# Easter Lily Growth and Development



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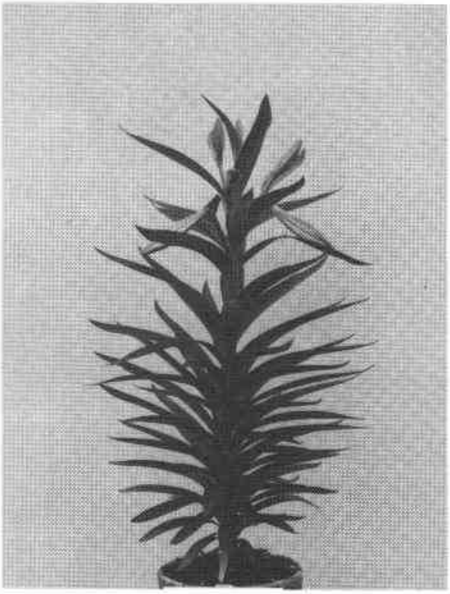
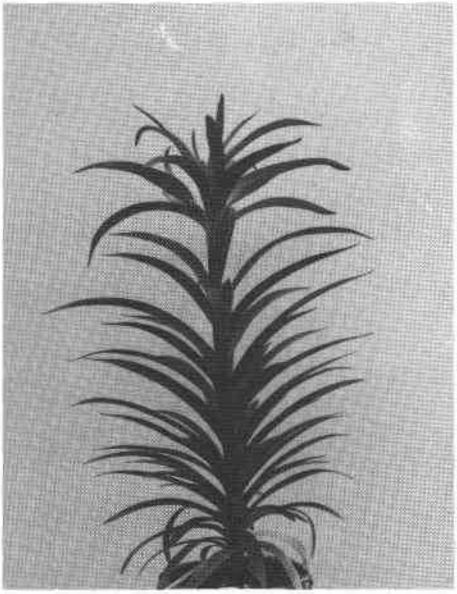
## COMMERCIAL CULTIVARS

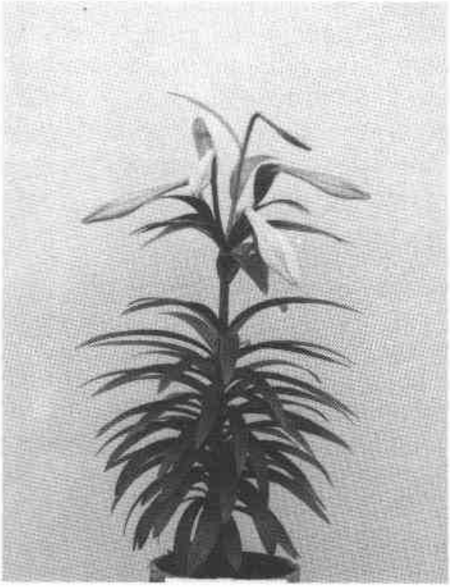


'Nellie White'



'Ace'

## NEW INTRODUCTIONS



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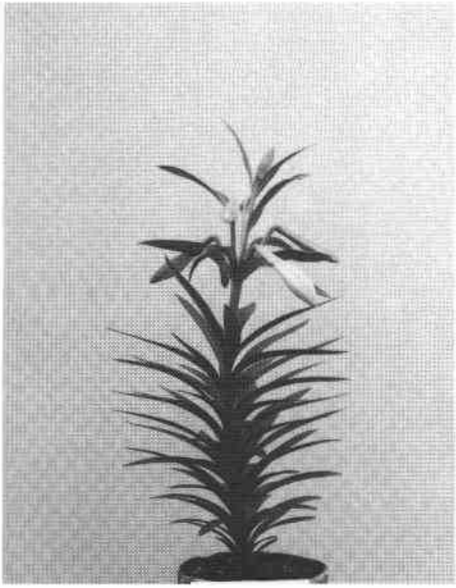

'Chetco' (OSU 73-106)

## Contents

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ABSTRACT

Production and marketing of the lily crop involves bulb growers, wholesale florists (jobbers), greenhouse forcers, and research horticulturists whose success depends in great measure on their knowledge of bulb physiology. Our knowledge of the growth and development of the Easter lily and its storage and forcing requirements has increased greatly in the last 25 years, but the influences of field and climatic factors on yield and forcing performance have not been studied fully.

Field, greenhouse, and controlled-environment facilities were used to determine plant/temperature relations in the phasic development of the Easter lily crop and its climatic adaptation. Weather monitoring (soil and air temperature) and plant growth analysis were used to evaluate the feasibility of predicting bulb yield, dormancy, maturity, and greenhouse forcing performance. The modifying influence of cultural practices on climate responses further illustrates the complexity of predictive instruments.

## INTRODUCTION

The successful production and marketing of the Easter lily, *Lilium longiflorum*, as a pot plant and cut flower involve some of the most sophisticated manipulations known to horticulture. Required are careful monitoring in the field, controlled temperature programming during handling and storage, and controlled environments during greenhouse forcing. Thus, bulb growers, jobbers, and greenhouse forcers must know their responsibilities in the marketing channels and know the underlying physiological principles involved in growing and forcing bulbs. The following discussions are designed primarily to relate seasonal and climatic influences on lily growth and development in the field to subsequent precooling in storage and greenhouse forcing.

A great deal has been written on storage and forcing requirements for Easter lilies and this has been summarized in various reviews (DeHertogh 1974, Langhans and Weiler 1967, Wilkins 1980). However, the influences of field and climatic factors as they impact yields and forcing qualities of lilies have not been studied.

Considerable information on field culture and its influence on Easter lily storage and forcing requirements has been gathered at the Pacific Bulb Growers' Research and Development Station at Harbor, Oregon, a nonprofit research facility provided by the Pacific Bulb Growers' Association and used since 1957 by staff members from Oregon State University, U.S. Department of Agriculture Western Regional Ornamental Plants Laboratory at Corvallis, Western Washington Research Center at Puyallup, and University of California at Davis to study a wide variety of lily bulb production problems. Universities throughout the United Stated also have used this station as a source of plant materials for storage and greenhouse studies.

Horticulturists utilizing the station have been interested in breeding and selecting cultivars better adapted for bulb production in this northern region, as well as for greenhouse forcing as pot plants and cut flowers. However, greater emphasis has been put on climate/plant relations and their influence on forcing requirements and performance. Crop monitoring for predicting bulb yield, maturity, dormancy, and sensitivity to forcing programs has been a primary objective.

## NATURAL DISTRIBUTION OF *LILIUM LONGIFLORUM*

Although Wilson (1925) considered *Lilium longiflorum* to be endemic only to the Liu-chiu (Ryukus) Islands (27°N), it has established itself as an escape on Taiwan (Formosa) at 23°N, and nearby islands, as well as on mainland China and throughout the Japanese home islands. This species is a subtropical plant that has become adapted to more temperate regions by natural selection and breeder influence. The commercial cultivars used on the Pacific Coast (coastal areas of southern Oregon and northern California) at 42°N must be considered northern strains of the species.

Seed from islands off the northern and southern coasts of Taiwan have made it possible for the writers to compare the performance of bulbs from these southern locations with our northern strains. The southern strains have shown variable responses to Oregon winters, depending on prevailing temperatures. During warm winters, they have grown rapidly and flowered in late March or early April, considerably ahead of our northern cultivars which bloom in early July. In cold winters, the Taiwanese seedlings have been greatly retarded and have flowered much later than our commercial cultivars. It is obvious that they have different temperature requirements for development.

The extension of the *Lilium longiflorum* habitat from a subtropical area to temperate areas required adaptation of the lily's sympodial growth form to the production of resting organs (Rees 1972). The basic sympodial pattern of growth exhibits some periodicity because lateral, basal development at the lower nodes is suppressed by apical dominance exerted by the terminal shoot and flower. As Rees points out, this periodicity would not be in phase with an external factor, but should the environment change to include dry or cold periods or if the habitat were extended further north, the plant could have adapted by developing a resting period between the death of the shoots and the replacement by basal buds. There is evidence to support these assumptions in the range of dormancy found between supposedly northern and southern strains of *Lilium longiflorum* and in the differences in their sensitivity to chilling treatment, both temperature and duration. Some strains, such as the southern 'Georgia' lily, "break bud" continuously during the growing season in northern areas ("summer-sprouting") and are thus useless for commercial production in northern climates. Seedling populations show a wide range of periodicity in development depending on origins.

This periodicity in lily bulb development and the sequential temperature requirements of the species for successive stages of development have prompted the use of weather stations in the Brookings-Harbor (Oregon) and Smith River (California) areas of production for studying crop/climate relations. In addition to recording stations at the Pacific Bulb Growers' Research and Development Station near Harbor, Oregon, and at the Westbrook Bulb Farms near Smith River, California, the U.S. Weather Bureau has a recording station at Brookings.

Seasonal air temperatures on Taiwan are as much as 8°C warmer in winter and 14°C warmer in summer than those at the Brookings Weather Station (Figure 1). The winter temperatures on Taiwan are similar in some respects to summer temperatures at Harbor, Oregon. Bulbs in Taiwan are much smaller at maturity than ours on coastal sites as a result of higher summer temperatures and early leaf senescence. Larger bulbs are possible at higher elevations on cool mountain sites on Taiwan.

## PHASES OF GROWTH AND DEVELOPMENT

Development can conveniently be separated into four phases (Roberts and others 1983) (Fig. 2). The first phase after field planting of the bulb in October is *shoot elongation*, which starts with the primary (mother) axis or shoot elongating out of the bulb and emergence. The aerial terminal meristem (shoot) continues to initiate leaf primordia, and a new, secondary (daughter) axillary meristem in the bulb begins to form at the base of the primary shoot axis or future flowering stem in December (Blaney and Roberts 1966a). Phase 2 commences with *flower initiation* of the apical meristem sometime after shoot emergence (December-January). Initiation occurs following sufficient bulb chilling or exposure of shoots to long photoperiods. Phase 2 is marked by successive leaf unfoldings from the primary aerial meristem and the commencement of scale initiation by the secondary axis below ground. The formation of a canopy results in progressive depletion of old (or mother) scale reserves during this growth phase. Phase 3, or *flower development* phase, commences with the appearance of visible flower buds on the primary axis and ends with the opening of the first flower (anthesis). The buds increase steadily in size and at one stage (20-25 mm, largest diameter) tip downward before opening. Scale initiation continues on the secondary axis below ground and new and old scales are continually being filled with reserves.

With anthesis, marked changes in initiatory activity begin and shifts in source/sink relations occur. With Phase 4, the postbloom or *senescence phase* (July-September), the secondary meristem shifts from scale to leaf primordia initiation, and old and new scales reach maximum rates of filling. With approaching harvest, the secondary axis develops a chilling requirement that is necessary for accelerated leaf initiation and eventual shoot elongation. Soil and air temperatures determine when Phase 4 ends, with leaf yellowing and senescence on the primary axis (high temperatures) or when harvest occurs and the secondary axis emerges (low temperatures) and becomes the primary axis.

