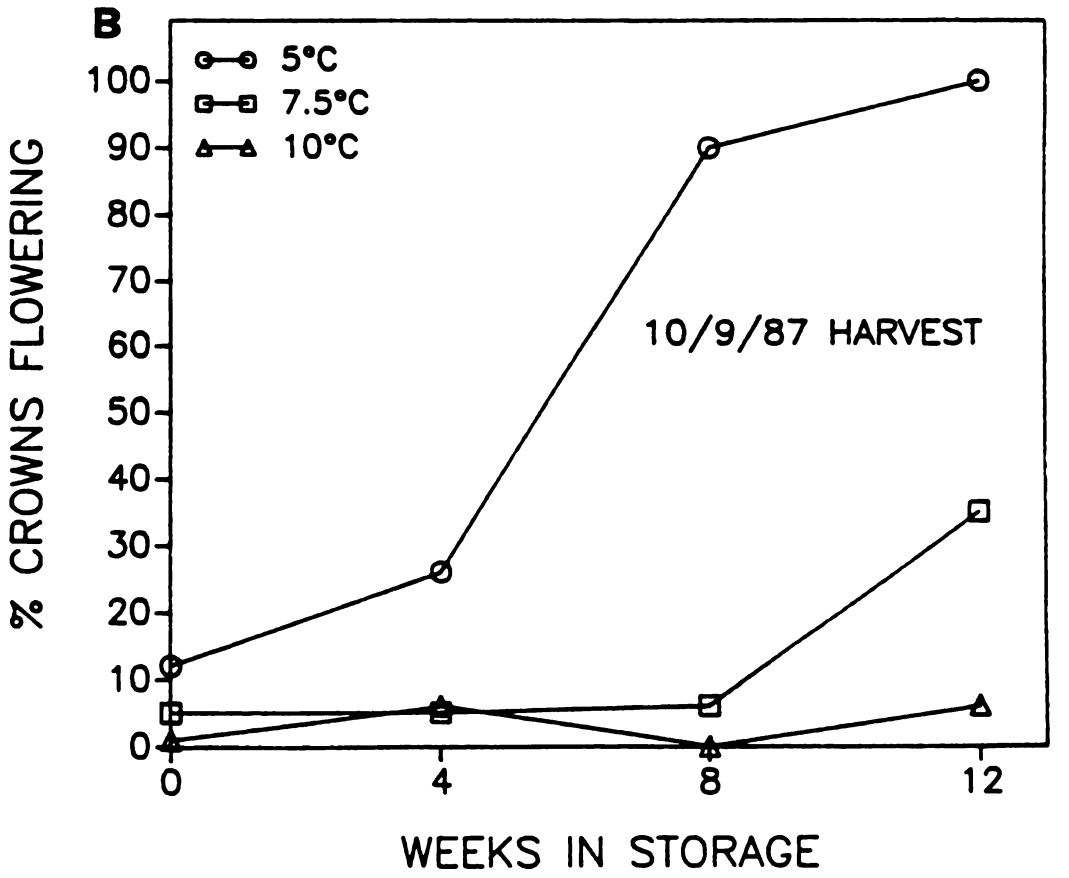

B
5°C
7.5°C
10°C
REGROWTH RATING
5
4
3
2
1
0
10/9/87 HARVEST
0
4
8
12
WEEKS IN STORAGE

Figure 4.14. Effect of storage temperature and duration on flowering of Dicentra spectabilis crowns harvested October 9, 1987. Percentages based on crowns with at least one broken eye.

