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Title: The Influence of Air and Soil Temperatures on the Growth and Development of Easter Lily, Lilium longiflorum, During Different Growth Phases

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Greenhouse-grown, September-harvested Lilium longiflorum cv. 'Nellie white' bulbs were used to determine temperature requirements during 5 pre-bloom and 1 post-bloom phases of development each of 1 month's duration. Plantes were subjected to 3 air temperatures(24°day/ 18°C night, 18°/13° and 13°/10°) in combination with soil temperatures at 30°, 24°, and equal to or lower than ambient air temperature during each growth phase and evaluated by growth analysis at the termination of each phase.

This study has substantiated that top growth needs high air temperature and daughter scale initiation and filling require high soil temperature. An air and soil temperature of 24°C was required for rapid flowering, leaf unfolding and stem elongation but at the expense of reserves in mother scales. Air temperature approaching 18°/13° during the month prior to anthesis favored maintenance of mother scales. Growth of daughter scales during the pre-bloom period was directly related to soil temperature rather than air tem-

perature with 30° soil temperature being no better than 24°. Soil temperature had no effect on flower bud expansion after buds-visible stage, air temperature being the determining factor thereafter. Growth of the flower bud, leaf unfolding rate or stem elongation were of equal value in monitoring crop growth rate and status.

Soil temperatures approaching 24°C favored scale primordia initiation, regardless of air temperature. Daughter meristem diameter, as well as the rate of scale primordia initiation decreased progressively from daughter bulb appearance toward anthesis of the mother axis. High soil temperatures also reduced daughter bulb apex diameter during early growth phases.

Since prevailing air and soil temperatures in the commercial lily growing sites are below those required for maximum growth and development of above- and below-ground organs during the pre-bloom period, it is concluded that air temperatures alone are adequate in monitoring field crop status and predicting ultimate yield potential during this period.

THE INFLUENCE OF AIR AND SOIL TEMPERATURES ON THE GROWTH AND DEVELOPMENT OF EASTER LILY, LILIUM LONGIFLORUM, DURING DIFFERENT GROWTH PHASES

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INTRODUCTION

In the Pacific Coast Area of Easter lily production(Curry county, Oregon and Del Norte county, California), commercial bulbs are harvested from mid-September to mid-October. Stem bulblets and yearling bulbs are harvested somewhat earlier for replanting in September and October to provide the next season's crop.

Warm growing seasons with above average air temperatures in this area have been associated with large crops and increased bulb size(79). The outstanding bulb harvest in 1966, following a warm spring(April to June), is remembered as "the year of the 'Ace'". A similar season in 1978 may well be called "the year of the 'Nellie White'". There are subtle, seasonal differences that sometimes favor one or the other of these commercial cultivars over the other, and it appears that Nellie White has the lower temperature requirements.

A warm weather cycle begining in 1977 has apparently continued through the 1979 and 1980 seasons with above average lily yields along the coast(81). In contrast, the very poor lily crops in 1964, 1971 and to some degree in 1975, appear to be associated with below average growing temperature. Furthermore, a pattern of warm winter(January to March) temperature followed by cool spring temperature is conducive to "summer sprouting", or the premature elongation of the daughter bulb axis(3,76).

Bulbs are usually planted 15 cm deep for winter protection. The temperature below ground varies from year to year, but not as much as

the air temperature. The lowest soil temperatures occur in December and January with little difference between the two months. The soil temperature increases to a peak in July and then cools down at a steady rate depending on air temperature and prevalence of fog. Comparing soil temperatures taken at the Pacific Bulb Growers' Research and Development Station, Harbor, Oregon during 1976 and 1977, it was found that the soil temperature at 15 cm depth was 5°C lower in February and 3.5° lower in July of 1976 than in 1977.

Newly developing storage organs, such as bulbs in lily and tulip, tubers in potato and corms in gladiolus, are capable of mobilizing carbohydrates from source sites of the plant, storage organ and leaves, and storing them as reserves(4,40,41). After replanting, the original sink organs become sources in supplying the carbohydrate demands of the newly expanding shoots(4,39,40).

Growth and development of the Easter lily plant can be divided into 3 major periods. 1). PRE- EMERGENCE: from planting in October to shoot emergence in late December or early January. The outer mother scales lose reserves to the mother axis as it elongates off the basal plate after replanting. The shoot apex continues to initiate leaf primordia until flower induction occurs near the end of this period (4). The first scales of the new daughter bulb are also initiated during the later part of this period. 4).PRE-BLOOM: from mother axis emergence to anthesis in late June or July. This above-ground axis keeps elongating and unfolding leaves while at the same time initiating and developing its flowers. The outer mother scales supply substrates to the expanding leaf canopy until such time that the canopy itself becomes self sufficient, after which the filling of

inner mother scales is continued. The daughter bulb meristem continues to initiate and fill scale primordia during this period. Since the mother and daughter axis are both utilizing reserves from mohter scales, they are competitive. 3). POST-BLOOM: from anthesis to bulb harvest in mid-September to mid-October. Daughter bulb apical meristem shifts from scale to leaf primordia initiation at the begining of this period. Both daughter and mother scale filling are at maximum during this period.

Both air and soil temperatures appear to influence sink strength in both above- and below-groung organs(9,11,31,46). Different organs may have different temperature requirements for maximum growth(99). Even for the same organ(24) temperature requirement could change with progressive development. Warm winters are conducive to early daughter bulb initiation and warm winters and springs favor early flowering. In 1979, the warm spring and summer temperatures resulted in above average lily bulb size, with more daughter scales and correspondingly fewer daughter leaf primordia at harvest. Soil temperatures which are warmer than air temperature during most of the growing season may influence some features of bulb development more than air temperature and air/soil temperature interactions may be crucial.

A previous growth chamber study showed the Easter lily plant to be very responsive to temperature increases during the pre-bloom period. However, soil temperatures were not considered in the study, and the pre-bloom period was materially shortened in the greenhouse stock plants used making it difficult to relate their temperature responses to field conditions.

The purpose of this study was to determine the influence of

various air and soil temperature regimes on the initiation(scales, leaves and flowers), expansion(stem, leaves and flowers), and filling (bulbing) of various above- and below-ground organs during specific phases of plant growth and development. This information would invaluable in monitoring crop growth and development, predicting bulb yield and maturity, and developing a model of lily plant growth/climate interactions.

LITERATURE REVIEW

Temperature effects on sinks

When rooted leaves of Phaseolus vulgaris and P. multiflora were transferred from warm(20°C) to cool(13°) root temperature with leaves held at the same air temperature sugars and starch accumulated in the lamina(46). Starch in the lamina decreased when roots were warm(20°), but increased when roots were cool(13°). Leaf starch content was sensitive to root temperature since warmer roots resulted in faster photosynthates translocation from the leaves. At high root temperature lamina also contained more water than when held at cool temperature. On basis of percent dry weight, root sugar was similar at both temperatures. This suggested that sugar utilization in roots or sink was controlled by root temperature and this in turn was reflected in leaf composition. The conversion of starch to sucrose in storage organs, such as potato tubers(48) and tulip bulbs(18) during low temperature could be the result of starch conversion as reported by Pressey and Shaw(71), who found that sugar accumulated in potato tubers exposed to low temperature as a result of increased invertase activity.

With the same air temperature, Nelson(68) found that the fresh weight, leaf area and water used by cotton seedlings decreased with a decreased soil temperature from 24°C to 12°. Carnation plants grown at soil temperatures of 21° and 31° produced better quality cut flowers than those at 18°(49). High soil temperature early in growing season, as a result of burning and mowing, increased the productivity of tall grass prairie(75). Spence and Humphries(88) used isolated, rooted

leaves of sweet potato to study the effects of root temperature on photosynthesis and found that 25° was the optimum temperature for tubering under their conditions.

Walker and Ho(99), using 25°C as a reference, found that carbon import by a tomato fruit was diminished by fruit cooling to 5° and enhanced by fruit warming to 30°. The carbon translocation rate are related linearly to the sucrose concentration in the sink, in this case the fruit. The rate of carbon import declined as the concentration of sucrose in the fruit increased and at a mean sucrose concentration of about 0.27% of the fresh weight import ceased. Moorby et al.(65) has found that lowering sink temperature decreased the rate of carbon translocation as has been observed in a number of other species such as Pisum sativa(56) and sugar beet(27). Pea pods maintained at 30° mobilized more ^{14}C-assimilates from source leaves than these at 20° and 10°(116). At higher temperature(35°) sucrose and starch reserves are catalyzed to hexose probably supporting the demand for hexose with enhanced respiration.

Gray(30) found that the weight of Easter lily scale bulblets formed at 22°C were significantly greater than those formed at 12° and without further increase at 27°. This indicates that 22° is near optimum for scale bulblet formation, mobilizing carbohydrates from mother scale source and transforming those into structural materials. The temperature optimum for bulbing in onion is also in the range of 20°-25°(12).

Sultana grape vines which produced more flowers per inflorescence, set more fruits, and developed greater shoot fresh weight, root dry weight and shoots per root at higher root temperature(117).

There was a progressive decrease in root weight of rose plants as the soil temperature increased from 11.3° to 22.2°C(84). Soil temperature of 21° to 30° did not increase flower production in rose(26), and flower production was significantly less at 30° soil temperature. Garden peas were most productive at soil temperature of 15° to 20°, producing the highest total and marketable yield, as well as plant dry weight(111). High soil temperature also decreased some of the mineral nutrients in plants(84, 111). Soil temperatures producing the greatest root growth are generally lower than those producing the greatest top growth(2, 84).

The air temperature surrounding the major sink in the plant plays an important role in controlling sink strength and its ability to draw assimilates from the source, which in turn increases the net carboxylating rate of the source leaves(43). It has been suggested that sinks held at different temperatures attract differential amounts of assimilates as a result of hormonal control derived from the sinks themselves(28, 116).

Sink effects on translocation

A sink is the region within the plant that utilizes the assimilates derived from the sources. Sources can be organs which contain carbohydrates such as photosynthesizing leaves and flower buds, storage organs, or even stem and roots. As defined by Warren Wilson(108) SINK ACTIVITY is "the rate of accumulation of dry weight per unit weight of sink tissue". SINK STRENGTH, also known as carbon import rate, is the product of sink activity and sink size(98). Apparently, sinks should have a profound effect on translocation through conducting tissue and

sieve tubes within the plant itself(106). Carbon translocation to the sink tissue is enhanced by sink region warming and is diminished by sink region cooling(27,33,65,97).

In the tomato plant, cooling the only sink fruit to 5°C resulted in a net export of carbon from the sink in contrast to the normal import of carbon(97). When the relative sink size is increased by defoliation or by shading part of the source photosynthetic area, the translocation rate of the assimilates produced by the remaining photosynthetic area increases(22,51,93).