## FIELD MONITORING OF DEVELOPMENT AND THE INFLUENCE OF WEATHER

The establishment of temperature requirements or optima for the various phases of crop development under field conditions by correlating growth components with weather factors is difficult if not impossible. However, such field monitoring sometimes confirms conclusions drawn from controlled environmental

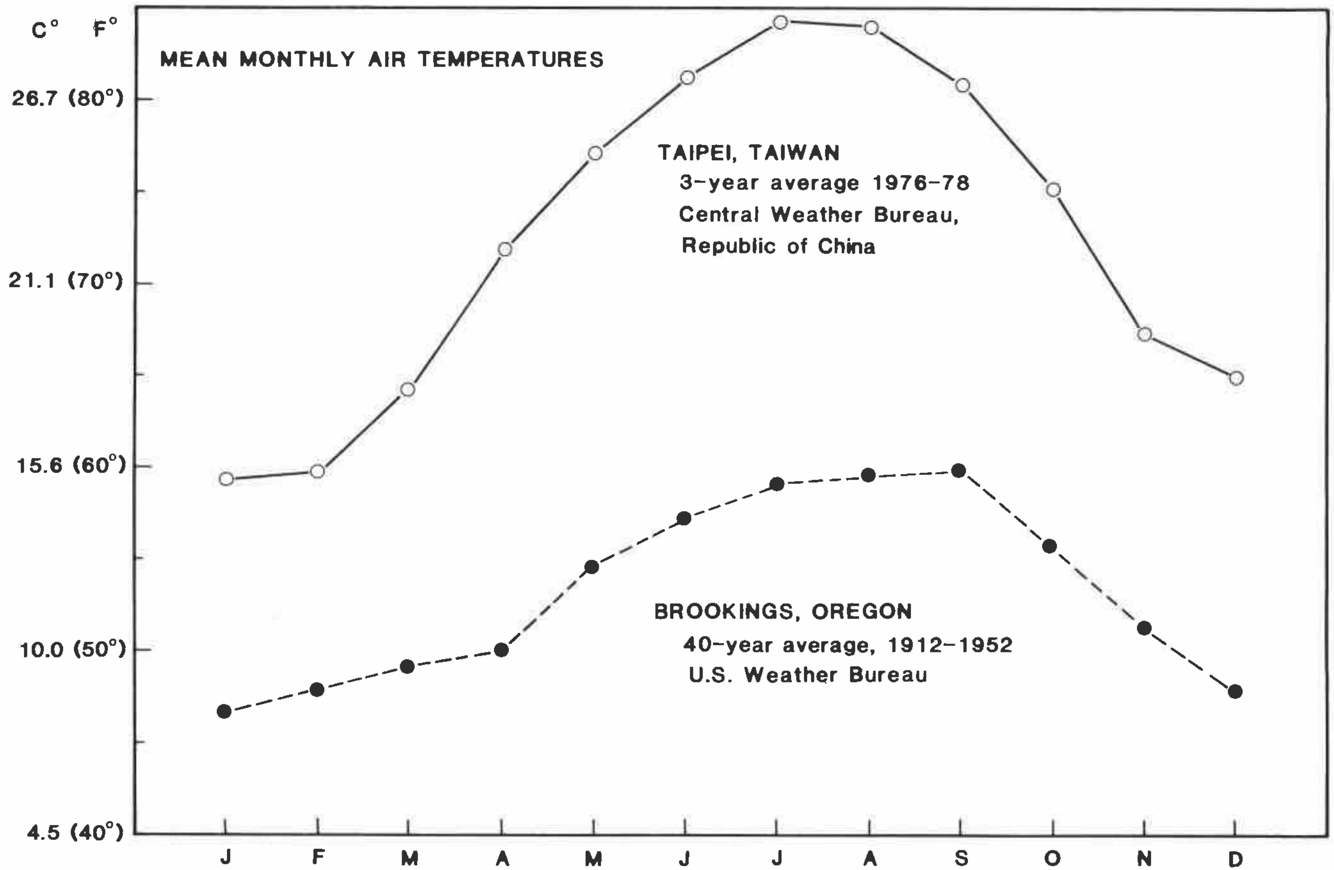


Figure 1. Comparison of mean monthly air temperatures on northern Taiwan (Taipei) with those on the southern Oregon coast (Brookings).

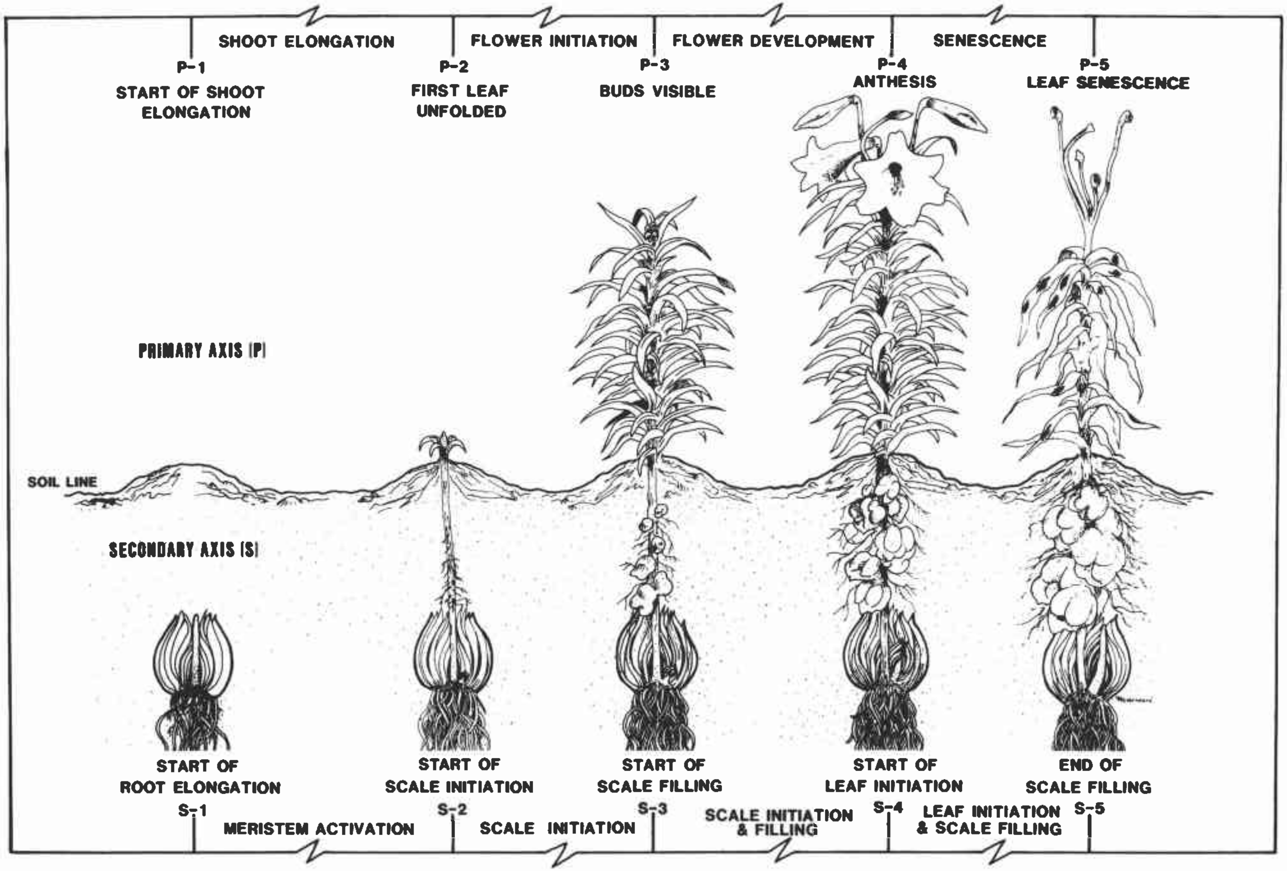


Figure 2. Schema of phasic development of above-ground (primary axis stages P-1 to P-5) and below-ground (secondary axis stages S-1 to S-5) organs in *Lilium longiflorum*.

facilities. The conclusions drawn from the field monitoring reported here are supported in most instances by controlled environment studies (Roberts and others 1983, Wang and Roberts 1983). These studies were designed to establish, under controlled environments, the temperature requirements, or optima, for initiation, elongation, and filling (bulbing) of above- and below-ground organs during the various phases of prebloom and postbloom development.

Mean monthly soil and air temperatures were taken at the Pacific Bulb Growers' Research and Development station during a 7-year period, 1976-1982 (Fig. 3). With the exception of 1976, the air temperatures were significantly above the 40-year averages for the area as based on Brookings Weather Station data (Table 1).

Samples from five grower fields and the Research Station were taken monthly from 1974-1982 to monitor seasonal crop development throughout the bulb-growing region. Before this period, samples were taken only at the Research Station site. Monthly sampling to monitor crop development was started at the station in 1963. Carefully sized planting stock was selected from the Research Station each fall and planted in grower-cooperator fields for sampling the next season, thus eliminating one source of sample variance. The bulbs were given the same care as commercial stocks. Starting in March or April each year, a sample of 10 bulbs each of 'Ace' and 'Nellie White' were taken each month for growth analysis. Analysis consisted of determining the length of the primary stem axis, the number of leaves unfolded, and the width of the largest flower buds initiated.

Bulbs were dissected to determine the number of primary (mother) and secondary (daughter) scales and their total fresh weight. The total number of secondary axis primordia (scale or leaf) was counted at the same time. At the time of shoot elongation, the number of primordia that were scales and the number that were leaves could be determined for the season.

The size (apex diameter) of the secondary meristem at each sampling, and the percentage of daughter axes that were "lifting off" the basal plate or sprouting also were determined. If the axes were elongating prematurely, they were termed "summer-sprouting" (Roberts and others 1955); if the axes elongated during normal harvest in September ('Ace') or October ('Nellie White') they were termed "fall sprouts." In both cases the length of the axes above the basal plate was recorded. A summary of some of these data for the September and October harvest samples is shown in Table 2.

The four growing seasons from 1974 through 1977 were only average or below in bulb yield at most locations for both 'Ace' and 'Nellie White.' There was a great deal of variation from grower to grower and on the same farm, so differences between seasons are difficult to evaluate. The seasons from 1978 through 1982 were generally more favorable for bulb growth, and this was reflected in increased bulb size of both cultivars on most farm sites. County agent surveys of crop yield for this period are in general agreement with these conclusions, especially when comparing the very best and poorest yields. The 1978, 1981, and 1982 seasons were particularly favorable for bulb growth and development of both 'Ace' and 'Nellie White' on most sites. An outstanding

Table 1. Summary of monthly heat unit accumulations (degree-days) at Brookings Weather Station, 1966-1982[1]

| Month | 1966 | 1967 | 1968 | 1969 | 1970 | 1971 | 1972 | 1973 | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| January | 540 | 543 | 560 | 659 | 466 | 574 | 628 | 578 | 577 | 561 | 526 | 495 | 488 | 565 | 529 | 372 | 600 |
| February | 513 | 439 | 370 | 551 | 360 | 511 | 489 | 379 | 505 | 483 | 540 | 371 | 453 | 501 | 360 | 373 | 460 |
| March | 531 | 549 | 431 | 454 | 403 | 551 | 449 | 537 | 478 | 507 | 571 | 554 | 373 | 418 | 478 | 419 | 512 |
| Total | 1,584 | 1,531 | 1,361 | 1,664 | 1,229 | 1,636 | 1,566 | 1,494 | 1,560 | 1,551 | 1,637 | 1,420 | 1,274 | 1,484 | 1,367 | 1,164 | 1,572 |
| April | 330 | 525 | 426 | 461 | 496 | 492 | 449 | 362 | 417 | 503 | 489 | 426 | 430 | 390 | 364 | 372 | 419 |
| May | 312 | 331 | 345 | 285 | 302 | 351 | 340 | 348 | 356 | 296 | 349 | 382 | 277 | 238 | 331 | 288 | 267 |
| June | 209 | 231 | 215 | 205 | 247 | 294 | 203 | 216 | 232 | 215 | 238 | 222 | 223 | 211 | 215 | 150 | 204 |
| Total | 851 | 1,087 | 986 | 951 | 1,045 | 1,137 | 992 | 926 | 1,005 | 1,014 | 1,076 | 1,030 | 930 | 839 | 910 | 810 | 890 |
| July | 211 | 179 | 224 | 180 | 214 | 231 | 162 | 215 | 166 | 150 | 169 | 193 | 177 | 129 | 118 | 174 | 164 |
| August | 199 | 199 | 167 | 189 | 212 | 127 | 127 | 247 | 162 | 208 | 153 | 175 | 173 | 107 | 176 | 134 | 144 |
| September | 130 | 124 | 171 | 184 | 140 | 177 | 220 | 171 | 245 | 223 | 192 | 211 | 155 | 56 | 155 | 166 | 111 |
| Total | 540 | 502 | 562 | 553 | 566 | 535 | 509 | 633 | 573 | 581 | 514 | 579 | 505 | 292 | 449 | 474 | 419 |
| October | 275 | 219 | 334 | 275 | 302 | 367 | 252 | 315 | 228 | 320 | 267 | 337 | 208 | 206 | 249 | 312 | 228 |
| November | 391 | 294 | 414 | 352 | 353 | 451 | 389 | 467 | 406 | 455 | 316 | 465 | 469 | 382 | 357 | 347 | 399 |
| December | 484 | 546 | 596 | .... | 557 | 644 | 642 | 467 | 504 | 575 | 505 | 500 | 617 | 444 | 421 | 447 | 476 |
| Total | 1,150 | 1,059 | 1,343 | .... | 1,212 | 1,462 | 1,283 | 1,249 | 1,138 | 1,350 | 1,088 | 1,302 | 1,294 | 1,032 | 1,027 | 1,106 | 1,103 |

[1]Quarterly degree-day totals are the sums of the negative departures of average daily air temperatures from 65°F. Therefore, the smaller the figure, the warmer the season or period in question.