A. Percent crowns with visible flower buds by 5 weeks post-break.

B. Percent crowns with at least one expanded flower within 180 days of potting.


A
% CROWNS WITH FLOWER BUDS
10/9/87 HARVEST
10°C
7.5°C
5°C
WEEKS IN STORAGE


B
% CROWNS FLOWERING
5°C
7.5°C
10°C
10/9/87 HARVEST
WEEKS IN STORAGE

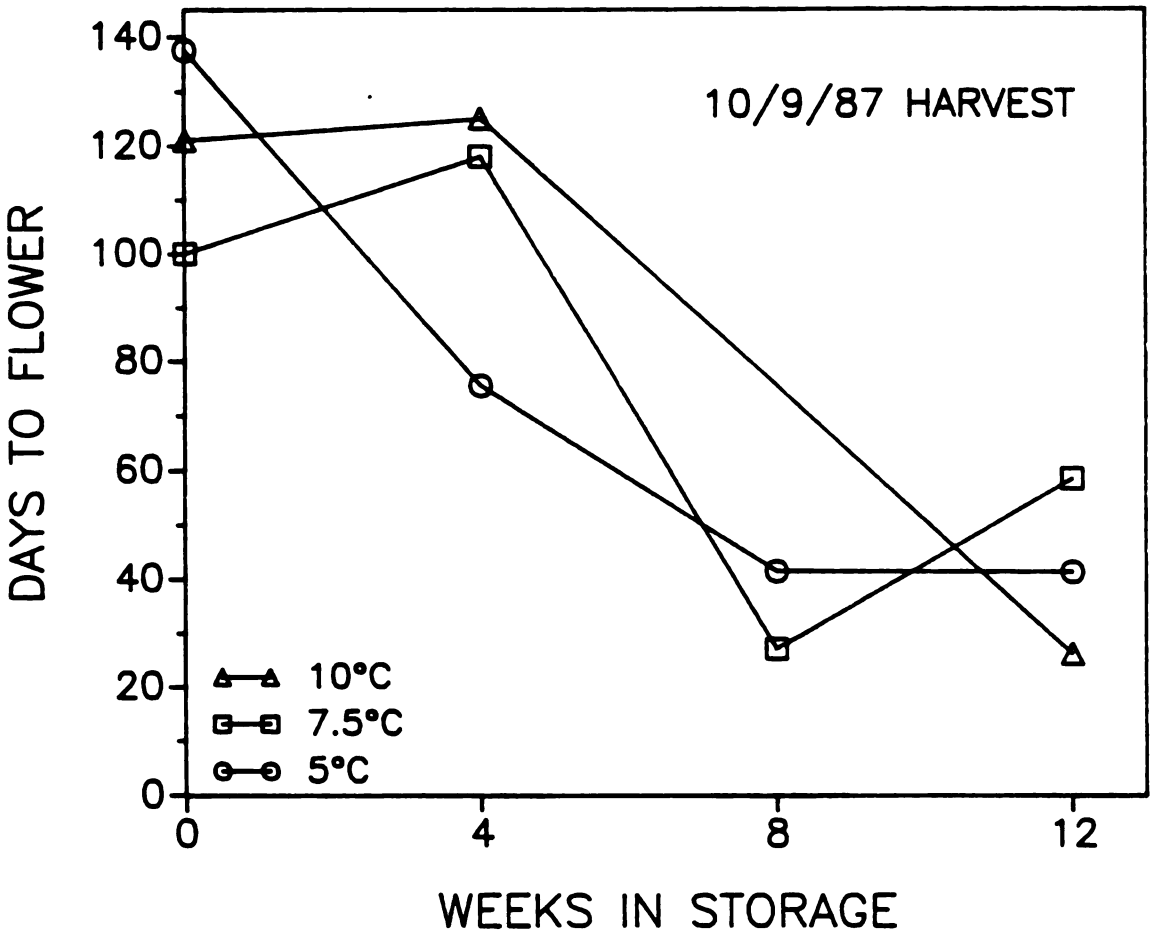


Figure 4.15. Effect of storage temperature and duration on days to flower for <u>Dicentra spectabilis</u> crowns harvested October 9, 1987. Means calculated for crowns with at least one broken eye.