Usually, the larger the sink tissue, the greater the amount and rate of carbon translocated into these tissue. This is not necessarily true for some plants or plant parts. Moorby and Milthrope(66) found that at any given temperature the rate of dry weight increase of the sprout on a single sprout potato is constant over a long period of time, and is proportional to tuber size, i.e., the source controls the translocation of assimilates flowing into the expanding sink. Changes in the level of starch and insoluble residues in the tomato fruit is dependent more on sink activity than on sink size. It has been determined that a high concentration of sucrose in the source and low concentration of sucrose in the sink is important in maintaining a rapid and normal carbon translocation from the source to the sink(93,97). Carbon translocation in sugar cane leaves continues after detachment but at a slower rate and the final concentration of sucrose is higher at the base of the leaf(36).

When translocation is slowed down by reducing sink size, the excess assimilates accumulate in the stem(22), and leaves(93). Many researchers have concluded that this accumulation of carbohydrates

decreases the photosynthetic rate of these source leaves(15,96).

Removing the shoot apex of the pea plant decreases its rate of translocation(59). Although the shoot apex is a relative strong sink, removing the shoot apex has no effect on the rate of sugar translocation out of sugar cane leaf(36). It has been suggested that the translocation process includes active uptake of assimilates into storage and growing areas(27).

The direction and rate of translocation can be altered by manipulating the sinks(102). Removing the grains from the ear of the wheat plant reduced the velocity of assimilates moving up the stem from the node that the flag leaf inserts and increased their downward velocity in the stem. However, the rate of assimilate moving out of the leaf was not affected by the removal of the grains. The translocation rate is slower in darkness than in light(33,65).

In cereal crops the flag leaf supplies almost all of the carbohydrate for filling of the grains. In the case of root and tuber crops, with the establishment of an effective canopy and the initiation of the storage organs, even the uppermost leaf supplies the underground organs(23). It is the relative strength of the sink that largely determines the pattern of assimilate movement.

It has been found that auxin produced by the sink does not control photosynthesis in the source leaves(51), nor the control of the assimilates moving through the peduncle(104).

Sink effects on photosynthesis

Many researchers have suggested that source leaf photosynthetic rate may be partially dependent upon the substrate requirements of

the sinks. The more substrate the sink needs, the higher the photosynthetic rate of the supplying leaves has to be in order to meet the greater demand. The rate of tuber formation in potato is nearly constant with time, although the Leaf Area Index(LAI) changes greatly. When LAI decreases toward the end of the growing season, net assimilation rate increases to compensate for the lost leaf surface(63). Removing potato tubers greatly decreases the net assimilation rate(E) of plant(69), as well as total dry weight accumulation(10,69). Quantities of assimilates normally moving to the tuber accumulated in stems and leaves in the form of sugars, starch and proteins after tuber removal. By artificially manipulating leaf area, Moorby(64) was able to show that decreasing the leaf area increased E of the remaining leaves in plants with rapidly developing tubers, i.e., increasing sink size stimulated leaf photosynthesis. Burt(10) showed that net assimilation of potato plants under high light intensity may be limited by their ability to utilize or store the products of photosynthesis.

If all the vegetative tillers of a wheat plant are kept defoliated, the net photosynthesis of the flag leaf on the main tiller was decreased by a reduction of grain number or increased by inhibition of photosynthesis of the ear itself(73). Austin and Edrich(1) found no marked change in assimilation rate of wheat after ear removal during the rapid grain development period. Their result was probably because the flag leaf had found some alternate sinks by not defoliating the vegetative tillers.

Hansen(35) working with apples has shown the uptake of $^{14}CO_2$ per cm^2 leaf area is greater on fruit-bearing shoots, often by a factor of 1.5 or more, than on non-fruit-bearing shoots. He also found(34) that

the considerable sink effects of apple fruits accelerated the translocation of photosynthates out of the nearby leaves. Hofstra and Nelson (42) observed a close relationship between rates of translocation of assimilates from leaves of different species of apple and rates of photosynthesis.

Partial defoliation of bean, corn and willow leads to increased photosynthesis in the remaining leaves, and a compensatory increase in levels of carboxylating enzyme, RuBP carboxylase, which is the enzyme responsible for the formation of 3-phosphoglyceric acid by incorporation of CO_2 and ribulose-1,5-biphosphate. This suggests that under normal field conditions photosynthetic rates are not only limited by physical resistance to CO_2 diffusion in the leaves but also limited by the concentration of the carboxylating enzymes(107). Partial defoliation also caused an increased chlorophyll content in the leaves of birch seedlings which in turn brought about a higher rate of photosynthesis(107).

Using detached rooted leaves, with roots being the sole sink and blade being the only source, it was found that the net assimilation rate was dependent upon the growth of the root system attached to the petiole(43,45).

Changes in net assimilation rate of pea leaflets were found to reflect closely the pattern of utilization during subtending fruit development, i.e., the fruit substrate demand modulated the photosynthesis of adjacent leaflets(25). Thorne and Koller(93) demonstrated that assimilate demand of soybean plants had a marked influence on source leaf photosynthesis and carbohydrate export. Starch concentration in the source leaf decreased more than 10-fold and sucrose increa-

sed 3-fold during a 8-day period when the other parts of the plant were shaded. They also found that RuBP carboxylase activity and inorganic phosphate concentration were all significantly higher in the unshaded leaf on the shaded plant than in the leaf of an unshaded plant. Net assimilation in the sugar beet leaf was found to be linked to the growth of storage root(33,47). Low root temperature reduced sink demand which in turn decreased net assimilation, especially in older leaves. Throne and Evans(92) designed an excellent experiment to show how sink demand controls canopy photosynthesis. Sugar beet has a larger storage root and greater leaf assimilation rate than spinach beet. Grafted plants of spinach beet on sugar beet roots increased assimilation rate of the spinach beet leaf, i.e., the photosynthetic rate of spinach beet leaves had been increased by introducing the larger sugar beet root sink. It has also been observed that the removal of fruits, upper leaves or growing point of Capsicum annuum increased the assimilation rate of the remaining leaves(54).

It is significant that some researchers have found no correlation between sink demand and source photosynthetic rate(1,28,67).

Temperature effects on translocation

Using growth as a measure of translocation, Swanson and Bohning (89) found that petiole temperature of 20°-30°C gave maximum sucrose transport out of bean leaves. The retarding effect of low temperature on translocation progressively decreased with time and at high temperature progressively increased(89,91). In milkweed the translocation loss of dry matter from the leaves at 30° was significantly greater than that at 20°, but in bean and tomato leaves the loss at 30° was

about the same as those at 20°(38). Respiration rate increases with temperature and consequently a considerable portion of the translocatable carbohydrates will be depleted before they reach the sink. The quantity of assimilates available for translocation was the limiting factor at high temperature, but this was apparently not due to any injury to the transport system(38,14). However, Coulson and Peel(16) did not observe a reduction in respiratory loss of ^{14}C at low temperature during the transport of ^{14}C-labelled assimilates suggesting that the respiration of conducting tissue was insensitive to temperature. It could be that the substrate for respiration during the testing period was being derived principally from the reserves already in the conducting tissue and not that of ^{14}C-assimilate being transported.

Giaquinta and Geiger(29) noted that above a critical temperature of 10°C for bean and 0° for sugar beet, the effect of temperature on the rate of mass transfer and speed of movement of ^{14}C-assimilates was consistant with the response found in physical processes and to be expected from changes in viscosity of sugar solutions. Canny(14) in his "Phloem Translocation" stated: "Temperatures from 0° to 10° are likely to slow translocation speeds to a fraction of that observed at 20° by the reduced supply of energy and increasing viscosity". But Coulson et al.(17) could find no recovery in respiration rate after transfering a sugar beet from low to normal temperatures, even though it had recovered its translocation rate. There was no apparent change in ATP level. Wardlaw(105) also contends that the movement of assimilates is not directly influenced by the metabolism in the sieve elements or surrounding cells.

In Helianthus seedlings translocation in the region of 10-20 cm

below the ^{14}C fed leaf reached a maximum between 30° and 35°C(119). The Q_{10} for translocation was more than 3 between 20° and 30°.

A cotton petiole temperature of 25°C was optimum for movement of assimilates out of the source leaf(14). The Q_{10} from 10° to 20° was about 2.5 with rapid decrease above 30°.

Webb and Gorham(109) and Webb(110) measured the rate of translocation of ^{14}C out of squash leaf following a pulse feed of $^{14}CO_2$, first at the node and later at various internodes held at a range of temperatures from 0° to 50°C. Translocation was at maximum at 25° and the process was interrupted at 0° and 50°. Returning to 25° from 0° allowed a slow resumption of ^{14}C translocation through the node, but the damage was permanent. Geiger(27) found that recovery of translocation from low back to normal(28°) temperature was very rapid in sugar beet. The difference observed by these researchers was probably due to the plant species differences, one being cold sensitive, the other cold resistant.

Canny and Phillips(13) assumed an effect-diffusion type of translocation, which has shown how the diffusion constant(K) of sucrose translocation can be affected by temperature. In their model:

$$K = r\, v^2 / 4\gamma$$

where v = streaming velocity of strands

r = radius of streaming protoplastic strands

γ = permeability coefficient of the surface of the protoplastic strands

Both v^2 and γ would be expected to increase with temperature. At too high temperature the strand surface becomes so permeable that γ is so

high that $r \cdot v^2$ to 4τ starts to decrease and the strands no longer function to accelerate the diffusion of the translocated substance, i.e., K decreases.

Wardlaw(104), working with wheat plants, found that the rate of movement of ^{14}C-assimilates out of the leaf was optimal at about 30°C. The movement of ^{14}C-assimilates through the stem was independent of temperature in the range 1° to 50°. After plants were exposed to very low(-5°) and very high(60°) temperatures for three days, the plants did not adapt and translocation remained low. He concluded that the movement of assimilates through the transport system is independent of temperature in range of 1° to 50°.

Other researchers, Bohning et al.(5) and Swanson and Whitney(90) working with beans, Mutsushima and Wada(60) working with rice, and Bouwer working with cotton(7), have all reported optimums between 25°-30° for translocation.

Effects of translocation on photosynthesis

When a shoot is girdled the translocation pathway is interrupted, and one would expect a reduction in translocation rate above the ring. Indeed, this is the case. Using this method Heinicke(37) showed that leaves above the ring responded with decreased photosynthesis which was also lower than that in the leaves under the ring. Severing phloem in the petiole decreased photosynthesis in the blade. These phenomena were later substantiated by Hofstra and Nelson(42).

Liu et al.(58) showed that translocation is one of the most important physiological factors controlling photosynthetic efficiency in bean plants. Cultivars with high vein loading and translocation

had higher photosynthetic rates.