Table 2. Summary of bulb growth analysis at time of September and October harvest (averages for 50 bulbs—10 bulbs from each grower)

| | September harvest weights | | | No. of daughter primordia | | | Ratios | | Late September | | Late October | | | September degree-days[1] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | Total | Mother | Daughter | Scales | Leaves | Total | Leaves/daughter bulb wt. | Daughter/mother bulb wt. | Apex diam. | Percent sprouting | Apex diam. | Percent sprouting | Sprout length | |
| | (g) | (g) | (g) | | | | (g) | (g) | (mm) | (%) | (mm) | (%) | (mm) | |
| | | | | | | | 'ACE' | | | | | | | |
| 1974 | 93.7 | 49.4 | 44.3 | 49 | 32 | 81 | .72 | .90 | 0.57 | 10% | .76 | 100% | 24 | 245 |
| 1975 | 86.2 | 53.6 | 32.6 | 47 | 40 | 87 | 1.22 | .61 | 0.71 | 20 | .76 | 100 | 21 | 223 |
| 1976 | 87.7 | 42.2 | 44.5 | 53 | 33 | 86 | .74 | 1.06 | 0.65 | 0 | .66 | 100 | 8 | 192 |
| 1977 | 101.0 | 56.5 | 44.5 | 51 | 35 | 86 | .79 | .79 | 0.67 | 20 | .69 | 88 | 18 | 211 |
| 1978 | 114.7 | 62.4 | 52.3 | 45 | 42 | 87 | .80 | .84 | 0.68 | 6 | .72 | 60 | 25 | 155 |
| 1979 | 100.6 | 52.4 | 48.2 | 61 | 27 | 88 | .56 | .92 | 0.53 | 0 | .64 | 93 | 3 | 56 |
| 1980 | 104.0 | 56.6 | 47.4 | 55 | 36 | 91 | .76 | .84 | 0.63 | 32 | .67 | 100 | 15 | 155 |
| 1981 | 108.7 | 54.6 | 54.1 | 57 | 47 | 104 | .87 | .99 | 0.63 | 94 | .66 | 100 | 23 | 166 |
| 1982 | 106.3 | 53.8 | 52.5 | 43 | 53 | 96 | 1.01 | .98 | 0.60 | 28 | .... | .... | .... | 111 |
| | | | | | | | 'NELLIE WHITE' | | | | | | | |
| 1974 | 81.8 | 39.7 | 42.1 | 49 | 36 | 85 | .86 | 1.06 | 0.53 | 0 | .61 | 100% | 11 | 245 |
| 1975 | 92.9 | 54.4 | 38.5 | 47 | 31 | 78 | .81 | .71 | 0.64 | 0 | .64 | 100 | 8 | 223 |
| 1976 | 103.2 | 49.2 | 54.0 | 53 | 30 | 83 | .56 | 1.10 | 0.61 | 2 | .63 | 6 | 5 | 192 |
| 1977 | 97.8 | 55.6 | 42.2 | 54 | 30 | 84 | .71 | .76 | 0.62 | 0 | .63 | 20 | 12 | 211 |
| 1978 | 125.0 | 62.9 | 62.1 | 49 | 42 | 91 | .68 | .99 | 0.63 | 0 | .66 | 10 | 6 | 155 |
| 1979 | 113.6 | 54.6 | 59.0 | 62 | 24 | 86 | .41 | 1.08 | 0.49 | 0 | .56 | 69 | 2 | 56 |
| 1980 | 107.4 | 56.0 | 51.4 | 57 | 34 | 91 | .66 | .92 | 0.56 | 0 | .64 | 94 | 5 | 155 |
| 1981 | 158.9 | 81.0 | 77.9 | 64 | 45 | 109 | .58 | .96 | 0.61 | 16 | .69 | 100 | 7 | 166 |
| 1982 | 143.3 | 70.1 | 73.2 | 56 | 47 | 103 | .64 | 1.04 | 0.62 | 0 | .... | .... | .... | 111 |

[1]Monthly degree-day totals are the sums of the negative departures of average daily temperatures from 65°F. Therefore, the smaller the figure, the warmer the month. National Climatic Center summaries. Soil temperatures would be even warmer.

'Nellie White' crop was produced in 1979; some California growers believe this to be one of the best 'Nellie White' bulb crops on record.

Although canopy formation (primary axis extension) in the lily plant starts in January on the southern Oregon and northern California coasts, significant gains in leaf dry weight do not occur until early April (Roberts and others 1964), and are completed with anthesis in late June or early July. It is reasonable therefore, in relating crop progress and harvest yield to seasonal temperatures, to divide the year in quarters as follows:

Fall (Oct-Nov-Dec): root and shoot elongation and meristem activation;

Winter (Jan-Feb-Mar): flower and scale initiation;

Spring (Apr-May-Jun): leaf unfolding, flower development, scale initiation and filling; and

Summer (Jul-Aug-Sep): leaf initiation, scale filling, and maturity development.

On the basis of grower records and those obtained from Research Station samples each year, it is evident that warm springs and summers are associated with large bulbs (Table 3). This is consistent with conclusions drawn from greenhouse and growth chamber experiments conducted under controlled environments (Roberts and others 1983, Wang and Roberts 1970). The initiation rate of bulb scale primordia from the new meristem, which formed the new secondary axis, during the prebloom period was more or less proportional to growing temperatures, reaching a maximum in 'Ace' at 18°C. 'Nellie White' had a lower optimum temperature. During flower development, the meristem produced as many scale primordia at 12°C as 'Ace' did at 18°C.

If we assume that warm springs and summers are essential for early maturing and large bulbs, and use Brookings Weather Station degree-day totals to measure relative warmth, we can determine to some extent the relation of the season to growth (scale initiatory activity) and development (scale filling) of the bulb crop. These data are presented in Table 3, with number of primordia on secondary meristem representing initiatory activity and bulb weight at final harvest indicative of bulb yield. With both 'Ace' and 'Nellie White' cultivars the largest bulbs and highest primordia counts were produced in years with above-average temperatures in April, May, and June. The two exceptions were in 1970 and 1973, when unusual crop responses occurred. The 1970 season had the second warmest winter on record, followed by a cool summer (Tables 1 and 3). This resulted in a high percentage of "summer-sprouting" or premature elongation of the secondary axis in June and July. The 1973 season also started out with above-average winter temperatures and a warm spring but then came the coldest summer on record, which resulted in "fall-sprouting" or advanced elongation of daughter axis in the field during September and October at the time of bulb lifting and packaging. Two of the largest crop years (1978 and 1981) also started out with warm winters, but these were followed by warm springs and summers that prevented premature sprouting and encouraged early and continuous scale filling or bulbing (Roberts and others 1983).

Table 3. Apparent relation between spring and summer heat accumulation, secondary bulb axis initiatory activity, and bulb scale weight at harvest for 'Ace' and 'Nellie White' cultivars

| Year[1] | Degree-day totals[2] | July leaf count[3] | | July primordia count[4] | | September harvest weight[5] | |
|---|---|---|---|---|---|---|---|
| | | A | NW | A | NW | A | AW |
| | | | | | | (g) | (g) |
| | | *Spring Quarter (A-M-J)* | | | | | |
| *1981 | 810 | 86 | 87 | 71 | 78 | 109 | 159 |
| *1979 | 839 | 78 | 65 | 69 | 73 | 101 | 114 |
| 1966 | 851 | 77 | 78 | 65 | 68 | 172 | 191 |
| *1982 | 890 | 72 | 82 | 79 | 87 | 106 | 143 |
| *1980 | 910 | 75 | 74 | 72 | 71 | 104 | 107 |
| 1973 | 926 | 74 | 69 | 47 | 49 | 74 | 100 |
| *1978 | 930 | 72 | 78 | 63 | 71 | 115 | 125 |
| 1969 | 951 | 73 | 72 | 61 | 68 | 124 | 125 |
| 1968 | 986 | 78 | 72 | 64 | 65 | 103 | 150 |
| 1972 | 992 | 62 | 62 | 56 | 58 | 103 | 163 |
| *1974 | 1,005 | 71 | 64 | 49 | 56 | 94 | 82 |
| *1975 | 1,014 | 61 | 62 | 53 | 53 | 86 | 93 |
| *1977 | 1,030 | 73 | 69 | 56 | 57 | 101 | 98 |
| 1970 | 1,045 | 80 | 74 | 73 | 75 | 112 | 138 |
| *1976 | 1,076 | 68 | 69 | 61 | 60 | 88 | 103 |
| 1971 | 1,137 | 73 | 69 | 52 | 49 | 92 | 113 |
| | | *Summer Quarter (J-A-S)* | | | | | |
| *1979 | 292 | 78 | 65 | 69 | 73 | 101 | 114 |
| *1982 | 419 | 72 | 82 | 79 | 87 | 106 | 143 |
| *1980 | 449 | 75 | 74 | 72 | 71 | 104 | 107 |
| *1981 | 474 | 86 | 87 | 71 | 78 | 109 | 159 |
| *1978 | 505 | 72 | 78 | 63 | 71 | 115 | 125 |
| 1972 | 509 | 62 | 62 | 56 | 58 | 103 | 163 |
| *1976 | 514 | 68 | 69 | 61 | 60 | 88 | 103 |
| 1971 | 535 | 73 | 69 | 52 | 49 | 92 | 113 |
| 1966 | 540 | 77 | 78 | 65 | 68 | 172 | 191 |
| 1969 | 553 | 73 | 72 | 61 | 68 | 124 | 125 |
| 1968 | 562 | 78 | 72 | 64 | 65 | 103 | 150 |
| 1970 | 566 | 80 | 74 | 73 | 75 | 112 | 138 |
| *1974 | 573 | 71 | 64 | 49 | 56 | 94 | 82 |
| *1977 | 579 | 73 | 69 | 56 | 57 | 101 | 98 |
| *1975 | 581 | 61 | 62 | 53 | 53 | 86 | 93 |
| 1973 | 633 | 74 | 69 | 47 | 49 | 74 | 100 |

[1]Years marked with asterisk are based on grower samples from commercial fields; other years are based on Research Station samples only. Bulbs were summer-sprouted in 1970, fall-sprouted in 1973.

[2]Monthly degree-day totals are the sums of the negative departures of average daily temperatures from 65°F. Therefore, the smaller the figure, the warmer the period. From Brookings, Oregon, Weather Station.

[3]Leaves unfolded on primary axis (mother).

[4]Scale and leaf primordia initiated on secondary axis (daughter).

[5]Average bulb weight in grams at harvest for both 'Ace' (A) and 'Nellie White' (NW).