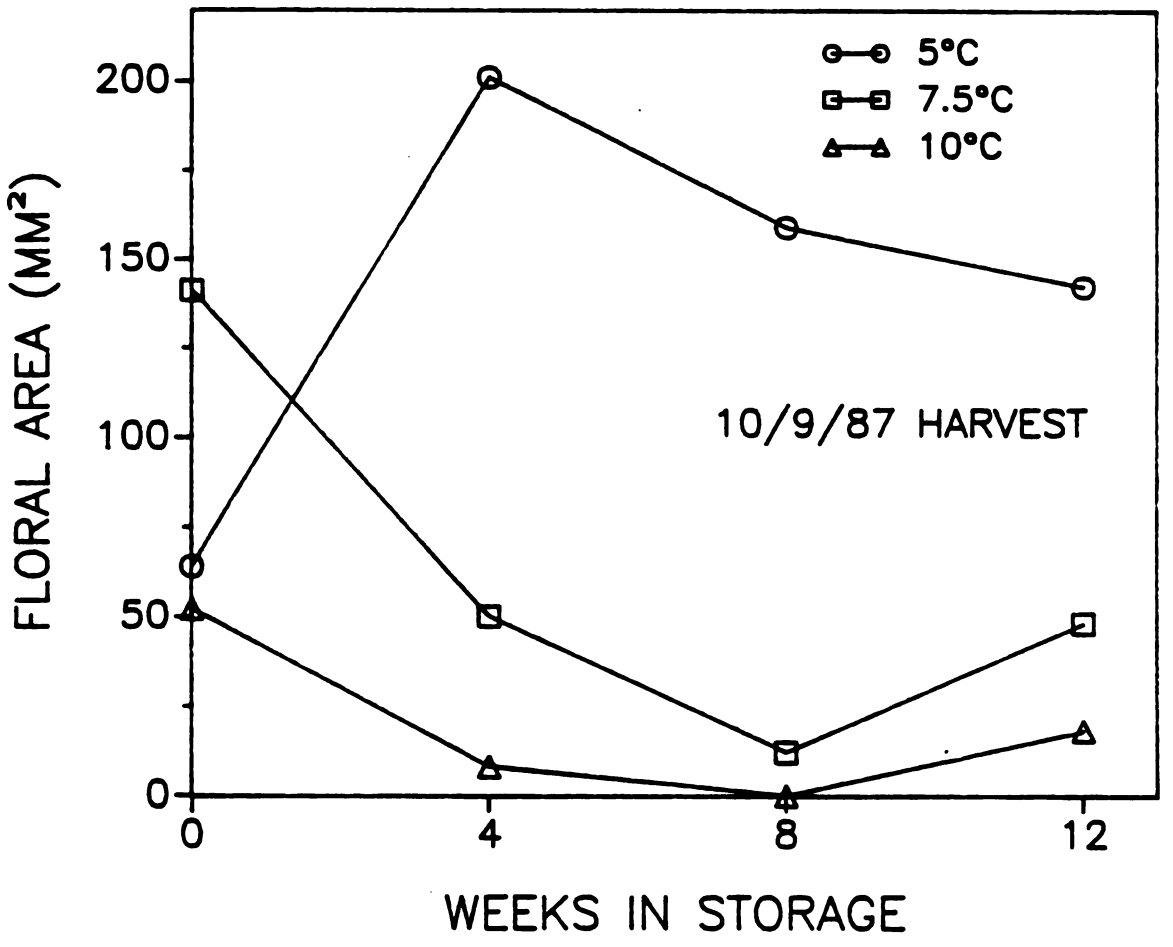


Figure 4.16. Effect of storage temperature and duration on floral production of Dicentra spectabilis crowns harvested October 9, 1987. Means based on crowns with at least one broken eye.

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CHAPTER 5

EFFECT OF TEMPERATURE ON EYE DEVELOPMENT OF *DICENTRA SPECTABILIS*

Chilling is required for rapid budbreak and subsequent stem elongation of fall-harvested *Dicentra spectabilis* when grown under greenhouse conditions. Chilled eyes also flower more quickly and more profusely than non-chilled eyes (Chapters 1,2,4). This implies that chilling promotes floral bud development as well as elongation of the flowering axis but anatomical data for *Dicentra* is lacking. The phenology of floral development during the growth cycle is unknown.

Langhans and Weiler (13) describe four consecutive stages in floral development. During flower initiation, there is a visible transformation of the meristem from vegetative to floral. Differentiation, the formation of the floral parts, follows initiation. During the maturation stage, the floral parts grow and sporogenesis occurs. The final step in flower development is anthesis, the opening of the flower bud.