Growth of Lilium longiflorum

The Easter lily, Lilium longiflorum, has a periodic growth habit. A "commercial" is a three-year-old bulb(19). "Commercials" are grown from "yearlings", which in turn are grown from "stem-bulblets". Stem-bulblets are continuously formed on stems below soil surface from mid-February to late summer with those forming first on lowest nodes reaching the greatest size(4). Like the bulb they increase in size until harvest. None of the stem-bulblets flower the first year of their initiation. The bulblet apex initiates scale primordia from their appearance until mother axis anthesis. It may produce scale leaves during growth and development. The diameter of stem-bulblets continues to increase at a fairly uniform rate until removed from the stem in September and October.

At harvest of the mother axis, one-quarter of the bulblets' leaf complement has been initiated. They are replanted by mid-October to grow to yearling bulbs. At planting time the daughter becoming mother axis has not lifted-off the basal plate, and it is impossible to distinguish scale from leaf primordia. Next year's flowering stem(mother axis) elongates not long after the stem-bulblets are replanted. The shoots start emerging above the soil surface in December. Flower initiation occurs in late February to early March which terminates leaf initiation. By late May or early June all leaves are fully expanded. Anthesis occurs from late June to mid-July.

The bulblet daughter is initiated by mid-December, and its meristem continues to initiate scale primordia until anthesis. The outer

mother scales shrivel and disintegrate rapidly as they are used in shoot growth from late February to late March. Their hydrolysis ceases in May when the new leaf canopy is sufficient to supply photosynthates for growth and development. Growth of the bulb continues until the yearling or commercial bulbs are harvested in September.

The yearling bulbs are replanted in October. Their growth cycle is similar to that of the stem-bulblet to yearling. Daughter bulb appears near mid-November(4). The last stem-bulblet scales are utilized by mid-April and the outer scales contributed by yearling bulb are also rapidly hydrolyzed until sometime in May. At harvest, over 30% of the total scale complement is made up of those initiated during the previous year. Daughter apices are vegetative at harvest.

Temperature affects the growth and development of Easter lily

Temperature is one of the major factors influencing the growth and development of the Easter lily(114). Flower buds develop more rapidly at 27°C than at 15° air temperature(70,115). After shoot emergence, at any temperature regime, light intensity controls plant height and at a given light intensity, higher temperature causes plants to grow taller. Plants under a 9-hour photoperiod are only one-half the height of those grown under an 18-hour photoperiod(86), Twenty-one degree day and night temperatures bring about more rapid flowering than any other temperatures(82). Smith and Langhans(86) found that a day temperature of 28° induced flowering in half the time required at 10° day and night temperatures(76 vs. 156 days) when night temperature was above 10°. White(112) found that less time was required for flowering when lily pots received initial rooting temperature of 21°-

27°. Box(8) likewise reported that plants grown at 21° air temperature flowered 15 to 20 days earlier than those at 16°. The chilling(vernalization) that bulbs receive before forcing profoundly influences their subsequent growth and development. Bulbs held at low temperature longer produce less flowers, but requires fewer days to flower(82).

McMurry(61) placed greenhouse grown lily plants under 24°C day and 18° night air temperature and irrigated them with water at 13°, 18°, 24° and 20°. Growth of both roots and bulbs was increased by water at temperatures of 24° and 29°. Death of lower leaves was increased by heating the irrigating water. However, heating soil to 21°-24° for three months in the field starting from mid-February and March or from mid-April to mid-June(100) caused "summer sprouting". Summer sprouting was triggered in the field in early spring, even though, the sprout did not appear above ground until early summer(79). Much higher than average winter temperature followed by below average summer temperature has caused early field fall sprouting before harvest which caused losses in marketable bulbs.

At lower elevations in northern Taiwan, the Republic of China, one of the original habitates of the Easter lily, anthesis occurs from late March to mid-April and the tops die down completely by mid-June. Bulbs are usually small compared with those harvested at Harbor, Oregon. The average air temperatures of April, May and June in Taipei, a northern city, for the years of 1976-1978 were 22.2°, 25.0° and 27.3°, respectively. In fact, the daytime temperatures were much higher than these. Average temperatures were 14.7°, 14.6° and 14.8° for the corresponding developmental stages in July, August and September in Harbor, Oregon, for the same years. Leaves of lily plants do not show

sign of senescence until after normal harvest dates in the Pacific Northwest. These and other studies suggest that above 20° air temperatures are too high for maintaining a functional leaf canopy after anthesis(55,81).

Gray(30) found that there is no critical temperature for scale bulblet formation. A 10°C increase from 12° to 22° nearly doubled the growth responses and 22° was near optimum for scale bulblet formation and development.

MATERIALS AND METHODS

Three hundred 'Nellie White' Easter lily yearling bulbs 14.0 to 16.5 cm in circumference were received from Pacific Bulb Growers' Research and Development Station, Harbor, Oregon on September 21, 1979. Upon receipt the bulbs were held in polyethylene bags (4 mil) with measured amounts of moist peat moss and the following sequence of case storage was given.

September 22--------October 4	2 weeks	18 ± 1°C
October 5----------October 18	2 weeks	15 ± 1°C
October 19----------November 15	4 weeks	10 ± 1°C

Vernalization at 10°C rather than 5° was used to provide sufficient bulb chilling to induce uniform emergence and flowering without excessive reduction in leaf numbers, thereby more nearly duplicating field-grown conditions.

Bulbs were planted in 10 cm clay pots on November 15, 1979 and placed on greenhouse benches with 13° ± 1°C day and 10° ± 1° night temperatures. These stock plants were maintained in this house until April 25, 1980, after which they were grown at 18° ± 1° day and 13° ± 1° night temperatures. Routine cultural procedures were followed. A solution containing 0.1% of Standard Calorado Mixture (681 gm ammonium nitrate, 454 gm muriate of potash, 227 gm magnesium sulfate, 227 gm phosphoric acid, 14 gm manganese sulfate, and 7 gm sodium tetra-borate) was used to irrigate plants three times a week to insure adequate nutrition at all growth phases.

Greenhouses were maintained at 3 different day/night air temperature regimes with provisions for soil temperature treatment combina-

tions(Table 1). Air temperatures in the 3 houses were monitored with

Table 1. Air temperatures used in combination with soil temperatures.

Air temperatures(°C) Day/night	Soil temperature(°C)			
24/18	30	24	24/18(=air)	cooled(<air)
18/13	30	24	18/13(=air)	cooled(<air)
13/10	30	24	13/10(=air)	cooled(<air)

a CR 5 Digital Recorder, Campbell Scientific, Inc., California, with sensors in each house located just above the plants. The house with 13°/10°C air temperature was not used after stage D(BV - 6 days) due to difficulties in controlling the temperature. Where soil temperatures were the same as ambient air temperatures they are designated as day/night(=air) temperatures(Table 1).

Insulated(styrofoam), bottom-heated rooting trays were used to control root temperature. Thermostatically-controlled, electric heating cables were put in the bottom of each tray to heat 12.5 cm of sand above a bottom board containing small drainage holes. Temperatures were maintained within $\pm$ 1°C by sensors buried in the sand.

Pots to be cooled were inserted through openings in specially designed cooling cases with their top rims held in place and sealed with rubber gaskets. Cool, outside air passed through the cases lowered the soil temperatures in the pots 1° to 5°C below the ambient air depending on the prevailing outside air temperature.

Growing temperature regimes, during 5 pre-bloom phases and 1 post-bloom phase of growth, were applied for 1-month duration commencing at specific morphological stages(Table 2).

Table 2. Morphological stages when plants were subjected to various growing temperature regimes of 1 month duration.

Phase designation	Morphological stage at beginning of treatment	Treatment duration Beginning	End
A	12-leaves unfolded	1/1	1/31
B	25-leaves unfolded	2/1	3/1
C	46-leaves unfolded	3/2	3/31
D	Buds visible(BV) - 6 days	4/1	4/30
E	Buds visible(BV) + 24 days	5/1	5/31
F	Anthesis(AN)	6/1	6/30

At the beginning of each treatment phase, 5 plants at that particular growth stage were selected at random from the stock plants for each temperature regime. Pots with soil to be heated were plunged in the sand-filled, bottom-heat trays to the depth of the lower pot rim. The samd was kept moist at all times to facilitate heat conduction. Where soil temperatures were kept the same as the ambient air, the pots were unfortunately placed on the open bench without benefit of insulation. Hence, soil temperatures in these pots would change faster than if they had been plunged in insulated trays in same manner as those to be heated.

On the last day of each treatment phase, plants were lifted from the pots for examination. They were washed free of culture media, taking care to retain all roots. Intact plants from each temperature regime were held in sealed plastic bags at 0°C until analyzed. All plants were dissected within 5 to 6 days.

Growth analysis consisted of carefully separating and counting mother scales and daughter primordia(scale and leaf). Daughter pri-

mordia were counted by excising the larger scales and examining the smaller primordia under a dissecting microscope. Daughter meristem diameter was determined with a micrometer in the microscope. Number of leaves unfolded was counted from the base of the stem up to the last leaf unfolded or to the second leaf below the first flower. Number of functioning leaves was the number of leaves unfolded during phases A to C or leaves which had not completely turned yellow during phases E and F. These numbers were used to estimate photosynthetic surface during each treatment phase. Stem length was distance from the basal plate to the last unfolded leaf insert at early stages or to the base of peduncle of the first flower after all the leaves had unfolded. Flower bud size was based on the widest diameter of the largest bud.

The fresh weight of roots, stem plus leaves, daughter scales, and mother scales were determined separately. These plant parts were dried at 65°C for 60 hours and their dry weight determined.

Since all plants were dissected at the end of each treatment phase, a new set of plants was selected from the stock plants for treatment in successive phases.

Plants subjected to 13°/10°C air and soil temperatures during phase A to D and 18°/13° air and soil temperatures during phases E and F were, in fact, held under the same conditions as the stock plants. Therefore, plants dissected at the beginning of phase A and at the end of each phase were not only used to compare the responses between treatments for any given phase, but also served as a basis for determining leaves unfolded, weight gain(or loss) of different plant parts and increase in daughter scale(leaf) primordia during the succeeding phase.

Photoperiod and light intensity were not under control during the course of the experiments.

Analysis of variance was used in interpreting the results. The 6 phases were viewed as 6 separate experiments and interphasic comparisons were not attempted.

RESULTS

Mother axis

Leaf unfolding rate. From shoot emergence to fully expanded canopy leaf unfolding rate was directly proportional to air temperature within the range used(Tables 3 and 4). Soil temperature had little or no effect on leaf expansion depending rather on the prevailing air temperature. Soil temperature above 24°C tended to hasten canopy formation but only when air temperature was low enough to be unfavorable to leaf expansion, i.e., below 18°. Plants with 13°/10° air temperature never reached the leaf unfolding rate of those with 24°/18° air temperature no matter how high the soil temperature. Since leaf expansion was completed before stage E(BV - 24 days), comparisons were not made for that phase. There was no significant air/soil temperature interaction after stage B(25-leaves unfolded). There was a significant reduction in number of functioning leaves after stage E, with the lower 1/3 senescing during phase E(BV - 24 days to AN- 6 days) in all treatments. High air temperature resulted in more leaf senescence (Table 3), but there is no evidence of soil temperature affecting leaf retention during phase E and F(AN - 6 days).