Two of the largest crops on record for the 1966-1982 period were produced in 1966 and 1981 for 'Ace' and 'Nellie White,' respectively. Both seasons started out with relatively cold winters that were followed by two of the warmest springs for the period. Summer temperatures in 1966, somewhat lower than those for 1981, were the fourth highest summer temperatures for the 17-year period (Tables 1 and 3). These observations and growth chamber research (Roberts and others 1983, Wang and Roberts 1983) led us to conclude that temperatures during canopy formation (spring) and flower bud development on the primary axis are critical in providing a long growing season for early development of the new daughter bulb and scale filling of the bulb. Weather data collected at the Pacific Bulb Growers' Research and Development Station for the 1976-1981 period (Fig. 3) show 1978 and 1981 had especially warm winters and springs, consistent with the conclusions drawn. The entire 1976 growing season (winter-spring-summer) was the coldest recorded for the 7-year period at the Research Station, producing one of the poorest crops. Comparison of weather data (Table 1) and crop performance (Tables 2 and 3) indicates that spring and summer temperatures and not winter temperatures are critical in producing outstanding crops. It may be significant that years having above-average spring temperatures also have above-average summer temperatures.

Growth (initiatory activity) and yield (scale filling) are closely associated with seasonal weather conditions. Growth rate and duration of period of constant growth rate determine bulb size potential (Roberts and Tomasovich 1975). The duration of growth is related to the time of flower initiation; early flower initiation is associated with long duration. Large yields of bulbs generally have been associated with near- or above-average spring temperatures which both promote earlier flower initiation and increase the rate and duration of constant growth (Roberts and others 1983, Wang and Roberts 1983). See Table 11 for supporting data.

Unlike most bulbous crops, lilies have a long growing season, growing below or above ground throughout the year in the field (Figs. 2 and 4). For this reason, many factors can influence growth and development differently at different times of the year. We will consider some of these factors, based on observations or research data, as we proceed through the growing season—from planting in October until harvest the following September.

## Primary Axis Elongation

### *Pre-emergence factors*

*Effects of cultivar*. Data have shown that 'Nellie White' outyields 'Ace' in most years (Table 2). This is substantiated by county agent records from grower fields and from packing shed data. Large differences in bulb size, bulblet production, and in field and greenhouse flowering potential have been demonstrated between *longiflorum* clones in our breeding program. This is not unusual and has been recorded for tulips, narcissus, and other bulbous crops (Rees 1972).

*Planting stock size*. The weight of lily bulblets and yearlings increases steadily, and under field conditions these increases are fairly uniform during

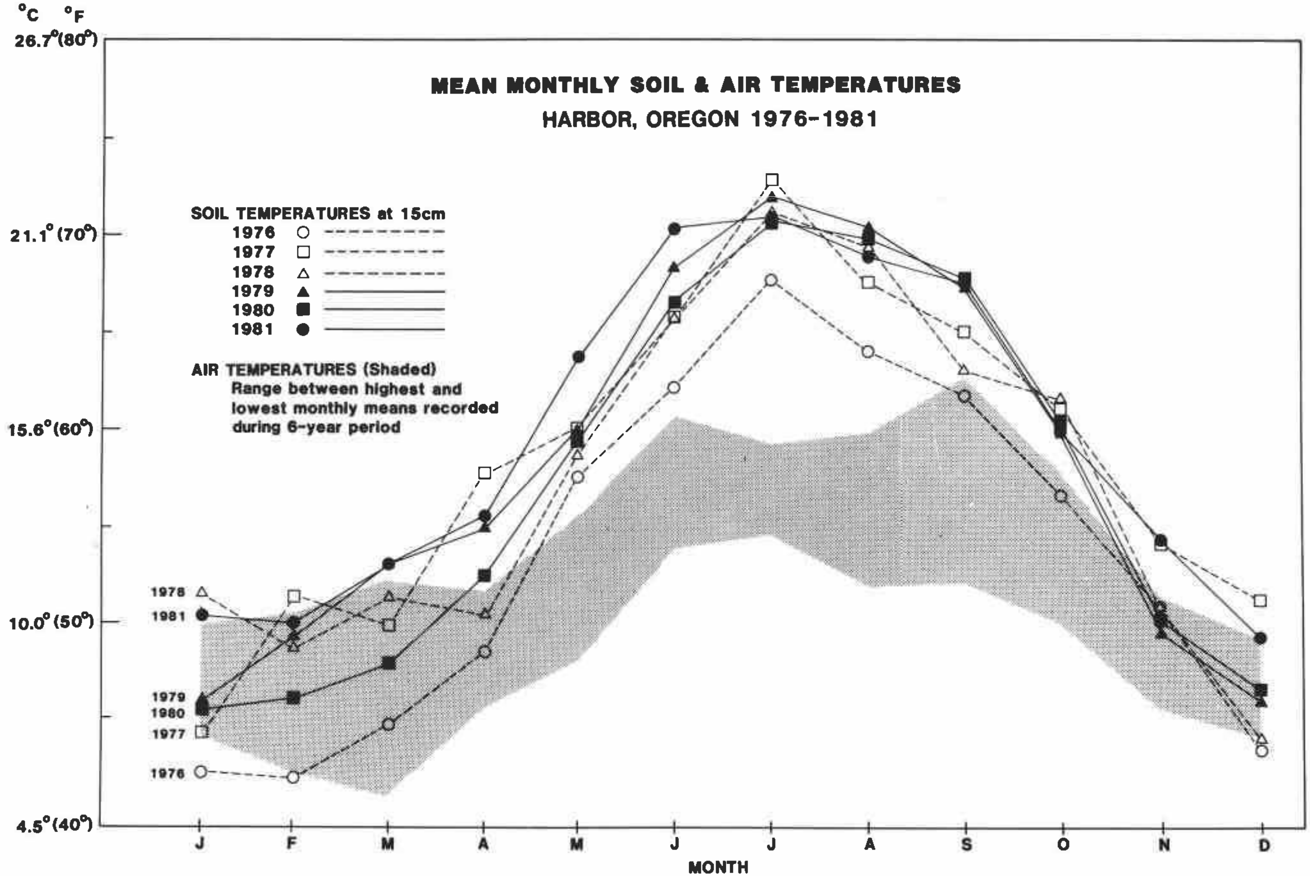


Figure 3. Mean monthly soil and air temperatures at Pacific Bulb Growers' Research and Development Station, Harbor, Oregon, for 1976-1981.

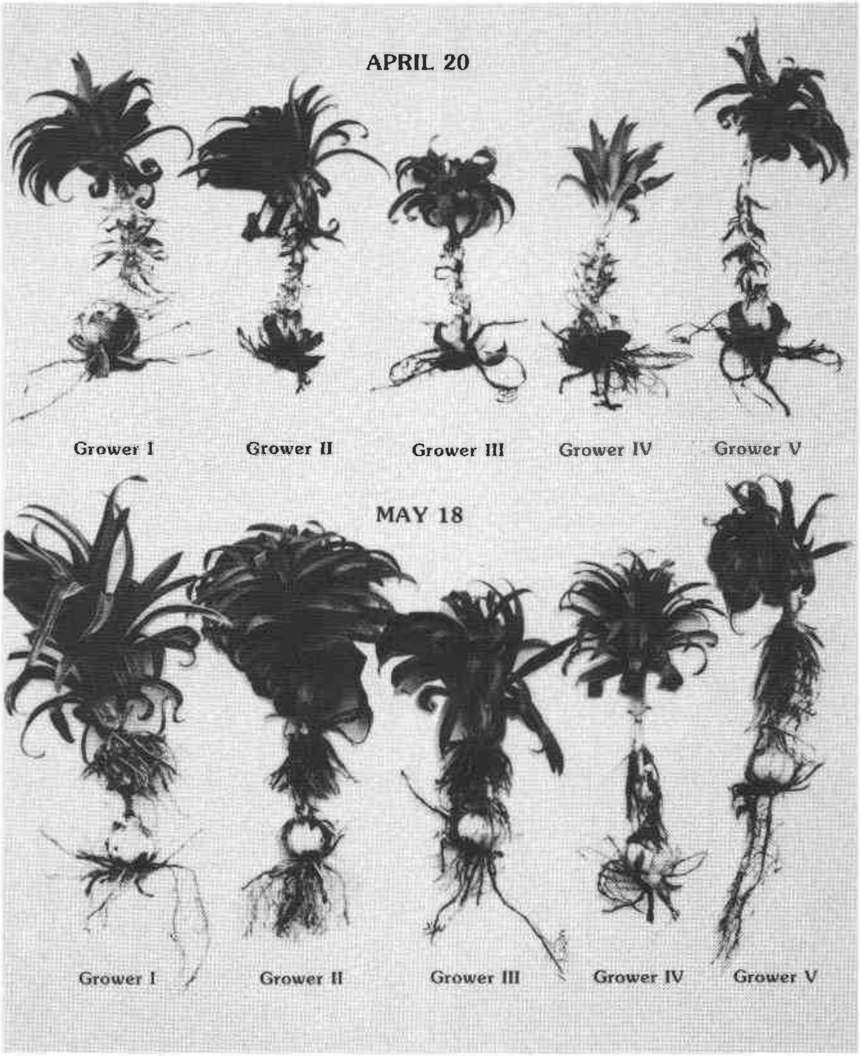


**Figure 4a. Appearance of samples of 'Croft' lily taken in April and May of 1956.**

canopy formation and until bulb harvest. Although planting stock size materially affects stem and canopy size and bulb yield potential, other factors may be of equal or greater importance. A 1964 nutrition study (Roberts and others) showed the rate of increase in bulb weight differed among grower fields with essentially the same size planting stock. The percentage gain in fresh weight from planting to harvest of bulblets growing to yearlings was 260, 434, 466, 493, and 552 for growers 5, 4, 1, 2, and 3, respectively; and for yearlings growing to commercials it was 176, 250, 278, 322, and 371 for growers 5, 2, 3, 1, and 4, respectively.

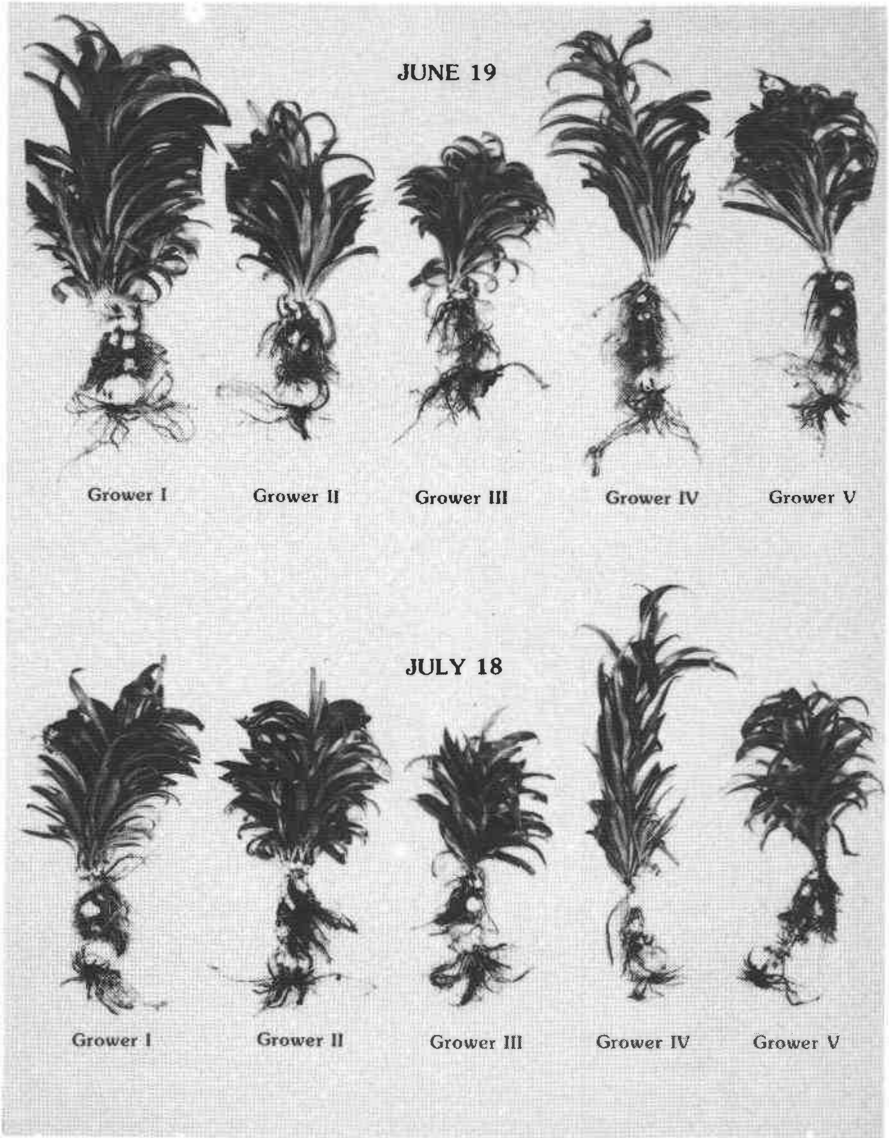


**Figure 4b. Appearance of samples of 'Croft' lily taken in June and July of 1956.**

If we include the weight variations caused by weather conditions between years (seasonal), it is impossible to predict the magnitude of the advantage to be gained from using larger planting stock. Kohl (1967) found that the number of leaves produced by the primary meristem or mother axis per unit of time was directly proportional to bulb size. Rees and others (1968) studied the effect of bulb size on growth pattern on tulips, using four bulb sizes planted at standard