In plants requiring vernalization, cold treatment induces the initiation of flower primordia (5). Initiation itself takes place after transfer to growing conditions. Many biennials and perennials require vernalization to

flower including lily (13), but many do not. Anatomical examination of tulip, narcissus, and hyacinth has shown that the meristem is never developmentally at rest (9).

Floral organogenesis in bulbs begins soon after flowering ends in spring and continues through subsequent warm and cold periods experienced in the field or in commercial handling. Flower formation itself is completed in several months under normal conditions (16).

Bryne and Halevy (3) have demonstrated similar floral phenology in herbaceous peony. Other plants such as bulbous iris (16), strawberry (1,12), and many woody perennials initiate floral primordia with the onset of cool fall temperatures and complete flower formation during chilling.

The purpose of this study was to examine floral development in Dicentra spectabilis at the anatomical level in relation to constant temperature.

MATERIALS AND METHODS

One year-old crowns of Dicentra spectabilis (L.) Lem. were harvested from southwestern Michigan fields (DeGroot Nurseries, Coloma, MI, on October 9, 1987. At harvest, ten field soil temperatures at 10 cm depth were measured. Records of soil temperatures were also obtained from the Trevor Nichols Experimental Farm, Fennville, MI (15). Crowns were harvested one week after minimum soil temperatures dropped below 10C. Loose soil was removed by shaking and any green material was trimmed, leaving the eyes intact. The crowns

were packed in a moistened 1:1 peat:perlite mixture in polyethylene-lined crates to avoid desiccation stress (4) and simulate *in situ* chilling, and held for 0, 4, 8, or 12 weeks at 5, 7.5, or 10C. Five crowns were sampled per treatment.

Fresh sections were cut freehand from several excised eyes from each crown and from roots of 5 mm diameter or more. Tissues were stained with aqueous solutions of safranin, fast green, aniline blue, and potassium iodide (10,11). Plant organs were examined using an Olympus zoom stereo microscope which allowed examination of structures too large for a dual objective microscope and too small for a standard stereoscope. Magnification ranged from 7.5X to 64X. The automatic photomicrographic system and variable illumination by three light sources provided a photographic record of perishable fresh sections.

RESULTS

Dicentra roots over 5 mm in diameter exhibited well-defined secondary growth (Figure 5.2a). Primary vascular elements were still present in these 6 month old tuberous roots although secondary xylem and phloem were well developed. Roots began to slough the papery brown cortex after 4 weeks at all temperatures, leaving behind smooth, white periderm. No other changes were observed in basic root morphology as crowns were chilled, except in staining. As storage was prolonged, root sections did not seem to

stain as darkly with potassium iodide. Starch content in the roots may have decreased over time as has been observed in strawberry (2).

Cross sections near the base of the eye contained widely spaced vascular bundles with little evidence of secondary growth (Figure 5.2b). Many small adventitious roots were noted in this area of junction between stem and rootstock. The eye itself (Figure 5.2c) was identified as an overwintering structure of scales that tightly enclosed primary and secondary buds (Figure 5.3). Vegetative meristems were dome-shaped and surrounded by 3 to 5 pairs of young leaves (Figure 5.2d).

A marked change in meristem shape from domed to pointed was associated with flower bud initiation (Figure 5.4a). With time, more leaves were formed around the dome and the meristem elongated into a spike bearing floral primordia (Figure 5.4b). At temperatures of 7.5 and 10C, many floral primordia developed in the highly etiolated eyes while the number of leaf primordia decreased. Elongation of the eye without opening of bud scales occurred as cortical and vascular cells in the central and basal regions lengthened. Some necrosis and disease in the etiolated tips was noted, reminiscent of tulip bud necrosis (6,7).

At 5C, eyes retained their integrity, presenting a firm and healthy appearance. Floral development was accompanied by leaf development and was less rapid than at 7.5 or 10C

(Table 5.1). Flower buds were first noted at 10C after 4 weeks of exposure, but only after 8 weeks at 5C.

DISCUSSION

Although early-harvested, unchilled *D. spectabilis* appeared to be endodormant, the eyes were undergoing major developmental changes. These changes involved cell elongation, meristem differentiation, and increasing vascular complexity, as well as previously demonstrated physiological modifications (Chapters 1,2,4).