Flower bud size(diameter). Air temperature contributed to early flower initiation more than soil temperature. Within the range of the air temperatures used, increasing temperature hastened flower bud development. High soil temperatures only magnified this effect (Table 5). During phase A(12- to 25-leaves unfolded), only 3 temperature regimes had resulted in flower initiation. Three other regimes were in early stages of flower initiation, while plants in remaining

regimes were still vegetative. Soil temperatures above 24°C were above optimum for flower bud development during phases A and B(25- to 46-leaves unfolded). Increasing soil temperature above 18° had similar effects on flower bud expansion during phase C(46-leaves unfolded to BV - 6 days) unless the air temperature was low(13°/10°). Both high air and soil temperatures hastened flower bud development during phase D(BV - 6 days to BV + 24 days), but air temperature exerted the greatest effect on flowering during phase E.

Stem length. During early phases of growth(A to C), increasing air and soil temperatures increased stem length. Increasing soil temperature from 24° to 30°C did not increase stem length Soil/air temperature interactions were evident only during phase A. Plants grown at relatively cool air temperature but with warm soil had stem lengths comparable to those obtained at relatively warm air temperatures without soil heating. From phase D through F(AN - 6 days to days), soil temperature did not significantly affect stem length. Plants grown at 24°/18° air temperature reached their final height at the end of phase D.

Stem dry weight. Generally, soil temperature above 24°C did not significantly enhance top growth as evidenced in leaf number(Table 3), stem length(Table 6) and dry weight(Table 7). Increasing air and soil temperatures during phase A progressively increased stem length and weight. A combination of 24°/18° air and 24° soil temperature produced the heaviest stems during phase B. During phases C and D, stem length and weight increased progressively with air temperature to 18° and soil temperature did not influence stem dry weight when air temperatures were above this. Neither air nor soil temperature

had any appreciable effect on stem dry weight after the establishment of canopy. The greatest gains in stem dry weight occured during phase F, when each plant had an average of 4 fast-growing flowerbuds. Data from a preliminary study of dry weight accumulation in developing flower buds are shown in Appendix 1.

Mother scale weight(fresh and dry). During the pre-bloom period, there were net losses in fresh weight of mother scales(Table 9), but dry weight started to accumulate slowly during phase D in those plants receiving 18°/13° air and lower than 24° soil temperatures(Table 11). Comparing dry(Table 11) with fresh (Table 9) weight gains(or losses) during phase A and B, it is evident that under various growing temperature regimes dry exceeded fresh weight losses. Since little shrinking of mother scales occurred during these 2 phases, it is evident that the space, originally occupied by starch in the mother scales, was replaced by water following hydrolysis and consumption of these reserves by other sinks and by respiration. In general, any increase in air temperature or increasing soil temperature above 18° caused increased fresh and dry weight losses.

Large fresh weight losses during phases C and D were due in part to the complete depletion of the outer mother scales. Soil temperature above 24°C was detrimental to fresh and dry weight accumulation in mother scales during phase F(the month after anthesis) and 18° seemed optimal(Table 9 and 11). However, the daughter bulb required higher air and soil temperatures to reach maximum development. The ratio of daughter to mother scale weight(D/M) decreased with decreasing soil temperatures(Table 8 and 10).

Daughter axis

Daughter scale weight(Fresh and dry). Fresh and dry weight changes in daughter scales followed similar patterns(Tables 9 and 11), except that dry weight accumulation appeared more sensitive to air temperature changes. Daughter scales made their greatest weight gains during phases A and B under a growing regime of 13°/10°C air in combination with 24° soil temperature. During phase C, the daughter bulb did not respond to increased air temperatures, whereas, soil temperature above 24° significantly increased daughter scale weight. Air temperature of 18/13° and soil temperature above 24° were required during phases D and E for the growth of daughter scales. High air temperature diminished scale filling or weight accumulation. After anthesis(stage F), high air (24°/18°) and soil(30°) temperatures enhanced daughter scale weight(Table 8 and 10). At this time, 30° soil temperature increased daughter scale filling at all air temperatures and at a rate 8-fold that of the mother scales. However, daughter and mother scale filling proceeded at same rate when soil temperature was near the ambient air temperature(Tables 9 and 11).

Daughter scale and leaf primordia initiation. Soil temperature near 24°C was optimum for daughter primordia initiation during the pre-bloom period(Figure 1 and 2). The advantage in scale primordia production with 24° over lower soil temperatures was even greater when the air temperature was also low(13°/10°). Temperature had no effect on initiatory activity after flower buds were visible. The initiation of daughter scale primordia was on a decreasing scale from time of daughter bulb appearance until anthesis of the mother axis.

Daughter bulb apex diameter. Daughter bulb apex diameter decreased with the approach of anthesis, but increased afterward (Table 12). During phases A and B, when air temperature was above 18°/13°, soil temperatures below 24° were required to enhance dome size. When air temperature was low(13°/10°) soil temperatures below 24° greatly increased the size of the daughter bulb meristem. Neither air nor soil temperature had much effect from phase C to F, although higher air temperature(24°/18°) during phase D reduced dome size. There were differences in apex diameter among temperature regimes at the end of phase F, but no pattern could be followed.

Scale dry matter

At harvest in the field in mid-September, 1979, scale contained an average of 35-38% dry matter(not reported here). At the time of planting, November 15, 1979 there was 28% dry matter in old mother scales and 36% in new mother scales(Table 13). One and one-half months later, December 31, 1979, percentage dry matter had decreased to 23% and 32% in old and new mother scales, respectively. The dry matter in old mother scales continued to decrease after shoot emergence. By stage E(BV + 24 days), old mother scales were completely withered and the new mother scales were partially depleted (Appendix 2). Dry matter in the daughter scales increased steadily as they grew in size.

Root dry weight

A soil temperature of 30°C significantly reduced root growth during phases A and B and 24° soil temperature appeared near optimum

(Table 14). Air temperature of 24°/18° and soil temperatures had no effect from phase C to E. There was no visible root responses to the temperature regimes used after anthesis.

Dry weight of the whole plant

Whole plant dry weights were not significantly different as a result of temperature regimes, except at the end of phase E, where high air temperature(24°/18°) resulted in decreased plant weight (Table 15).

DISCUSSION

Flower bud initiation was completed during phase B which terminated leaf initiation. The initiation of leaf primordia on mother axis was not greatly influenced by soil temperatures above 13°C, nor significantly hastened by successively higher air temperatures. However, development of these primordia and the unfolding and expansion of the young leaves were affected by both air and soil temperatures, i.e., high temperatures favored these growth responses. Temperature effects on leaf initiation has been found to be less profound than on leaf unfolding(44). In this study, the rate of stem elongation also determined the speed of leaf unfolding(Tables 4 and 6). The availability of substrates to the growing leaves and stems was also a limiting factor in determining leaf unfolding rate in some plants. The provision of initiation sites with stem elongation contributes to leaf expansion rate in potato(6). In Easter lily, leaf primordia can accumulate as a rosette around the apical meristem until such time as conditions are favorable for stem elongation.

Root temperatures of 18° to 24°C most favored foliage expansion, which is similar to that observed for strawberry(77) and potato(31). However, air temperatures above 18° were required for Easter lily to reach a maximum rate of leaf unfolding, a high temperature response shared by cucumber(62,32). Bouwer(7) concluded that the rate of net assimilation is rather insensitive to soil conditions which can cause distinct variations in leaf growth. The principal effect of low soil temperature would be a decrease in leaf area followed by a reduction in photosynthetic tissue for carbohydrate assimilation with the net

result of overall reduction in plant growth.

Top growth was correlated closely with air temperature(Tables 3, 5 and 6). Warm soil temperatures further enhanced the effect of high air temperatures on leaf unfolding rate. This study shows that plants grown at a combination of 24°C soil and lower air temperatures could produce the same amount of top growth as those grown at 5° higher air temperatures without soil heating. Under greenhouse conditions, the cost for soil heating would be less than the maintaining of air temperature. Soil heating could also be used to induce early flowering (Table 5), if this were desirable. However, under field conditions soil temperature early in the season is too low to influence top growth. High air temperature increased shoot elongation and dry weight accumulation from shoot emergence to one month before anthesis. The optimum soil temperature(24°) enhanced these responses only from shoot emergence to visible bud stage. Thus, top growth in Easter lily , under field conditions, would be in direct proportion to prevailing air temperature, since soil temperatures never reach optimum.

Air temperature of 24°C accompanied by 24° soil temperature for three months following shoot emergence greatly accelerated the growth of flower buds. Smith and Langhans(86) found that increasing day or night temperatures from 15.6° to21.1° could reduce the time to flowering by 8-15 days. Air temperature of 26.7° accelerated flowering, which was most effective after shoot emergence. Initial rooting temperatures of 21.1° to 26.7° shorten the time to flowering over lower temperatures (112). At any lower temperature water supply could be a limiting factor in above-ground growth. It was concluded that the high growth potential was supported by high soil temperatures, which increased the

water absorption by the roots.

Since leaf number is fairly constant for a given size planting stock(4), leaf unfolding rate could provide an accurate estimate of prevailing air temperature and a predictive measure of crop development. This study supports the assumption that the rate of leaf unfolding (number of leaves), stem elongation(plant height) and flower development in mother axis have the same optimums, 24°C, of both air and soil temperatures during the pre-bloom period(Table 17), and can be used interchangeably in monitoring growth rate and predicting subsequent growth phases(79).

As a result of supplying reserves to other sinks, the weight of the older mother scales was inversely related to the growth of these developing sinks. Mother scale weight was best maintained at 18°C soil temperature and 18°/13° air temperature during phases E and F, one month before and one month after anthesis, that is, balance between old scale depletion and younger mother scale filling. Dry weight was more sensitive to temperature changes than fresh weight. It is evident that with some treatments dry exceeded fresh weight losses during the first two months(Tables 9 and 11). Since little shrinking of mother scales was found during these phases, it suggests that the space in the old mother scales, originally occupied by starch, was replaced by water after the consumption of these reserves by the expanding sinks, as well as, by respiration. Some of the outer mother scales appeared translucent, suggesting hydrolysis had taken place.

Expanding leaves are the major apical sinks. The young,expanding leaves of soybean import carbohydrates from older leaves below(94). In the case of bulbous plants, scales also supply carbohydrates to the

expanding leaves. Generally, leaves have been found to terminate carbon import when they are half-expanded(94,95), and export of carbon follows immediately. In this study, lily plants showed a net loss in dry weight during the two earliest growth phases under greenhouse conditions. Between 25 and 45 leaves were unfolded on the mother axis before dry weight loss of the whole plant ceased(Table 3 and 15). However, mother reserves were still being used for stem and leaf growth at all air and soil temperatures until all leaves were fully expanded. Mother scales were still losing dry weight during phase E, if plants were under 24°/18°C air temperature.