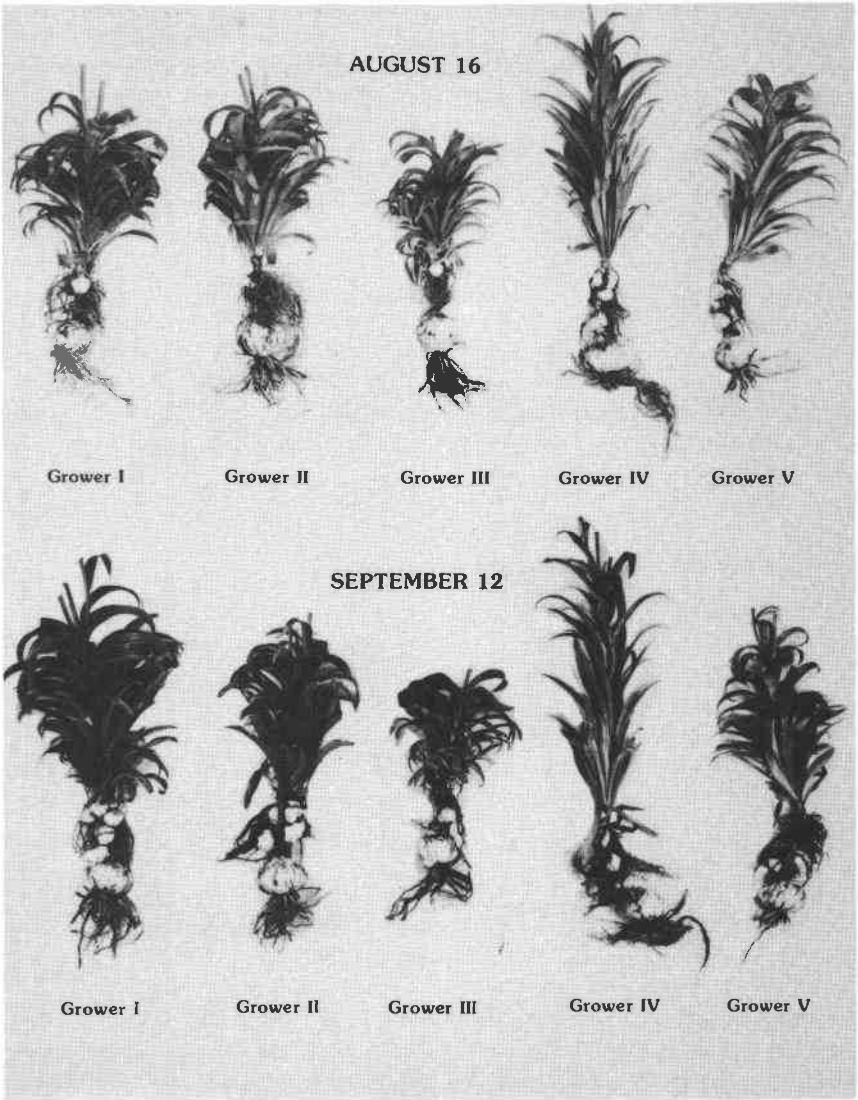


**Figure 4c. Appearance of samples of 'Croft' lily taken in August and September of 1956.**

spacings. Similar patterns of leaf area increase and decrease were obtained with plants from all sizes of bulbs, but peaks were higher in plants from large bulbs. However, he also found that relative growth rates (based on dry weight increase) decreased with increasing bulb size.

*Time of planting.* Commercial practice has demonstrated that October is the desirable time to plant lily bulblets and yearlings in Northwest fields (Blaney and Roberts 1967, Roberts and Blaney 1957). Earlier planting can result in premature starting of shoot growth which may subject the shoot to undue winter stress or spring frosts. Later fall plantings may meet with unfavorable weather conditions both for planting operations and bulb establishment. Cold storage of bulbs through the winter followed by early spring planting has given poor results. Some years, spring plantings have shown poor rooting, low leaf numbers, and a tendency for the bulbs to develop numerous lateral meristems or multiple "noses" or growing points (secondary axes).

Since the autumn planting date is seriously limited by weather conditions and time required in attaining adequate bulb size, the trend has been toward earlier planting (as early as mid-August) in Northwest fields. Therefore, the influence of time of planting on subsequent performances of the crop depends on how advanced the bulb stock was when harvested, how well the bulb will continue to develop during pathogen treatment and storage before replanting, and prevailing soil conditions (primarily soil temperatures) after planting.

Factors most likely to influence bulb yield the following year as a result of planting date would be those which will ultimately influence leaf number (leaf area) and leaf area duration (Rees 1972). Unlike Dutch bulbs (tulips, narcissus, and bulbous iris), the lily has an indeterminate leaf number that is determined by time of flower induction. Planting stock of a given size ordinarily will produce the same number of leaves in the canopy year after year unless planting date, planting stock size, planting depth, or soil temperatures drastically change growth rate or time of flower induction. Early planting while soil temperatures are in the 10° to 15°C range is conducive to extended leaf primordia formation before sufficient chilling at 5°C has brought about flower induction. Large planting stock grows faster and consequently can produce more leaves before flower initiation. However, effective leaf area in lilies can change constantly, with new leaves unfolding up to time of flower anthesis and older basal leaves senescing after flowering and as the plant matures and canopy shading increases. Appreciable loss of basal leaves normally will not occur until after flowering.

Using data obtained in West Coast fields from 1974 through 1982 (Table 11), it is possible to compare June bulb weight with the number of leaves unfolded on the primary axis by the last week in April before appreciable basal leaf loss (Fig. 5). The relationship between leaf number and bulb size development evidently is stronger in 'Nellie White' than in 'Ace' during the period of canopy formation.

These results suggest that early canopy formation and large leaf numbers favor larger bulb size or conversely, as Kohl (1967) has established, large bulb development favors more rapid leaf initiation and unfolding (growth rate). In any case, large bulb years are associated with early canopy formation, early flowering, and early bulb filling. The relationship between leaf numbers and harvest yield (September) becomes less positive (see *Leaf removal studies*, p. 30.). The evidence available for Easter lilies thus far would suggest that the association between large leaf numbers and larger bulb sizes is the result of a more rapid formation of photosynthetic surface (and thus longer leaf-area duration) rather than gain or advantage in total photosynthetic surface.

*Planting depth.* Lily planting depths have varied with bulb size, soil type, and location. Large yearlings were first planted with the tops of the bulbs 15 to

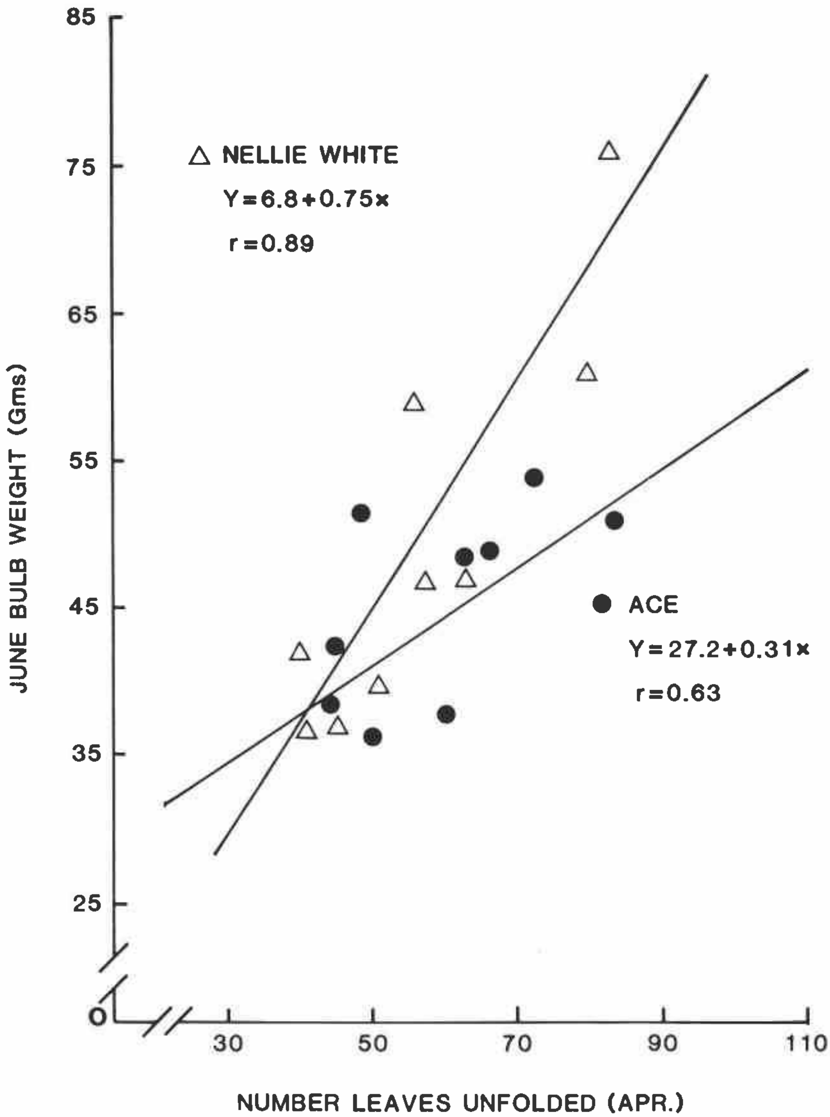


**Figure 5. Relationship between June bulb weight and number of leaves unfolded on the primary axis by the last week in April and before appreciable basal leaf loss, 1974-1982. (See data in Table 11.)**

20 cm (6-8 in.) below the soil surface, especially in light, sandy loam soils. With the advent of deep mounding, after planting to a height of 7 to 10 cm (3-4 in.) to protect the bulbs during severe winter weather and improve drainage and aeration, the below-ground (wheel track) depth has been reduced somewhat to 10 to 15 cm (4-6 in.), putting the top of the bulb 18 to 25 cm (7-10 in.) below the

top of the mound. Thus, growers speak of planting depth as distance from top of mound to top of the bulb and mound height as distance from wheel track to top of mound.

The influence of planting depth on such growth responses as primary axis (mother shoot) emergence (date), leaf number (canopy area) and rate of leaf unfolding, primary scale weight, secondary (daughter) initiatory activity (scale and leaf primordia numbers), secondary scale filling, and axis elongation (sprouting), have been the subject of considerable speculation without research information being available. A study designed to answer some of these questions was established by McCorkle at the Pacific Bulb Growers' Research and Development Station, Harbor, Oregon, on September 10, 1975.