Crowns clearly did not require vernalization to induce flowering. Initiation of floral meristems occurred at 5C but development was more rapid at 7.5 and 10C, temperatures which do not satisfy the chilling requirement for stem elongation (Chapter 4). In fact, Lopes (14) found that chilling at 5C inhibited flower initiation in plants kept vegetative by constant pinching.

Despite rapid floral organogenesis, warmer temperatures did not promote successful flowering of *Dicentra spectabilis* since flower axes were not able to elongate (Chapter 4, Figure 4.12). The result of these opposing factors was the occasional dwarfed plant with one expanded flower and essentially no leaves or stems, or a vigorous plant with a few aborted buds but no flowers.

TABLE 5.1. Effect of storage temperature and duration on percent of Dicentra crowns with floral buds as observed in fresh sections at 7.5 to 64x magnification. 5 crowns per treatment. No floral buds were observed at 0 weeks.

STORAGE TEMPERATURE	WEEKS IN STORAGE 4	8	12
5C	0	40	--
7.5	0	80	100
10	20	100	100

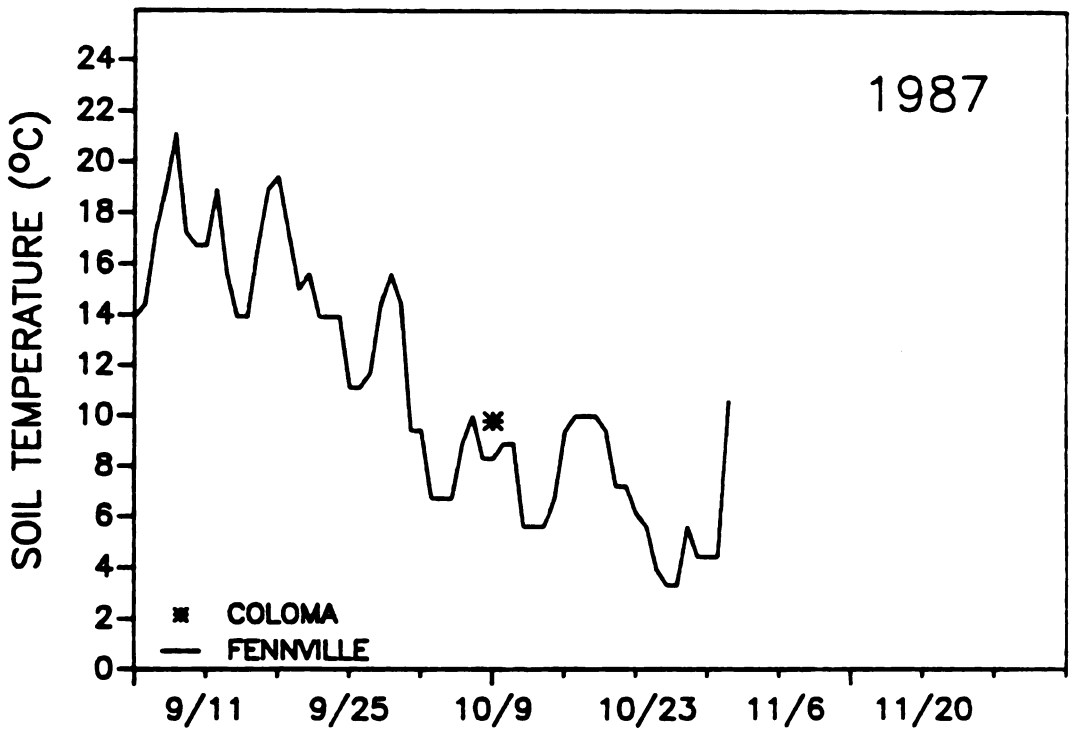


Figure 5.1. Minimum daily soil temperatures at 10 cm depth at Trevor Nichols Experimental Farm, Fennville, MI, and average soil temperature at 10 cm depth at 10:00 am in *Dicentra spectabilis* field in 1987 in Coloma, MI. Coloma SE=0.1.