A sink draws substrates from the closest source(94), so, root growth should be primarily supported by mother scales(39,40). Most of the dry matter accumulated during the months between buds visible and anthesis stayed in the top, i.e., stem,leaves and flower buds. Approximately 10% of the dry matter gained during the month before anthesis went into scales if the air temperature was near 18°/13°C. Stem dry weights at anthesis did not differ with air and soil temperatures. The reduction in whole plant dry weight at 24°/18° air temperature was through reduced scale and root weight. This suggests that air temperature can cause either excessive respiration and/or reduced photosynthesis to a point where there is a carbohydrate deficit in above-ground parts. A preliminary study showed that developing flower buds had very high respiration rates which could be brought even higher by raising the air temperature. Plants accumulated considerable dry weight during the month before anthesis, even with a substantial decrease in leaf area. This same phenomenom has been observed in wheat and potato(6,64), where the leaf area index decreased during the rapid

grain filling period or when tubers expand dramatically.

Since the newly expanded leaves are not able to supply sufficient assimilate for the expanding leaves and stem during early stages of their growth, rapid leaf canopy expansion accompanying warmer air and soil temperatures was at the expense of mother scale reserves. Young expanding leaves provide the mother axis with a mobilization sink which is essential to stem elongation(78) and development of flower primordia at early phases before they themselves become strong sinks. Thenty-four degree air and soil temperatures,favoring rapid leaf unfolding, also tend to create a strong above-ground sink. Scale filling was greatly enhanced after anthesis, when they are the principal sink for assimilates.

The average stem dry weight after senescence of the tops was 6.37 grams(not shown). This means an average of 3-4 grams of dry matter originally in the stem and leaves had been translocated to the bulb and roots, as well as, being used as substrate for respiration during senescence. This movement of dry matter from canopy to storage organ during the final stages of growth have also been observed in other crops, such as potato(64) and wheat(72), which accounts for about 10% of their economic yield.

Most of the research work concerning the daughter apical meristem has been done with reference to greenhouse forcing. Wang et. al. (101) reported that prior to flower initiation(mother axis), bulbs receiving excessive 5°C cold induction had smaller apices(diameter) which in turn produced less leaves and flowers. Large iris rhyzomes with large apical meristems produce more flowers(21).

Current data show a decrease in daughter bulb apex diameter as the mother axis approached anthesis(Table 12). The rate of scale primordia initiation was decreasing from daughter bulb initiation to anthesis of the mother axis(Figure 1), and the apical meristems were becoming progressively smaller. During the 2 months after daughter bulb appearance(phases A and B), above 24°C soil temperature resulted in smaller daughter apical meristems. However, these smaller daughter apical meristems were initiating scale primordia at a faster rate than the larger meristems. It appears that the enhancement of initiatory activity resulted in a reduction of apical meristem size.

As the size of daughter bulb apical meristem decreased during the development of flower buds, one would consider that the developing flower buds exert some influences on the initiatory activity and the size of daughter apical meristem during the pre-bloom period.

Sinnott(85) reported as early as 1921 that the size of a plant organ is not dependent upon the body size of the plant on which it is borne, but rather on the size of the growing point from which it is developed. This explains the larger daughter apical meristem associated with the larger bulb, which in turn produces more flowers(52). However, on basis of our September lily harvest data taken from the field, large bulbs do not necessarily have large dome size(Appendix 3). The size of the growing points varies from year to year, and could be influenced by environmental factors(20). In consequence, the size of apical meristem, as well as the morphology of apical meristem, are not likely to be reliable harvest maturity indices, HMI(21,80).

Lily bulb size is determined , supposedly, by the number of scales and/or the size of these scales. But, these do not always

correlate in field data. In 1978, bulb size was above average, although the number of scales was average. In 1979, above average bulb size was associated with more scales.

Tuber size has been shown to determine the final yield of potato. Growth of the potato tuber is the result of cell proliferation and enlargement. At harvest, tuber size has increased 12,000 fold in volume and this is accompanied by a 90 to 370 fold increase in cell number, as well as by a 40 to 90 fold increase in cell size, according to the position of the cells in the tuber(83). Onion bulb enlargement is the result of lateral enlargement of cells at the leaf base.

Lily scales are modified leaves, hence their growth is also subject to the factors determining the size of a true leaf. These factors are 1). the number of primordial cells, 2). rate of cell division, 3). duration of cell division, 4). size of individual mature cells. Number of cells in a scale primordium is determined by the size of apical meristem(85). The integrated effect of the former 3 factors determines the total number of cells in a scale. The last factor has the most influence on the scale size. There is no information available so far on the duration of cell division in Easter lily scales and the potential cell size.

Because lily scales are modified leaves, it is resonable to assume that cell division ceases at a certain time after the appearance of the primordium(74). The percent dry weight of the whole daughter bulb increased slowly from the bulb's first appearance until one month after anthesis(Table 13), which suggests that the density of the daughter bulb was increasing. If the cells enlarge with the deposition of the stored foods, earliness of scale initiation and duration

of scale filling are also important factors determining the final bulb size.

During the pre-bloom period, initiatory activity was at maximum at 24°C soil temperature(Figure 2). This was particularily evident when air temperature was not optimum for growth. Daughter scale initiation and filling were responsive to high temperature indicating that substrate levels were adequate and carbon translocation to these sinks were probably not a limiting factor(65,99). It has been established that tissue cultured lily bulblets require high sugar concentration in the culture medium for maximum bulb and root growth. Soil temperature at 24° provides the best substrate levels in the initiation site and in the daughter scales. The relative high temperature requirement for bulbing in lily daughter scales is different from that of the potato tuber in which high soil temperature decreases tuber growth,especially at high air temperature(31). High air temperature (27°Day/22°Night) favored grain development with the corresponding increase in the rate of cell division in the endosperm tissue of wheat plant, but with a shortened period of stem growth(103). High temperature resulted in a more rapid initiation of daughter scales thus providing a longer duration for bulb filling and consequently the development of larger and early maturing bulbs(79). Using pre-germinated seeds for early onion seedling development(57), and planting tall grass prairie on warm soil following burning and mowing(75). have also substantially increased final yield at harvest. In the case of onion, the percentage yield of large bulbs was also increased.

Daughter primordia produced at and several weeks after anthesis are morphologically plastic(4). They are subject to the influence of

soil temperature, and both field observation and growth chamber studies (81) have shown that high soil temperatures favor scale rather than leaf formation in early summer. An early spring with above average air and soil temperatures continuing into summer resulted in higher scale counts and larger daughter bulb in the field in 1979. These bulbs were more dormant than the bulbs in other years, since the dormancy factor accumulates in the daughter scales at high temperature(100).

This year's daughter scales become next year's mother scales. Their diamensions can increase from initiation until the bulb is harvested at the end of next growing season. Factors unfavorable for the early initiation of scale primordia during the pre-bloom period would be subsequently reflected in reduced bulb size at harvest(4), because they would get less time for filling.

During the pre-bloom period the top did not have significant amounts of assimilates transported downwards for bulb growth, however, the daughter bulb never ceases to increase in size. It is suggested that carbohydrates translocated into the daughter bulb have been drawn rather than pushed(27). When sprouting lily bulbs are placed in sealed bags in moist, dark storage at 24°C, bulbs are formed at the top of the stems(Figure 3). A terminal bulb was formed when the sprouted bulbs were placed under above 21°, nonflower-inducing conditions with short photoperiods(Figure 4).

It is obvious from this study that daughter and mother scales have different patterns of growth before anthesis of the mother axis. During the first year, the daughter bulb is always a sink, but older mother scales are sources while younger ones are still sinks. In tulip, the older mother scales are totally consumed by current growth

of other sinks. The shift from sink to source in daughter scales is also observed in tulip(39,40). Using the reserves in mother scales to build a daughter and to supply the reproductive growth is believed to be a survival mechanism of the lily plant.

This study has substantiated that top growth and daughter scale primordia initiation and filling require relative high temperatures An air and soil temperature of 24°C is required for rapid flowering, leaf unfolding and stem elongation but at the expense of the reserves in the mother scales. Air temperatures approaching 18°/13° during the month prior to anthesis favors maintenance of the mother scales. Flower size, leaf unfolding rate or plant height can be used to measure crop growth rate and earliness. High soil temperature approaching 24° favors scale initiation. Soil temperature above 24° enhances daughter scale filling. Under field conditions, growth of the lily crop has a positive correlation to the prevailing air temperature during the pre-bloom period. Another growth chamber experiment is under way to study the carryover effects of different air temperatures at different growth phases on scale number and scale filling at harvest.

FIGURE 1. GAIN IN DAUGHTER PRIMORDIA DURING EACH GROWTH PHASE AS INFLUENCED BY AIR AND SOIL TEMP.

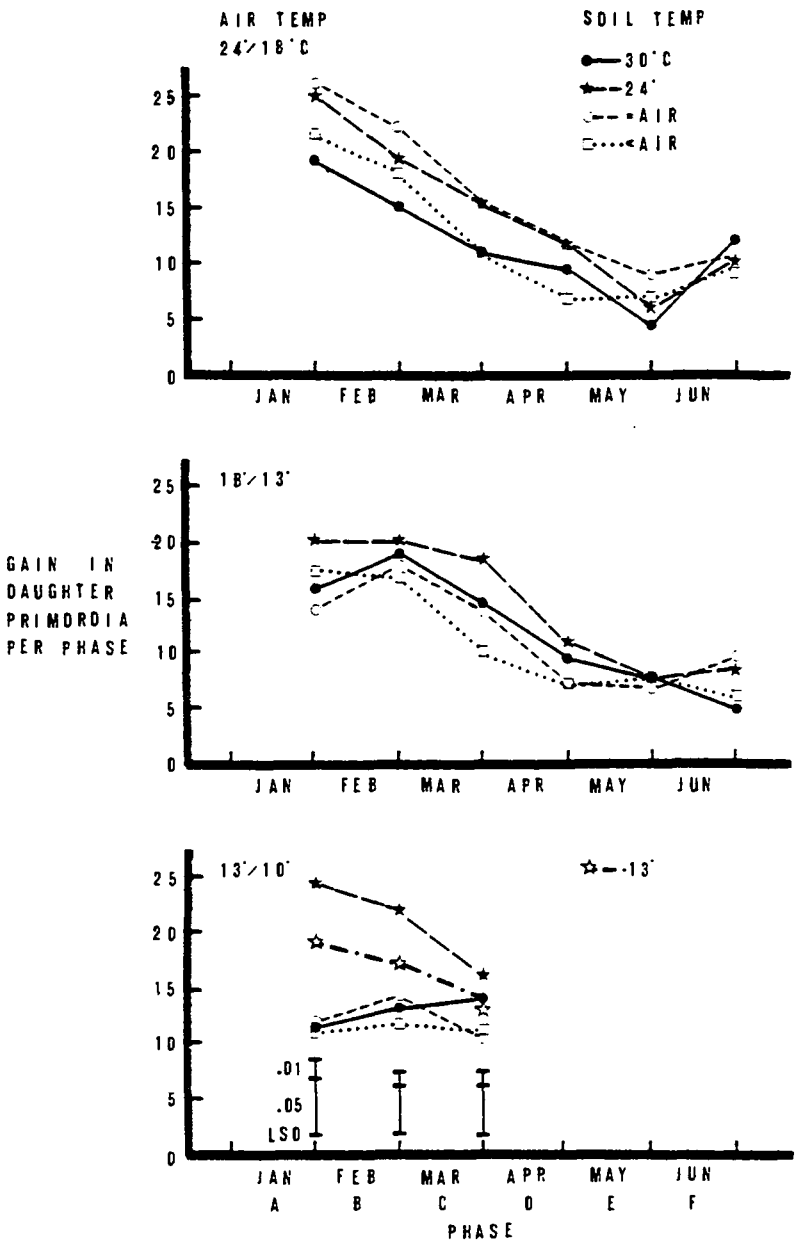

FIGURE 2. GAIN IN DAUGHTER PRIMORDIA DURING EACH GROWTH PHASE AS INFLUENCED BY SOIL TEMP.