The study included two experiments using two commercial cultivars, 'Ace' and 'Nellie White.' Each cultivar experiment consisted of nine treatments—three planting depths of 3, 10, and 18 cm and three mounding heights of 0, 8, and 15 cm in all combinations. The 40-50 gram yearling planting stock was planted in double-staggered rows at a density of 6 bulbs per 30 cm of row space. The rows were 107 cm apart. These carefully selected bulbs were planted in treatment row segments at random in nine treatment blocks replicated five times. Five-bulb samples were harvested on each of five dates for growth analysis and statistical evaluation.

Planting depth and mounding height did not significantly influence primary axis shoot emergence or the number of leaves and their rate of unfolding on the flowering axis (Tables 4 and 5). However, shallow planting (3 cm) or excessive mounding (15 cm) reduced weight of daughter bulb at harvest. This reduced the total weight of the bulb. Shallow planting also reduced primary scale weight in both 'Ace' and 'Nellie White,' but excessive mounding (15 cm) reduced primary scale weight in 'Ace' only. Mounding 8 cm was superior to no mounding or excessive mounding with 'Nellie White.'

The most significant influence of planting depth and mounding was on secondary axis development. Although excessive mounding (15 cm) significantly reduced the weight of secondary scales in both 'Ace' and 'Nellie White,' it did not influence the number of primordia initiated by the daughter meristem (Table 5). Although deep planting (10-18 cm) tended to favor increased weight of secondary scales, it was accompanied by significant reductions in number of secondary primordia (scales and leaves). A combination of medium planting depth with no mounding (or 8-cm mounds at most) produced the largest bulbs with maximum numbers of daughter primordia in 'Ace,' whereas deeper planting (18 cm) and some mounding (8 cm) produced the largest 'Nellie White' bulbs. These findings warrant further study because they suggest differences in the responses of the two cultivars.

The most striking result of this study was to find that shallow planting, regardless of mounding practice, greatly increased the incidence of "summer-sprouting" (Table 6). This was accompanied by increased numbers of daughter primordia (scales and leaves), showing the advanced development of this secondary axis. The ratio of secondary to primary scale weight substantiates this further. Temperature records taken at 3, 6, and 9 cm throughout the year showed the soil to be warmest at the 3-cm soil depth from January through

Table 4. Influence of planting depth and mound height on ultimate[1] fresh weight of primary (mother) and secondary (daughter) bulb scales, on total bulb weight, and on initiatory activity of mother and daughter meristems

| Mound height | Planting depth | Weight | | Total bulb weight | No. of secondary primordia | No. of primary leaves | Ratio of daughter/ mother weight |
|---|---|---|---|---|---|---|---|
| | | Primary scales | Secondary scales | | | | |
| (cm) | (cm) | (g) | (g) | (g) | (g) | | |
| | | | 'Ace' | | | | |
| 0 | 3 | 81.8 | 64.0 | 146.7 | 102 | 97 | .79 |
| | 10 | 91.3 | 71.2 | 162.5 | 104 | 97 | .78 |
| | 18 | 79.3 | 47.8 | 127.0 | 86 | 101 | .60 |
| 8 | 3 | 76.6 | 56.1 | 132.7 | 105 | 99 | .73 |
| | 10 | 90.2 | 68.7 | 158.8 | 100 | 100 | .76 |
| | 18 | 98.0 | 67.5 | 156.5 | 94 | 98 | .69 |
| 15 | 3 | 64.6 | 46.5 | 111.1 | 104 | 194 | .72 |
| | 10 | 86.7 | 67.2 | 153.9 | 100 | 101 | .78 |
| | 18 | 84.0 | 58.5 | 142.5 | 86 | 105 | .69 |
| | LSD .05 | 5.0 | 3.5 | 7.8 | 5.3 | 7.3 | .... |
| | LSD .01 | 6.8 | 4.8 | 10.7 | 7.4 | 10.1 | .... |
| | | | 'Nellie White' | | | | |
| 0 | 3 | 56.7 | 34.5 | 91.0 | 92 | 75 | .61 |
| | 10 | 71.8 | 49.2 | 122.8 | 85 | 83 | .70 |
| | 18 | 75.6 | 45.9 | 121.1 | 78 | 84 | .61 |
| 8 | 3 | 52.1 | 35.9 | 88.7 | 105 | 81 | .69 |
| | 10 | 76.7 | 45.3 | 120.4 | 88 | 86 | .59 |
| | 18 | 90.3 | 48.5 | 138.6 | 81 | 88 | .54 |
| 15 | 3 | 51.6 | 36.6 | 83.8 | 91 | 75 | .71 |
| | 10 | 74.1 | 35.4 | 109.3 | 81 | 81 | .48 |
| | 18 | 82.4 | 46.2 | 127.0 | 85 | 84 | .56 |
| | LSD .05 | 4.9 | 5.7 | 7.8 | 10.1 | 6.6 | .... |
| | LSD .01 | 6.8 | 7.8 | 10.7 | 13.9 | 9.1 | .... |

[1]Ultimate fresh weight refers to fresh weight at September harvest date.

April, approximately uniform in temperature from 3 to 9 cm from June to August, and warmest at 9 cm from October to November. May, September, and December were transition months. The warmer temperatures at 3 cm during the spring could account for the advanced spring development of the secondary axis when the bulbs are planted shallowly. This advanced development could, in turn, increase the likelihood that the secondary axis would sprout prematurely if exposed to cool temperatures in late spring and summer.

*Plant density*. Commercial crops of lilies grown in West Coast fields are planted at a wide variety of spacings. However, planting stock consisting of 4-, 5-, and 6-in. (10.2, 12.7, and 15.2 cm in circumference) yearlings are most

Table 5. Summary of influence of planting depth and mound height on harvest weight of primary (mother) and secondary (daughter) bulb scales and on initiatory activity of mother and daughter meristems[1]

| | | Weight | | | Ratio | | |
|---|---|---|---|---|---|---|---|
| | | Primary scales | Secondary scales | Total bulb weight | daughter/ mother weight | No. of primary leaves[2] | No. of secondary primordia[3] |
| | | (g) | (g) | (g) | (g) | | |
| **'Ace'** | | | | | | | |
| Mound height (cm) | 0 | 84.1 | 61.3 | 145.4 | .73 | 99 | 97 |
| | 8 | 88.3 | 64.1 | 152.4 | .73 | 100 | 100 |
| | 15 | 78.4 | 57.4 | 135.8 | .73 | 103 | 97 |
| Planting depth (cm) | 3 | 74.3 | 55.8 | 130.2 | .75 | 100 | 104 |
| | 10 | 89.4 | 69.0 | 158.4 | .77 | 100 | 102 |
| | 18 | 87.1 | 57.9 | 142.0 | .67 | 102 | 89 |
| LSD .05 | | 2.9 | 2.0 | 4.5 | .... | 4.2 | 3.1 |
| LSD .01 | | 3.9 | 2.8 | 6.2 | .... | 5.8 | 4.2 |
| **'Nellie White'** | | | | | | | |
| Mound height (cm) | 0 | 68.0 | 43.5 | 111.6 | .64 | 81 | 85 |
| | 8 | 73.0 | 42.9 | 115.9 | .59 | 85 | 91 |
| | 15 | 69.4 | 37.4 | 106.7 | .54 | 80 | 86 |
| Planting depth (cm) | 3 | 53.5 | 34.3 | 87.8 | .64 | 77 | 96 |
| | 10 | 74.2 | 43.3 | 117.5 | .59 | 83 | 85 |
| | 18 | 82.7 | 46.1 | 128.9 | .55 | 85 | 81 |
| LSD .05 | | 2.8 | 3.3 | 4.5 | .... | 3.8 | 5.8 |
| LSD .01 | | 3.9 | 4.5 | 6.2 | .... | 3.3 | 8.0 |

[1]Based on study by W. R. McCorkle at Pacific Bulb Growers' Research and Development Station, Harbor, Oregon, September 1975.

[2]Number of leaves on flowering stem.

[3]Total number of scale and leaf primordia on secondary axis.

often planted 4 to 6 bulbs per foot (30 cm) in double, often staggered rows. The mounded or ridged rows are traditionally 40 to 42 inches (101-107 cm) apart, but some are planted at 36 inches (91 cm) to increase plant density. There have been few studies on the effect of planting density on lily yields in this country or abroad. However, detailed studies have been made of tulips and narcissus in England and The Netherlands. Rees and others (1968) found planting density had no effect on flowering date in narcissus, but high densities increased stem length by more than 20 percent. Flower number increased almost linearly with increasing density, but flower number per bulb decreased from unity to 0.87 at the highest density. Lifted bulb weight per unit area increased with increase in

Table 6. Influence of planting depth and mound height on initiatory activity (scale primordia) and premature elongation (summer-sprouting) of secondary axis (June 3, 1976)

| | | 'Ace' | | 'Nellie White' | |
|---|---|---|---|---|---|
| Mound height | Planting depth | Daughter primordia | Summer-sprouting | Daughter primordia | Summer-sprouting |
| (cm) | (cm) | | (%) | | (%) |
| 0 | 3 | 53.6 | 40 | 52.7 | 47 |
| | 10 | 42.4 | 0 | 46.9 | 0 |
| | 18 | 43.1 | 0 | 41.8 | 0 |
| 8 | 3 | 56.9 | 53 | 58.5 | 53 |
| | 10 | 43.3 | 7 | 43.6 | 0 |
| | 18 | 44.1 | 0 | 45.1 | 0 |
| 15 | 3 | 54.6 | 33 | 58.6 | 47 |
| | 10 | 45.8 | 0 | 46.4 | 0 |
| | 18 | 47.4 | 0 | 47.8 | 0 |

Based on study by W. R. McCorkle at Pacific Bulb Growers' Research and Development Station, Harbor, Oregon; 3 replications, 5 bulbs per sample, mean of 15 bulbs.

planting density following the equation proposed by Bleasdale and Nelder (1960), but did not reach an asymptote within the range of densities employed (to 150 bulbs/m-$^{3}$). There was a corresponding increase in the weight of round bulbs.

Plant density of Easter lilies was studied at the Pacific Bulb Growers' Research and Development Station at Harbor, Oregon, during the 1980-1981 and 1981-1982 seasons by L. J. Riddle. Replicated plots of 5- to 6-in. (13-15 cm) 'Ace' and 'Nellie White' yearlings were planted to compare 4, 5, 6, 7, and 8 bulbs per foot (30 cm) of row. Rows were spaced 40 inches (102 cm) apart, giving population densities of 52, 65, 78, 91, and 104,000 bulbs per acre, respectively. Yields were lower than normal at the station in the 1981-1982 season; the 1980-1981 season was above average. However, in both growing seasons, increasing plant density increased gross income per acre potential, primarily by increasing number of bulbs per acre with only slight decreases in average bulb size (Table 7). Higher densities also decreased the incidence of "summer-sprouting" and weed growth but increased the number of unsalable bulbs.

Rees (1972) concluded from narcissus studies that there are quite large seasonal differences in both optimum planting rates and in financial returns. In Rees' narcissus experiments (Rees and Turguand 1969), he found that optimal planting rates are considerably higher than those used commercially in the United Kingdom. The same situation appears to be true for commercially grown lilies along the West Coast of this country. Planting methods (beds versus ridges) and bulb densities are selected on the basis of convenience in the use of equipment and labor. The planting density is considerably below the potential in salable bulbs. Methods for conducting and evaluating density trials are well established for narcissus and tulips, but further research is necessary for *Lilium*.