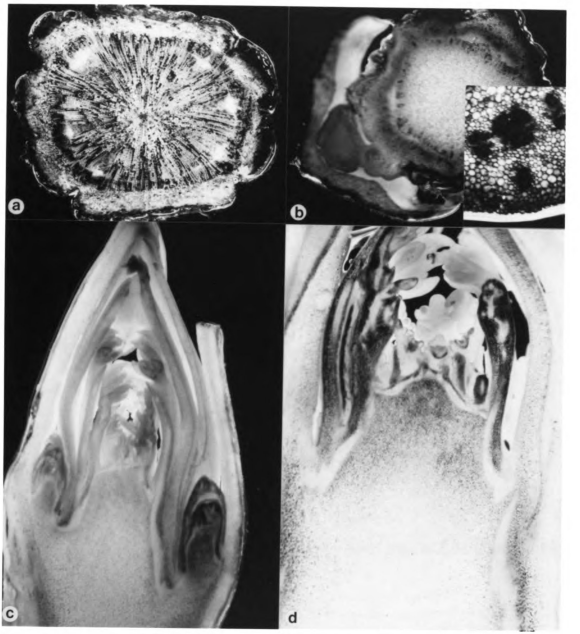
Figure 5.2. Vegetative anatomy of fall-harvested *Dicentra spectabilis*.

A. Root, cs.

B. Base of eye, cs.

C. Vegetative eye, ls.

D. Vegetative meristem, ls.


a
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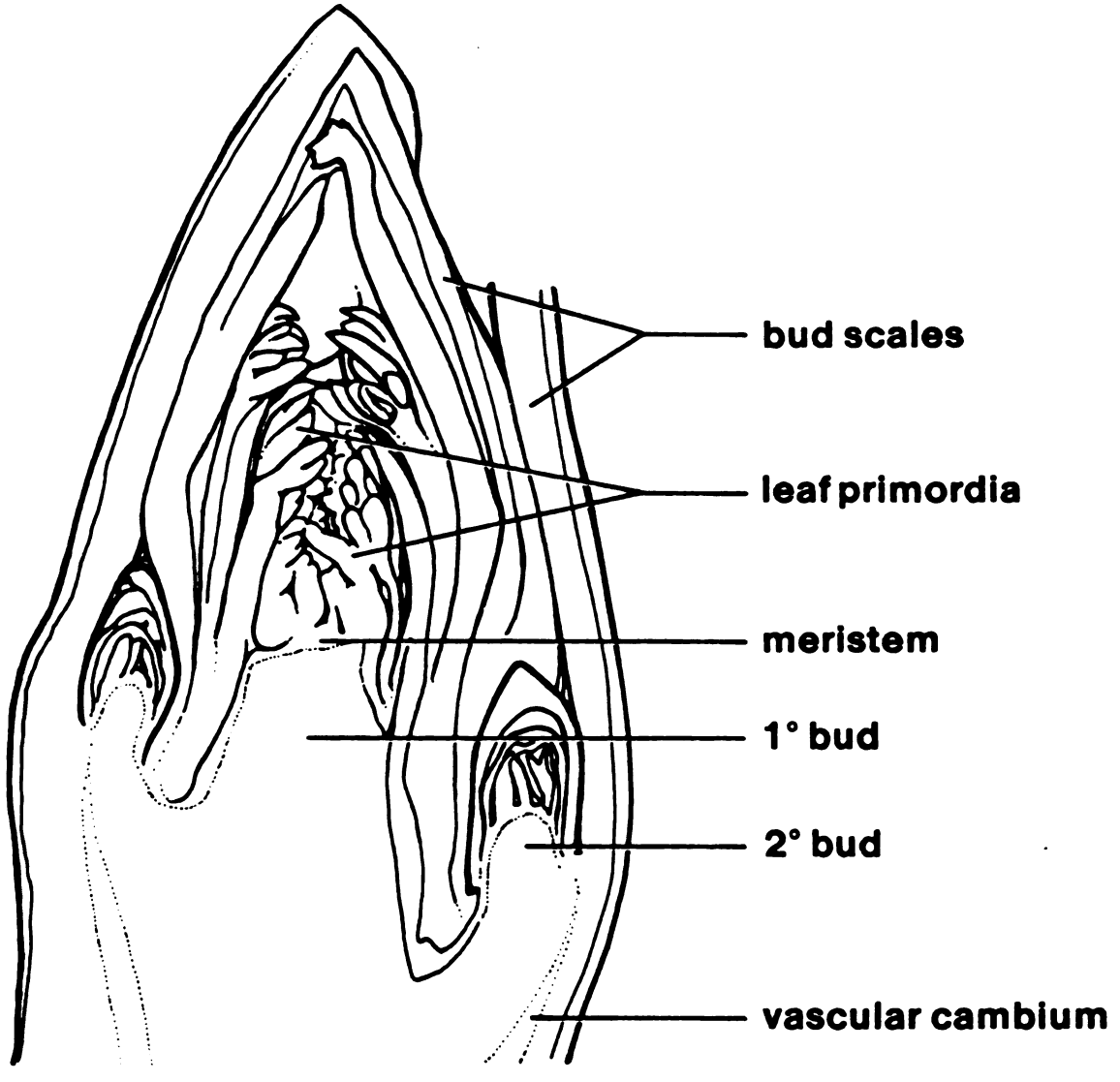