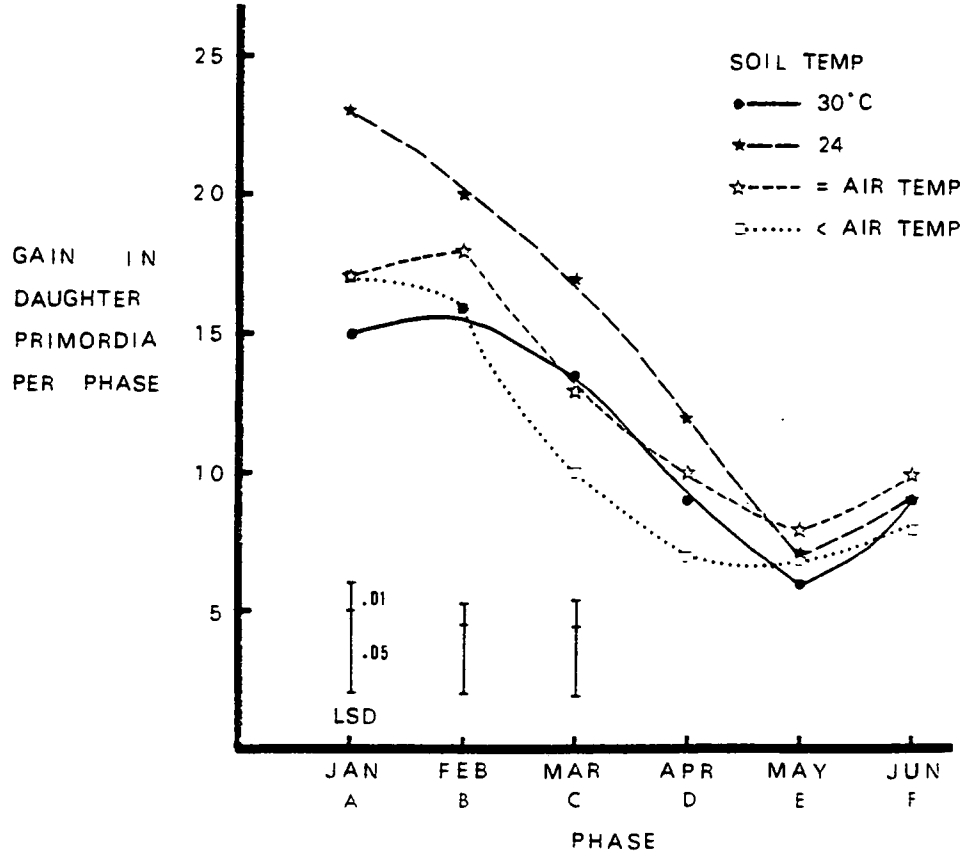

Figure 3. Bulb is formed at the top of the stem when sptouting lily bulb is places in sealed bag in moist, dark storage at above 24°C.

Figure 4. A terminal bulb is formed when the plant is placed under non-inducing(flowering) temperatures(21°C) and short photoperiods.

Table 3. Number of functioning leaves at the end of various growth phases as influenced by air and soil temperatures.[z]

Temperature (°C) Air Day/Night	Soil	Growth Phase A	B	C	D	E	F
24/18	30	32	45	64[y]	71	40	36
	24	32	45	65[y]	69	37	38
	24/18	30	43	67[y]	69	37	37
	cooled	30	40	65[y]	66	37	38
		31	43	65	69	38	37
18/13	30	25	37	66	65	44	37
	24	24	39	58	66	43	37
	18/13	26	32	58	66	44	36
	cooled	22	33	56	67	48	35
		22	35	59	66	45	36
13/10	30	18	33	53			
	24	23	35	51			
	13/10	12	25	46			
	cooled	13	25	44			
		16	29	48			
	$LSD_{.05}$	3.5 1.7	4.1 2.0	6.3 3.1	NS SN	4.9 2.5	NS NS
	$LSD_{.01}$	4.7 2.3	5.4 2.7	8.4 4.2	NS NS	6.6 3.3	NS NS
	Air	**	**	**	NS	**	NS
	Soil	**	**	*	NS	NS	NS
	A x S	**	NS	NS	NS	NS	NS

[z] Functioning leaves are defined as leaves unfolded before stage E and leaves having not completely turned yellow afterward.

[y] All leaves unfolded during phase C.

Table 4. Number of leaves unfolded during each one-month treatment period.

Temperature (°C) Air Day/Night	Soil	Growth Phase A		B		C		D	
24/18	30	30		33		39		25	
	24	30		33		40		23	
	24/18	28		31		42		23	
	cooled	28		28		40		20	
			29		31		40		23
18/13	30	23		25		41		19	
	24	22		27		43		21	
	18/13	14		20		33		20	
	cooled	20		21		31		21	
			20		23		35		20
13/10	30	16		21		28			
	24	21		23		26			
	13/10	10		13		21			
	cooled	11		13		19			
			14		17		23		
	$LSD_{.05}$	3.5	1.7	4.1	2.0	6.3	3.1	NS	NS
	$LSD_{.01}$	4.7	2.3	5.4	2.7	8.4	4.2	NS	NS
	Air	**		**		**		NS	
	Soil	**		**		*		NS	
	A x S	**		NS		NS		NS	

* and ** significant at 5% and 1% levels respectively. NS, not significant.

Table 5. Flower bud size at the end of each one-month treatment(mm).

Temperature(°C) Air Day/Night	Soil	Growth Phase A		B		C		D		E	
24/18	30	0.98		3.3		7.6		15.1		FB[x]	
	24	0.68		2.8		7.1		14.7		FB	
	24/18	0.60		2.6		7.4		14.2		FB	
	cooled	P[z]		1.9		7.1		13.9		FB	
			0.68		2.6		7.2		14.5		
18/13	30	P		2.4		5.2		10.7		25.5	
	24	P		2.2		5.0		10.8		27.8	
	18/13	V[y]		1.3		5.7		9.2		23.5	
	cooled	V		1.2		5.1		9.2		30.0	
			0.08		1.8		5.3		10.0		26.7
13/10	30	V		1.5		4.0					
	24	V		1.4		3.8					
	13/10	V		0.7		2.9					
	cooled	V		0.6		2.7					
			0.00		1.1		3.4				
	$LSD_{.05}$	0.21	0.11	0.4	0.2	0.7	0.3	1.2	0.6		
	$LSD_{.01}$	0.29	0.14	0.5	0.3	0.9	0.5	1.6	0.8		
	Air	**		**		**		**		**	
	Soil	**		**		**		*		NS	
	A x S	NS		NS		**		NS		NS	

[z] Not all plants had started flower initiation.
[y] All plants vegetative.
[x] Full bloom.

Table 6. Stem length(cm) at the end of various growth phases as influenced by air and soil temperatures.

Temperature(°C) Air Day/Night	Soil	Growth Phase A		B		C		D		E		F	
24/18	30	9.7		10.0		16.6		25.1		23.2		23.8	
	24	8.1		10.3		16.7		25.8		25.0		26.3	
	24/18	8.2		9.4		16.4		24.0		25.9		24.3	
	cooled	7.9		8.1		14.9		23.1		26.5		24.3	
			8.5		9.4		16.2		24.5		25.1		24.7
18/13	30	7.9		8.8		13.6		17.2		25.3		23.6	
	24	7.5		8.8		13.0		15.6		25.8		24.1	
	18/13	5.2		6.9		11.2		15.6		24.2		23.6	
	cooled	5.5		7.2		11.7		16.7		23.7		25.1	
			6.5		7.9		12.4		16.3		24.8		24.1
13/10	30	7.0		7.4		11.2							
	24	6.0		7.9		11.0							
	13/10	4.9		6.4		10.2							
	cooled	3.9		5.9		8.8							
			5.6		6.9		10.3						
	$LSD_{.05}$	0.8	0.4	1.2	0.6	1.7	0.9	2.7	1.4	NS	NS	NS	NS
	$LSD_{.01}$	1.1	0.5	1.6	0.8	2.3	1.2	3.7	1.8	NS	NS	NS	NS
	Air	**		**		**		**		NS		NS	
	Soil	**		**		**		NS		NS		NS	
	A x S **	NS		NS		NS		NS		NS		NS	

** Significant at 1% level. NS, not significant.

Table 7. Stem dry weight at the end of each one-month treatment period as result of various air/soil temperature regimes(gm.).

Temperature(°C) Air Day/Night	Soil	Growth Phase A	B	C	D	E	F
24/18	30	1.87	2.47	5.67	9.30	12.58	10.45
	24	1.71	3.31	5.45	9.10	12.55	9.89
	24/18	1.40	2.87	5.76	7.98	12.71	10.45
	cooled	1.57	2.59	5.06	7.30	12.45	9.82
18/13	30	0.97	2.31	5.35	7.78	13.09	9.43
	24	1.31	2.85	4.89	7.30	12.63	9.53
	18/13	0.57	2.13	4.46	6.73	10.71	10.42
	cooled	0.83	1.87	4.41	8.06	12.45	10.65
13/10	30	0.66	1.68	4.41			
	24	0.93	2.29	4.50			
	13/10	0.38	1.40	3.48			
	cooled	0.40	1.32	3.28			
	$LSD_{.05}$	0.10	0.53	0.89	1.37	NS	NS
	$LSD_{.01}$	0.22	0.71	1.20	1.85	NS	NS
	Air	**	**	**	**	NS	NS
	Soil	**	**	**	*	NS	NS
	A x S	NS	NS	NS	NS	NS	NS

* and ** significant at 5% and 1% levels respectively. NS, not significant.