Table 7. Effect of planting density in 'Nellie White' Easter lily on average bulb size and distribution of sizes (1981 and 1982 crops)[1]

| Density | Year | Percentage of bulb sizes: Commercial | 7-8 in. | 8-9 in. | 9-10 in. | 10-inch and above | Average bulb size |
|---|---|---|---|---|---|---|---|
| | | (%) | (%) | (%) | (%) | (%) | (in.) |
| 4 bulbs/row foot 52,000/acre 13/m² | 1982 | 0.3 | 8.3 | 51.6 | 35.6 | 4.0 | 8.7 |
| | 1981 | 0.0 | 0.0 | 4.5 | 19.0 | 76.0 | 10.3 |
| 5 bulbs/row foot 65,000/acre 16/m² | 1982 | 0.0 | 14.3 | 59.3 | 24.6 | 1.6 | 8.5 |
| | 1981 | 0.0 | 0.0 | 3.0 | 34.0 | 62.0 | 10.1 |
| 6 bulbs/row foot 78,000/acre 19/m² | 1982 | 0.3 | 20.3 | 57.0 | 20.3 | 2.0 | 8.4 |
| | 1981 | 0.0 | 0.0 | 10.0 | 63.0 | 26.0 | 9.6 |
| 7 bulbs/row foot 91,000/acre 22/m² | 1982 | 2.6 | 32.6 | 54.3 | 10.3 | 0.0 | 8.1 |
| | 1981 | 0.0 | 0.0 | 15.0 | 50.0 | 34.0 | 9.6 |
| 8 bulbs/row foot 104,000/acre 26/m² | 1982 | 3.6 | 35.0 | 47.6 | 13.6 | 0.0 | 8.0 |
| | 1981 | 0.0 | 4.0 | 30.0 | 40.0 | 26.0 | 9.3 |

[1]Based on study by L. J. Riddle at the Pacific Bulb Growers' Research and Development Station, Harbor, Oregon.

***Prebloom factors***

*Canopy formation* (primary axis elongation and old scale depletion). At harvest the narcissus, tulip, and hyacinth bulbs contain a reproductive structure. A lily (*L. longiflorum*) or Easter lily bulb does not contain flower primordia or reproductive structure at time of harvest or planting. Rather, the leaf complement (number), stem length, and flower number vary greatly with bulb size, season, and planting density. Lily leaves are produced by the primary axis until floral initiation occurs; no active aerial vegetative apices are present after floral initiation.

A general review of canopy formation in *L. longiflorum* is found in papers describing the 3-year developmental cycle of the bulb (Blaney and Roberts 1966a) and observing the seasonal changes in weight of leaves and bulbs in commercial grower fields (Roberts and others 1964). Seasonal differences in time of primary axis emergence, rate of leaf unfolding, time of anthesis, and number of leaves in canopy as shown in Table 8 (data from Harbor, Oregon, 1963-1982). A more detailed picture of gains or losses in dry weight of various organs of 'Nellie White' Easter lily during various phases of growth is shown in Figure 6. The data used in this figure were obtained from controlled growth chamber studies (Roberts and others 1983).

Table 8. Seasonal differences in rate and extent of primary axis development in 'Ace' and 'Nellie White' Easter lilies (from 30-40 gram planting stock)[1]

| Year | Emergence date | Flower buds visible | Full bloom[2] | Total no. of leaves (July) | No. of secondary primordia (July) |
|---|---|---|---|---|---|
| | | | 'Ace' | | |
| 1981 | Dec 16, 1980 | ..... | Jun 23 | 86 | 71 |
| 1970 | Dec 19, 1969 | May 23 | Jul 4 | 80 | 73 |
| 1969 | Dec 20, 1968 | Jun 4 | Jul 16 | 73 | 61 |
| 1982 | Dec 26, 1981 | ..... | Jul 13 | 72 | 79 |
| 1978 | Jan 1, 1978 | ..... | Jun 25 | 72 | 63 |
| 1977 | Jan 3, 1977 | May 27 | Jul 3 | 73 | 56 |
| 1980 | Jan 7, 1980 | ..... | Jul 2 | 75 | 72 |
| 1971 | Jan 7, 1971 | Jun 4 | Jul 28 | 73 | 52 |
| 1976 | Jan 8, 1976 | ..... | Jul 8 | 68 | 61 |
| 1983 | Jan 11, 1983 | ..... | ..... | ..... | ..... |
| 1979 | Jan 15, 1979 | ..... | Jul 5 | 78 | 69 |
| 1968 | Jan 15, 1968 | May 21 | Jul 3 | 78 | 64 |
| 1974 | ..... | ..... | Jul 15 | 71 | 49 |
| 1975 | ..... | ..... | Jul 15 | 61 | 53 |
| 1973 | Jan 22, 1973 | May 28 | Jul 3 | 74 | 47 |
| 1972 | Jan 27, 1972 | Jun 4 | Jul 13 | 62 | 56 |
| 1966 | Jan 28, 1966 | May 26 | Jul 12 | 77 | 65 |
| 1963 | Feb 1, 1963 | Jun 13 | Jul 16 | 66 | ..... |
| 1967 | Feb 2, 1967 | Jun 8 | Jul 23 | 71 | ..... |
| 1965 | Feb 6, 1965 | May 25 | Jul 13 | 70 | 56 |
| 1964 | Feb 15, 1964 | Jun 10 | Jul 20 | 56 | 51 |
| | | | 'Nellie White' | | |
| 1982 | Dec 14, 1981 | ..... | Jul 13 | 82 | 87 |
| 1981 | Dec 23, 1980 | ..... | Jun 23 | 87 | 78 |
| 1970 | Dec 30, 1969 | May 22 | Jul 5 | 74 | 75 |
| 1978 | Jan 1, 1978 | ..... | Jun 25 | 78 | 71 |
| 1969 | Jan 5, 1969 | Jun 4 | Jul 14 | 72 | 68 |
| 1980 | Jan 7, 1980 | ..... | Jul 2 | 74 | 71 |
| 1976 | Jan 8, 1976 | ..... | Jul 8 | 69 | 60 |
| 1979 | Jan 9, 1979 | ..... | Jul 2 | 65 | 75 |
| 1968 | Jan 15, 1968 | May 19 | Jul 1 | 72 | 65 |
| 1983 | Jan 16, 1983 | ..... | ..... | ..... | ..... |
| 1977 | Jan 17, 1977 | May 27 | Jul 3 | 69 | 57 |

*(continued next page)*

Table 8. Seasonal differences in rate and extent of primary axis development in 'Ace' and 'Nellie White' Easter lilies (from 30-40 gram planting stock)[1]—(Continued)

| Year | Emergence date | Flower buds visible | Full bloom[2] | Total no. of leaves (July) | No. of secondary primordia (July) |
|---|---|---|---|---|---|
| 1973 | Jan 19, 1973 | May 26 | Jul 6 | 69 | 49 |
| 1975 | ..... | ..... | Jul 15 | 62 | 53 |
| 1974 | ..... | ..... | Jul 15 | 64 | 56 |
| 1972 | Jan 28, 1972 | Jun 2 | Jul 12 | 62 | 58 |
| 1966 | Feb 1, 1966 | May 23 | Jul 10 | 78 | 68 |
| 1967 | Feb 5, 1967 | Jun 6 | Jun 20 | 67 | ..... |
| 1965 | Feb 6, 1965 | May 29 | Jul 12 | 65 | 62 |
| 1971 | Feb 7, 1971 | Jun 10 | Jul 28 | 69 | 49 |

[1]Data from canopy formation study at Pacific Bulb Growers' Research and Development Station, Harbor, Oregon, using station samples only.

[2]When one-half of the plants have an open flower.

*Growth rate.* The early establishment of a "critical leaf surface" results in long growing seasons (duration of canopy) favorable to total net assimilation and high yields. Prebloom weather factors and planting stock size can affect specific growth rate and thereby affect canopy duration.

Rees (1972) has used dry weight and leaf area change with time to calculate the net assimilation rates and crop growth rates in tulip and narcissus during the growing season. His values are similar to those obtained with a range of other temperate crops such as kale, sugar beet, gladiolus, wheat, barley, grass swards, and potato. He concluded that bulbous plants in general and tulips in particular are susceptible to a potential loss of dry matter production because of their short growing season and early senescence. Potential dry matter production is maximized if the peak leaf area index coincides with the peak incoming solar radiation (intensity and duration). This would be near midsummer in an average season, but week-to-week variations in net assimilation can be as great as the maximum differences in values obtained from early spring to fall harvest because of extended periods of fog or heavy overcast in the Brookings-Smith River region of southern Oregon and northern California.

*Shoot emergence.* The Easter lily has a long growing season on the West Coast, extending from shoot emergence in late December to harvest in late August or early October the following year. Leaf canopy formation, beginning shortly after shoot emergence, is completed with the appearance of visible flower buds in late May or early June (Table 8). Leaf numbers on 30 to 40 grams planting stock (4-in. circumference) of 'Ace' and 'Nellie White' have varied from 56 (1964) to 86 (1981) in 'Ace' and 51 (1964) to 87 (1981) in 'Nellie White.' Since planting depth does not influence leaf number and rate of leaf unfolding significantly (Tables 4 to 6) and planting stock size was constant throughout these studies, planting date and/or winter and spring temperatures appeared to influence final leaf number significantly. Early planting in the autumn and

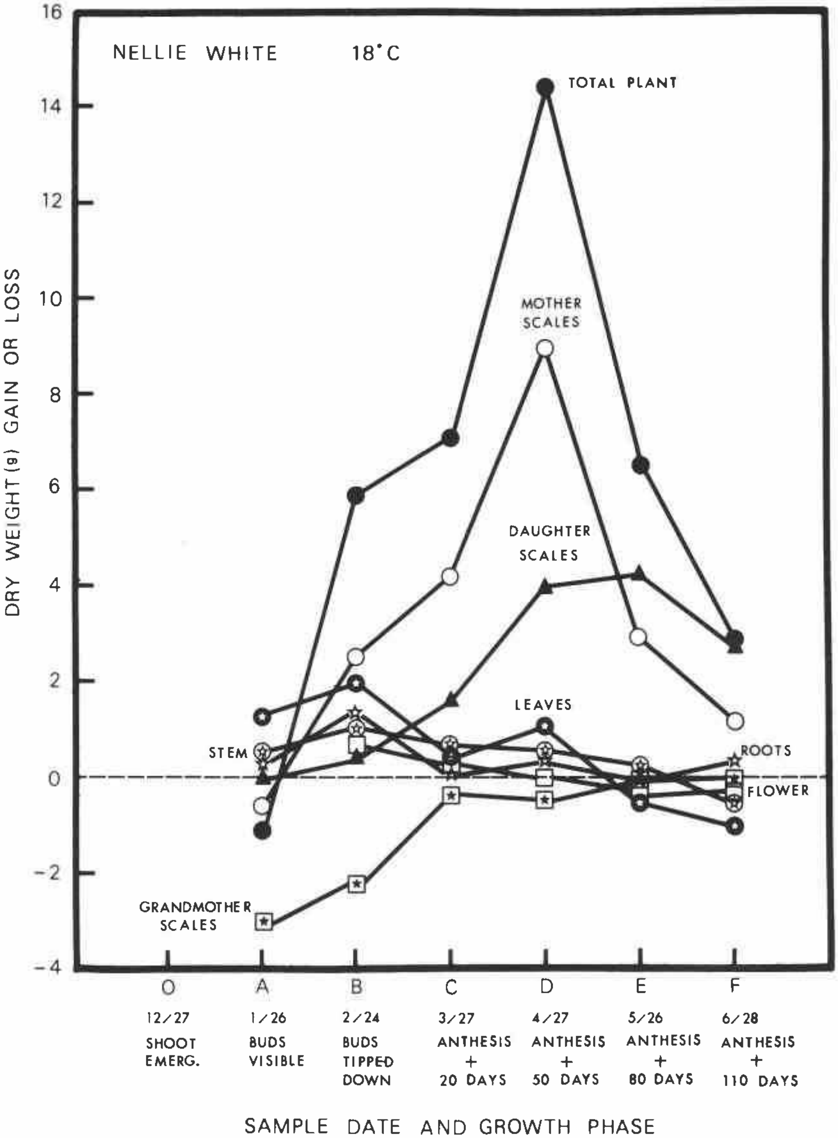


**Figure 6. Distribution of monthly gains or losses in dry weight of various organs of 'Nellie White' Easter lily during various phases of growth. Growth chamber at 18°C and near optimum for most stages.**

warm soil temperatures result in greater initiatory activity and leaf primordia formation before sufficient bulb chilling has occurred to induce flowering and terminate leaf making (temperatures are fairly constant all year at regular 6- to

9-in. (15-23 cm) planting depth). There does not appear to be a consistent relationship between date of shoot emergence or flowering and the leaf number on the primary axis (Table 8). However, there is a degree of relationship between early development of the secondary axis (July primordia count) and the leaf number on the secondary axis in 'Nellie White.' There does not appear to be any significant relationship between leaf number and bulb weight at harvest (Tables 4 and 5).