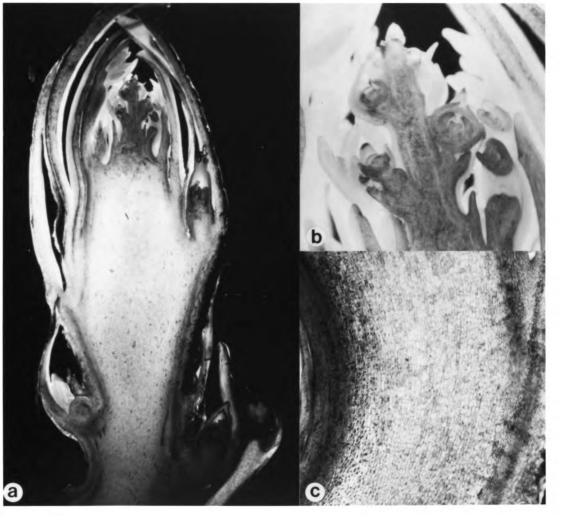
Figure 5.3. The eye of Dicentra spectabilis.

Figure 5.4. Anatomy of floral eyes of Dicentra spectabilis.

A. Floral eye, ls.

B. Floral meristem, ls.

C. Zone of elongation in floral eye, ls.


a
b
c

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SUMMARY

Each of four separate growth responses in Dicentra spectabilis--eye etiolation, budbreak, stem elongation, and flowering--had a different time/temperature requirement as summarized in Chapter 4. Stem elongation, for example, was promoted by 4 weeks of storage at temperatures of 5C or less. Below the "chilling threshold", the rate of subsequent elongation was dependent upon temperature and length of exposure. Above some critical temperature between 5 and 7.5C, there was no promotion of stem elongation but, rather, promotion of eye etiolation.

This work did not test hypotheses of mechanism, but a few can be suggested as bases for future physiological studies of Dicentra and bud dormancy. The quantitative response to chilling at $\leq$5C could be due to temperature-dependent sythesis/metabolism of a growth promoter/inhibitor such as gibberellin or other plant growth regulators. The important reaction could also be one involving conversion of respiratory substrates or their distribution through the phloem in the developing stem. The lag time of 4 weeks may be necessary to build up sufficient quantities of the substance or its precursor before transfer to growing conditions.

More unusual is the sharp change in response at the chilling threshold, reminiscient of sudden injury in chilling sensitive tissues. This on/off response to temperature by Dicentra could depend on a change in membrane structure or protein conformation, which could then promote or prohibit the quantitative response of stem elongation. Perhaps this same mechanism could also control the promotion of eye etiolation, acting as an input/output logic gate, returning one answer for temperatures below the threshold and another for temperatures above it.

Obviously, a great deal of research needs to done in order to test these hypotheses. The current work serves to characterize the chilling requirements and demonstrate that Dicentra spectabilis could prove an excellent subject for further basic research on dormancy and growth of perennial plants.