Table 8. Fresh weight(gms) of daughter scales(D), mother scales(M) and total bulb(T) as influenced by air and soil temperatures during various growth phases.

Temperature(°C)		Growth Phase											
Air	Soil	A			B			C			D		
Day/Night		D	M	T	D	M	T	D	M	T	D	M	T
24/18	30	0.41	35.1	35.5	0.89	32.9	33.8	1.66	21.8	23.5	2.94	19.2	22.1
	24	0.53	39.7	40.2	1.00	34.1	35.1	1.70	22.1	23.8	2.98	17.8	20.8
	24/18	0.41	37.5	37.9	0.67	33.8	34.5	1.42	23.5	24.9	2.10	20.5	22.6
	cooled	0.34	40.0	40.3	0.47	36.5	37.0	0.90	24.7	25.6	1.55	19.2	20.8
18/13	30	0.41	32.2	33.6	0.94	33.4	34.4	1.73	24.4	26.1	3.75	17.5	21.3
	24	0.50	39.8	40.3	1.15	34.4	35.6	2.14	29.1	31.2	2.86	21.5	24.4
	18/13	0.18	41.4	41.6	0.29	36.8	37.1	0.91	29.5	30.4	1.51	27.8	29.3
	cooled	0.26	38.4	38.7	0.28	38.8	39.0	0.70	30.9	31.6	1.25	26.0	27.3
13/10	30	0.18	39.6	39.8	0.62	33.5	34.1	2.11	25.2	27.3			
	24	0.73	41.6	42.3	1.29	31.3	32.6	2.03	28.8	30.8			
	13/10	0.14	41.0	41.1	0.23	39.2	39.4	0.62	34.1	34.7			
	cooled	0.16	45.2	45.4	0.22	39.6	37.1	0.69	29.4	30.3			
	$LSD_{.05}$	0.17	NS	NS	0.26	NS	NS	0.46	7.4	7.6	0.58	5.3	5.3
	$LSD_{.01}$	0.22	NS	NS	0.35	NS	NS	0.62	10.0	10.2	0.78	7.1	7.2
	Air	*	*	NS	NS	NS	NS	NS	**	**	NS	**	**
	Soil	**	NS	NS	**	NS	NS	**	NS	NS	**	*	NS
	A x S	**	NS	NS	**	NS	NS	**	NS	NS	**	NS	NS

* and** significant at 5% and 1% levels respectively. NS, not significant.

Table 8(continued)

E			F			
D	M	T	D	M	T	D/M
2.56	18.6	21.2	13.2	21.5	34.7	0.61
3.12	20.0	23.1	8.9	24.8	30.7	0.36
3.14	18.0	21.1	8.6	22.1	30.7	0.39
2.75	18.1	20.9	8.6	25.1	33.7	0.34
3.94	21.6	25.5	10.0	21.5	31.5	0.47
3.62	21.9	25.5	8.6	24.3	32.9	0.35
2.70	21.9	24.6	6.8	26.4	33.2	0.26
2.14	22.7	24.8	6.1	23.0	29.1	0.26
0.83	NS	NS	2.4	NS	NS	0.15
1.12	NS	NS	3.3	NS	NS	0.21
NS	**	**	**	NS	NS	*
**	NS	NS	**	NS	NS	**
**	NS	NS	NS	NS	NS	NS

Table 9. Gain(+) or loss(-) in daughter(D), mother(M) and total(T) fresh weight during monthly treatment periods (gms).

Temperature(°C) Air Day/Night	Soil	Growth Phase A D	A M	A T	B D	B M	B T	C D	C M	C T
24/18	30	+0.41	-5.2	-4.8	+0.75	-8.1	-7.4	+1.43	-17.4	-16.0
	24	+0.53	-0.6	-2.4	+0.53	-7.2	-6.7	+1.47	-17.1	-15.6
	24/18	+0.41	-2.8	-2.4	+0.53	-7.2	-6.7	+1.19	-15.7	-14.5
	cooled	+0.34	-0.3	0.0	+0.33	-4.5	-4.2	+0.67	-14.5	-13.8
18/13	30	+0.41	-7.1	-6.7	+0.80	-7.5	-6.7	+1.50	-14.8	-13.3
	24	+0.50	-0.5	0.0	+1.01	-6.6	-5.6	+1.91	-10.1	- 8.2
	18/13	+0.18	+1.1	+1.3	+0.15	-4.2	-4.0	+0.68	- 9.7	- 9.0
	cooled	+0.26	-1.9	-1.6	+0.14	-2.2	-2.1	+0.47	- 8.3	- 7.8
13/10	30	+0.18	-0.7	-0.5	+0.48	-7.5	-7.0	+1.88	-14.0	-12.1
	24	+0.73	+1.3	+2.0	+1.15	-9.7	-8.6	+1.80	-10.4	- 8.6
	13/18	+0.14	+0.7	+0.8	+0.09	-1.8	-1.7	+0.39	- 5.1	- 4.7
	cooled	+0.16	+4.9	+5.1	+0.08	-4.1	-4.0	+0.46	- 9.8	- 9.3
	$LSD_{.05}$	0.17	5.2	NS	0.26	NS	NS	0.46	7.4	7.6
	$LSD_{.01}$	0.22	NS	NS	0.35	NS	NS	0.62	10.0	10.2
	Air	*	*	NS	NS	NS	NS	NS	**	**
	Soil	**	NS	NS	**	NS	NS	**	NS	NS
	A x S	**	NS	NS	**	NS	NS	**	NS	NS

* and ** significant at 5% and 1% levels respectively. NS, not significant.

Table 9(continued):

D	D M	D T	E D	E M	E T	F D	F M	F T
+2.32	-14.9	-12.6	+1.05	-9.2	-8.2	+10.66	+2.2	+12.8
+2.36	-16.3	-13.9	+1.61	-7.8	-6.2	+ 6.33	+5.5	+11.8
+1.48	-13.6	-12.1	+1.63	-9.8	-8.2	+ 6.09	+2.8	+ 8.9
+0.93	-14.9	-14.0	+1.24	-9.7	-8.5	+ 6.07	+5.8	+11.9
+3.13	-16.6	-13.5	+2.43	-6.2	-3.8	+ 7.50	+2.2	+ 9.7
+2.24	-12.6	-10.4	+2.11	-5.9	-3.8	+ 6.06	+5.0	+11.1
+0.89	- 6.3	- 5.4	+1.19	-5.9	-4.7	+ 4.25	+7.0	+11.4
+0.63	- 8.1	- 7.5	+0.63	-5.1	-4.5	+ 3.53	+3.7	+ 7.2
0.58	5.3	5.3	0.83	NS	NS	2.4	NS	NS
0.78	7.1	7.2	1.12	NS	NS	3.3	NS	NS
NS	**	**	NS	**	**	**	NS	NS
**	*	NS	**	NS	NS	**	NS	NS
**	NS	NS	**	NS	NS	NS	NS	NS

Table 10. Daughter(D) and mother(M) scale dry weight(gms) at the end of each one-month treatment.

Temperature(°C) Air Day/Night	Soil	Growth Phase A D	A M	B D	B M	C D	C M	D D	D M	E D	E M	F D	F M	
24/18	30	0.08	8.74	0.21	6.47	0.41	4.50	0.77	4.72	0.72	4.35	4.01	6.58	0.61
	24	0.09	8.08	0.17	5.54	0.38	3.94	0.77	4.41	0.87	5.23	2.57	7.17	0.36
	24/18	0.11	8.14	0.14	6.06	0.35	4.44	0.58	5.39	0.91	4.58	2.60	6.50	0.40
	cooled	0.07	9.00	0.10	6.70	0.21	4.99	0.42	5.09	0.77	5.16	2.54	8.02	0.32
18/13	30	0.08	8.31	0.20	6.29	0.38	4.66	1.03	4.74	1.22	6.51	3.04	6.44	0.47
	24	0.09	8.37	0.22	5.89	0.46	5.22	0.76	5.81	1.14	7.00	2.41	6.95	0.35
	18/13	0.04	10.74	0.05	7.42	0.18	6.04	0.36	6.89	0.84	7.18	2.14	8.27	0.26
	cooled	0.05	8.68	0.05	8.05	0.13	5.89	0.33	6.82	0.64	7.33	1.80	6.99	0.26
13/10	30	0.03	9.60	0.12	7.10	0.51	5.58							
	24	0.14	8.57	0.25	5.98	0.44	5.69							
	13/10	0.03	10.87	0.04	8.60	0.12	6.72							
	cooled	0.04	11.73	0.04	8,14	0.12	6.34							
	$LSD_{.05}$	0.04	1.02	0.06	2.26	0.11	1.60	0.16	1.37	0.26	1.47	0.78	NS	0.15
	$LSD_{.01}$	0.05	1.37	0.08	3.04	0.15	2.20	0.22	1.85	0.36	1.98	1.05	NS	0.21
	Air	*	**	*	*	NS	**	NS	**	*	**	**	NS	*
	Soil	**	*	**	**	**	NS	**	*	*	NS	**	NS	**
	A x S	**	NS	**	NS	**	NS	**	NS	**	NS	NS	NS	NS

* and ** significant at 5% and 1% levels respectively. NS, not significant.

Table 11. Daughter(D), mother(M) and total(T) bulb dry weight gain(or loss -, gms) during each one-month treatment period as influenced by air and soil temperatures.

Temperature(°C) Air Day/Night	Soil	Growth Phase A D	A M	A T	B D	B M	B T	C D	C M	C T
24/18	30	0.08	-2.90	-2.82	0.18	-4.40	-4.20	0.37	-4.10	-3.73
	24	0.09	-3.56	-3.47	0.14	-5.33	-5.19	0.34	-5.66	-4.32
	24/18	0.11	-3.50	-3.39	0.11	-4.81	-4.70	0.31	-4.16	-3.85
	cooled	0.07	-2.64	-2.57	0.07	-4.17	-4.10	0.17	-3.61	-3.44
18/13	30	0.08	-3.33	-3.25	0.17	-4.58	-4.41	0.34	-3.94	-3.60
	24	0.09	-3.27	-3.18	0.19	-4.98	-4.79	0.42	-3.38	-2.96
	18/13	0.04	-0.90	-0.86	0.02	-3.45	-3.43	0.14	-2.56	-2.42
	cooled	0.05	-2.96	-2.91	0.02	-2.82	-2.80	0.09	-2.71	-2.62
13/10	30	0.03	-2.04	-2.01	0.09	-3.77	-3.68	0.47	-3.02	-2.55
	24	0.14	-3.07	-2.93	0.22	-4.89	-4.67	0.40	-2.91	-2.51
	13/10	0.03	-0.77	-0.74	0.01	-2.27	-2.26	0.08	-1.88	-1.80
	cooled	0.04	0.09	0.13	0.01	-2.73	-2.72	0.08	-2.26	-2.18
	$LSD_{.05}$	0.04	1.02	2.05	0.06	2.26	2.26	0.11	1.60	1.67
	$LSD_{.01}$	0.05	1.37	2.74	0.08	3.04	3.04	0.15	2.20	2.50
	Air	*	**	**	*	*	*	NS	**	**
	Soil	**	*	*	**	**	**	**	NS	NS
	A x S	**	NS	NS	**	NS	NS	**	NS	NS

* and ** significant at 5% and 1% levels respectively. NS, not significant.

Table 11(continued):

D			E			F		
D	M	T	D	M	T	D	M	T
0.65	-2.00	-1.35	0.36	-2.54	-2.18	3.24	0.40	3.64
0.65	-2.31	-1.66	0.51	-1.66	-1.15	1.80	0.99	2.79
0.46	-1.33	-0.87	0.55	-2.31	-1.76	1.83	0.32	2.15
0.30	-1.63	-1.33	0.41	-1.73	-1.32	1.77	1.84	3.61
0.91	-1.98	-1.07	0.86	-0.38	0.48	2.27	0.26	2.53
0.64	-0.91	-0.27	0.78	0.11	0.89	1.64	0.77	2.41
0.22	0.17	0.41	0.48	0.29	0.77	1.37	2.09	3.46
0.21	0.10	0.31	0.28	0.44	0.72	1.03	0.81	1.84
0.16	1.37	1.39	0.26	1.47	1.52	0.78	NS	NS
0.22	1.85	NS	0.36	1.98	2.04	1.05	NS	NS
NS	**	**	*	**	**	**	NS	NS
**	*	NS	*	NS	NS	**	NS	NS
**	NS	NS	**	NS	NS	NS	NS	NS

Table 12. Daughter bulb apex diameter(μm) following one-month growth at various air/soil temperature regimes.

Temperature(°C) Air Day/Night	Soil	Growth Phases A	B	C	D	E	F
24/18	30	380	340	370	380	370	540
	24	390	410	380	380	380	510
	24/18	410	400	380	380	420	490
	cooled	430	440	400	390	380	490
18/13	30	380	380	390	420	380	460
	24	380	430	350	420	420	550
	18/13	470	480	410	410	390	540
	cooled	440	470	400	410	410	500
13/10	30	380	340	370			
	24	460	410	390			
	13/10	580	520	400			
	cooled	560	580	400			
	$LSD_{.05}$	35	53	40	NS	NS	52
	$LSD_{.01}$	47	41	NS	NS	NS	NS
	Air	**	**	NS	**	NS	NS
	Soil	**	**	*	NS	NS	NS
	A x S	**	*	NS	NS	NS	**

* and ** significant at 5% and 1% levels respectively. NS, not significant.

Table 13. Percent of dry matter in old mother(OM), new mother(NM) and daughter(D) scales at the end of each growth phase as influenced by various air/soil temperature regimes.

Temperature(°C)		Growth Phase													
Air	Soil	A		B			C			D		E		F	
Day/Night		OM	NM	OM	NM	D	OM	NM	D	NM	D	NM	D	NM	D
24/18	30	15	29	11	23	24	9	23	24	25	27	23	28	31	33
	24	11	25	10	19	17	9	19	17	25	26	26	28	29	29
	24/18	14	26	10	21	22	9	21	22	26	28	26	29	29	30
	cooled	14	27	12	21	21	13	21	21	27	27	29	28	32	30
18/13	30	15	30	10	22	21	9	22	22	27	28	30	29	30	30
	24	13	25	9	20	19	11	20	22	27	27	32	30	29	28
	18/13	19	30	13	23	17	12	23	20	25	24	33	30	31	32
	cooled	15	26	14	24	18	11	24	19	26	26	32	30	30	30
13/10	30	16	28	14	24	19	9	24	24						
	24	11	24	10	22	19	8	22	22						
	13/10	21	30	15	26	17	10	26	19						
	cooled	20	29	16	25	18	12	25	17						
	$LSD_{.05}$	4.6	3.5	3.9	2.8	NS	2.0	NS	3.2	NS	NS	3.1	2.0	NS	2.0
	$LSD_{.01}$	6.1	4.7	5.2	3.8	NS	2.6	NS	4.3	NS	NS	4.2	NS	NS	2.6
	Air	**	NS	**	**	NS	NS	NS	**	NS	NS	**	**	NS	NS
	Soil	**	**	**	**	NS	**	NS	**	NS	NS	*	*	NS	**
	A x S	NS	*	NS	NS	NS	**	NS	NS	NS	NS	NS	NS	NS	NS

* and ** significant at 5% and 1% levels respectively. NS, not significant.

Table 14. Root dry weight (gms) during each growth phase following various air/soil temperature treatments.

Temperature (°C) Air Day/Night	Soil	Growth Phase A	B	C	D	E	F
24/18	30	0.73	0.81	2.07	2.35	3.00	3.58
	24	0,94	1.55	1.87	2.70	3.20	3.45
	24/18	1,03	1.53	1.42	2.97	3.23	3.42
	cooled	0.97	1.41	1.95	2.68	3.84	3.11
18/13	30	0.47	1.10	2.39	3.04	4.05	3.18
	24	0.90	1.30	2.34	3.00	3.76	3.45
	18/13	0.79	1.71	2.58	2.52	3.64	3.77
	cooled	0.78	1.29	2.36	3.12	3.78	3.41
13/10	30	0.44	0.94	2.19			
	24	0.86	1.30	2.00			
	13/10	0.64	1.15	1.96			
	cooled	0.77	1.02	2.30			
	$LSD_{.05}$	0.21	0.37	0.43	NS	0.61	NS
	$LSD_{.01}$	0.28	0.49	0.59	NS	0.81	NS
	Air	**	*	**	NS	NS	NS
	Soil	**	**	NS	NS	NS	NS
	A x S	NS	NS	NS	NS	NS	NS

* and ** significant at 5% and 1% levels respectively. NS, not significant.

Table 15. Dry weight(gms) of whole plant as influenced by various air and soil temperature regimes.[z]

Temperature(°C) Air Day/Night	Soil	Growth Phase A	B	C	D	E	F
24/18	30	9.72	9.96	12.65	17.14	20.65	24.62
	24	10.73	10.57	11.64	16.98	21.85	23.08
	24/18	10.57	10/60	12.97	16.92	21.43	22.97
	cooled	11.54	10.80	12.21	15.49	21.22	23.49
18/13	30	10.73	9.90	12.78	16.59	24.87	22.09
	24	10.50	10.26	12.91	16.87	24.53	23.34
	18/13	12.14	11.31	13.26	16.50	22.37	24.60
	cooled	10.38	11.26	12.79	18.33	24.20	22.85
13/10	30	10.73	9.84	12.69			
	24	10.50	9.92	12.63			
	18/13	11.92	11.19	12.28			
	cooled	12.94	10.52	12.04			
	$LSD_{.05}$	NS	NS	NS	NS	3.00	NS
	$LSD_{.01}$	NS	NS	NS	NS	4.04	NS
	Air	NS	NS	NS	NS	**	NS
	Soil	NS	NS	NS	NS	NS	NS
	A x S	NS	NS	NS	NS	NS	NS

[z] The whole plant dry weight at the begining of phase A was 12.15 gms.
* and ** significant at 5% and 1% levels respectively. NS, not significant.

Table 16. The optimum temperatures for the growth of different parts of a Easter lily during different growth phases.

Plant part	Growth Phase A		B		C		D	
	Soil	Air	Soil	Air	Soil	Air	Soil	Air
Flowers	30	24/18	30	24/18	30	24/18	30	24/18
Leaves	24	24/18	24	24/18	24	24/18	24	24/18
Stem	30	24/18	24	24/18	24	24/18	24	24/18
Mother scales	cooled	13/10	air	13/10	NI	13/10	NI	18/13
Daughter scales	24	13/10	24	NI[z]	24	[y] NI	24	18/13

	E		F	
	Soil	Air	Soil	Air
Flowers	24	24/18		
Leaves				
Stem				
Mother scales	NI	18/13	NI	NI
Daughter scales	24	18/13	NI	24/18

[z] No influence. [y] indicates 'above'.

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APPENDIX

Appendix 1. Dry weight of flower buds at different stages.[z]

Length(cm)	4-5[y]	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14
Width(cm)	1.5	1.7	1.8	2.0	2.2	2.3	2.6	2.6	2.7	3.3
Fresh weight(gms)	2.9	3.9	4.8	6.2	7.2	8.2	9.7	10.7	11.8	13.7
Dry weight(gms)	0.45	0.60	0.74	0.88	1.00	1.12	1.29	1.27	1.41	1.52

14-15	15-16	opening
3.4	3.6	4.1
14.9	15.9	17.3
1.60	1.62	1.63

[z] Flower buds were taken on July 2, 1980, and were then divided into different groups according to their length.
[y] Values are the average of 5 flower buds.

Appendix 2. Number of old(O) and new(N) mother scales at the end of each growth phase as a result of various air/soil temperature regimes.

Temperature (°C)		Growth Phase								
Air	Soil	A		B		C		D	E	F
Day/Night		O	N	O	N	O	N	N	N	N
24/18	30	14	37	15	35	9	28	28	27	24
	24	15	33	13	34	13	31	27	25	24
	24/18	17	33	13	35	10	32	32	27	25
	cooled	18	35	14	34	12	32	32	27	25
18/13	30	12	33	13	34	33	31	26	26	25
	24	15	34	14	33	13	34	32	27	26
	18/13	14	35	11	34	13	33	41	29	26
	cooled	15	34	11	34	10	36	36	29	26
13/10	30	15	34	11	34	8	33			
	24	11	37	15	34	12	32			
	13/10	16	36	17	36	12	35			
	cooled	12	34	11	34	13	34			

Appendix 3. Bulb weight(gms) and daughter bulb apical meristem diameter(mm) of two Easter lily cultivars for 7 consecutive years.[z]

Year	Date of sampling	Cultivar	Weight (gms)	Apex diameter (gms)
1980	Sept 30	Ace	149.4[y]	0.67
		NW	141.2	0.60
1979	Oct 2	Ace	118.7	0.54
		NW	153.7	0.52
1978	Sept 28	Ace	108.7	0.66
		NW	119.9	0.63
1977	Sept	Ace	101.1	0.73
		NW	106.3	0.64
1976	Sept 10	Ace	89.2	0.63
		NW	130.0	0.70
1975	Sept 19	Ace	93.8	0.69
		NW	94.9	0.64
1974	Sept 17	Ace	123.1	0.59
		NW	95.5	0.51

[z] Bulbs taken at Pacific Bulb Growers' Research and Development Station, Harbor, Oregon, for all years.
[y] Values are averages of 10 bulbs.