*Leaf removal studies.* The importance of leaf area or leaf numbers to bulb production in lilies has been a subject of considerable speculation. The effects of leaf removal in flower harvesting on gladiolus corm development have been determined (Roberts and Milbrath 1943, Compton 1957). Timmer and Koster (1969) found when whole leaf blades were removed before flowering in tulip, yield was reduced by up to 80 percent, but after flowering the reduction was about 50 percent.

Effects of leaf removal on lily bulb development were studied at the Pacific Bulb Growers' Research and Development Station in 1963-1964 using the 'Croft' cultivar. Large 'Croft' yearlings (40-50 g) were planted in autumn 1963, using the standard commercial practice of double-staggered row (6 bulbs per 30 cm of row) with mounding. At time of complete canopy formation (buds visible when terminal leaves separated), leaf removal treatments were as follows:

L-10: 10 basal leaves retained;
L-20: 20 basal leaves retained;
L-30: 30 basal leaves retained;
L-40: 40 basal leaves retained;
R-10: 10 basal leaves removed;
R-20: 20 basal leaves removed;
R-30: 30 basal leaves removed; and
R-40: 40 basal leaves removed.

Twelve plants were picked at random to receive each of the above treatments. The plants averaged approximately 65 leaves per plant at time of treatment, and there was an average of 55, 45, 33, and 28 leaves remaining on the plants after R-10, R-20, R-30, and R-40 treatments, respectively. At harvest on September 29, growth was analyzed to determine the effects of leaf removal on number of flowers produced, weight of old and new scales and bulblets, and number of new primordia (scales and leaves) formed.

This study showed that considerable leaf surface near the base of the plant can be removed when buds are first visible without reducing bulb yield. In fact, approximately half the leaves could be removed from the base of the plant without reducing bulb yield (Table 9). However, the terminal leaves seemed especially important in maintaining bulb weight—half or more of them were required to produce a normal yield. Leaf removal had less influence on initiatory activity (daughter primordia count) than on bulb scale filling. Sixty percent of the leaves could be removed at the time flower buds were visible without reducing the initiatory activity of this secondary meristem.

A greenhouse study (Roberts and Blaney 1968) determined the effects of vernalization and partial defoliation on flowering and correlative relationships

Table 9. Effects of leaf removal on certain growth and developmental responses in field-grown 'Croft' Easter lily (1963-1964)

| Treatments | | Weight | | | | No. of flower buds | Total primordia (secondary axis) |
|---|---|---|---|---|---|---|---|
| | | Old scales (g) | New scales (g) | Total bulb (g) | Total bulblet (g) | | |
| Basal leaves retained | Leaves removed[1] | | | | | | |
| Intact (control) | 0 | 75.4 | 69.6 | 146.7 | 33.4 | 3.0 | 71 |
| 10 | 55 | 28.2 | 12.4 | 40.6 | 8.0 | 1.4 | 45 |
| 20 | 45 | 33.1 | 15.8 | 48.9 | 10.2 | 2.2 | 54 |
| 30 | 35 | 37.2 | 23.0 | 60.2 | 16.9 | 2.7 | 60 |
| 40 | 25 | 46.6 | 26.2 | 72.8 | 29.7 | 3.2 | 60 |
| Basal leaves removed | Leaves retained[1] | | | | | | |
| 10 | 55 | 59.6 | 67.7 | 126.7 | 28.7 | 2.8 | 75 |
| 20 | 45 | 84.2 | 72.7 | 156.9 | 35.2 | 2.8 | 73 |
| 30 | 35 | 62.7 | 66.1 | 128.8 | 35.9 | 3.2 | 78 |
| 40 | 25 | 42.6 | 39.0 | 81.6 | 27.1 | 2.8 | 66 |
| Critical value | | | | | | | |
| 1% | | 13.6 | 14.4 | 18.0 | 15.8 | 0.85 | 8.7 |
| 5% | | 10.2 | 10.9 | 13.6 | 12.0 | 0.64 | 6.6 |

[1]Based on average of 65 leaves per plant.

in 'Croft' Easter lily. Plants were subjected to several defoliation treatments where various numbers of young or mature leaves were removed at different positions on the flowering shoot during successive stages of its elongation. The young, expanding leaves were essential to progressive elongation of the primary axis, especially through flower bud initiation with shoots from partially vernalized plants. These young, expanding leaves favored rapid leaf unfolding, internode elongation, complete flower bud development and maintenance of primary axis dominance by creating a strong mobilization sink or inhibiting the secondary axis. Prolonged chilling (vernalization treatment) reduced leaf numbers but increased internode lengths sufficiently to make stems longer. Chilled plants also were less dependent on leaves during early stages of axis elongation for maintaining growth rate and continuing flower bud development. Defoliation did not influence flower induction or initiation in plants receiving sufficient vernalization stimulus. Removing young leaves when approximately 30 percent of the leaf complement was unfolded enhanced development of the secondary axis significantly but resulted in abortion of most of the initiated flowers. The correlated inhibition of the secondary axis, especially in the partially vernalized plant, appeared to depend in great measure on the young, expanding leaves until the developing flower buds formed a strong sink.

Removal of basal leaves before buds were visible always resulted in weight loss in the mother and daughter portions of the bulb. This loss was greatest in the mother scales and was proportional to the number of leaves removed. The removal of the very young, expanding leaves conserved the reserves in the mother scales. Leaf removal before buds became visible, regardless of age or position on the axis, reduced weight of the mother scales more than that of the daughter scales.

Quinlan (1966) found that the shoot tip in apple was supplied with assimilates from leaves on the upper part of the shoot and the root system was supplied assimilates from the lowermost leaves. A leaf in the middle region exported assimilates both upward and downward. He concluded that partial defoliation caused changes in the pattern of distribution of assimilates from the remaining leaves, tending to compensate for the loss of part of the photosynthetic system. This would indicate, as also suggested by Joy (1964) when working with translocation in sugar beet, that vascular connections cannot be the only factor determining the pattern of distribution of assimilates from a particular leaf. The balance of photosynthetic supply from all the leaves on the plant also may influence the distribution pattern. Hartt and others (1964) found that actively growing lalas and suckers of sugarcane, which are sinks, increased the percentage of translocation downward, but that roots exert no force attracting the translocation. Defoliation above or below a fed leaf increased translocation to the stem, and the removal of upper leaves had greater effect than the removal of lower leaves. These data are similar to our findings with the Easter lily. Hartt was of the opinion that since translocation from a blade is increased by the removal of the other blades and can take place in a blade detached from the stalk, a major force of translocation is within the leaf blade itself.

These lily leaf removal studies suggest that removal of leaves at very early stages allows time for compensatory increases in size of remaining leaves and hence reduces net loss in leaf surface (Roberts and Blaney 1968). As much as 50 percent of the plant's young leaves could be removed from the plants with partially vernalized bulbs without appreciably depleting reserves from mother or daughter scales. A plant from a fully vernalized bulb in our greenhouse experiments had insufficient leaves for flower development, for development of the new daughter, and for maintaining the reserves in the mother scales.

Leaf surface in lily seems to be most critical in the field during the winter and early spring to assure early and rapid leaf canopy formation and flowering, thus assuring a long growing season for scale filling and maturation processes. After anthesis, as much as 40 to 50 percent of the older (basal) leaf surface can be lost or removed without appreciably reducing bulb size or secondary axis initiatory activity. It should be appreciated, however, that the younger leaves in upper parts of the canopy are essential to bulb development (especially scale filling and leaf initiation) and maintaining correlative relationships between various organs even after anthesis. Research (Roberts and Fuchiami 1972b) in the greenhouse has shown that the exposure of the senescing mother axis to 6 weeks of short days at 10°C (50°F) induced the secondary axis to flower at an earlier date than did plants exposed to long-day treatment. Besides flowering two weeks earlier, the short-day plants produced 30 percent fewer leaves and one less flower than those receiving the long-day treatment at the same temperature.

*Plant height relations* (stem length). Height control in lilies can be a problem in both field production and greenhouse forcing. Cultural practices in the field are best facilitated when plants are fairly short, and the florist trade is increasingly demanding shorter pot plants. Height control in the future will be solved genetically by breeding and selecting shorter cultivars. Breeding lines or cultivars to control plant height are becoming available in both white Easter lilies and the colored Asiatics and Oriental hybrids.

A degree of height control is being accomplished in greenhouse forcing by using A-Rest (ancymidol) applications (Wilkins 1980), and in the field through the use of deflowering sprays at bud visible stage (see section on deflowering studies, p. 38.).

A number of factors influence stem length in lilies. Wilkins (1980) found excessive temperatures (above 18.3°C) during early stages of forcing, excessive watering, night lighting at low intensities, and growing under long days to be conducive to excessive plant height. Smith and Langhans (1962) found height in lilies to be markedly influenced by photoperiod. Plants under an 18-hour photoperiod were twice as tall as those under a 9-hour photoperiod. Kohl (1967) cites references to show that light intensity can be an important factor in determining the height of lilies. Shading or high density planting in lilies increases plant height. Rees and others (1968) found planting density had no effect on flowering date in narcissus, but high densities increased stem length by more than 20 percent.

Leaf number, as influenced by bulb size, date of planting, and time of flower induction and initiation (chilling requirement satisfied), is considered to influence stem length. Stem length appears, however, to be more the result of internodal stretch as cells that are still plastic elongate in the stem. Unpublished data have shown that when shoots from vernalized bulbs are grown in total darkness they can be some 6 meters (20 ft.) tall. Roberts and Blaney (1968) also have shown that the basal internodes of partially vernalized plants are much more plastic or able to stretch than are those of fully vernalized plants. Removing terminal leaves seriously impaired stem elongation, whereas removing basal leaves increased plant height.

Leaf length appears to be inversely related to stem segment lengths (Blaney and Roberts 1966b). Comparison of the data for leaf and stem segment lengths shows that the longer the leaves, the shorter the stem segment, irrespective of storage treatment. Precooling increasingly elongated the internodes with each progressively later harvest. The progressive lengthening of the leaves of plants from nonvernalized bulbs harvested from July to September and the abrupt shortening of the leaves with the October harvest suggest a profound seasonal change in the physiological mechanism responsible for subsequent leaf expansion (Roberts and Blaney 1968).

Under West Coast field conditions, the chilling requirement for lily floral induction will be satisfied between mid-December and mid-January under normal circumstances (Fig. 2). Leaf number on the primary axis varies from year to year, depending on planting date, how near soil temperatures at planting depth are to the optimum (15°C) for leaf initiation, how long before the chilling requirement for flower induction is achieved, and how rapidly floral initiation occurs. Induction would be most rapid between 5° and 10°C and initiation would be most rapid at temperatures above this; that is, warm winters would favor rapid flower initiation and cessation of leaf initiation once flower induction has occurred.

During the 1974-1982 period, the number of leaves on the primary axis of 30 to 40 grams planting stock (samples from five growers in the Brookings-Smith River area) varied from 61 to 86 in 'Ace' and 62 to 87 in 'Nellie White' (Table 10). Stem length varied from 32.2 to 43.7 cm in 'Ace' and 28.7 to 35.1 cm in 'Nellie White.' There does not seem to be any consistent relationship in 'Ace' among leaf number, stem length, and daughter bulb weight. However, with the 'Nellie White' cultivar there are relationships of certain shoot and bulb parameters that are seasonal and that may be significant. Shoots that developed during the warmer spring seasons of 1978, 1980, 1981, and 1982 had a tendency to develop more leaves on the primary axis, were consistently shorter, and had greater daughter bulb weight. These data lend further support to the conclusion that leaf number has little relationship to stem length. They suggest that the rate of development of the secondary axis exerts a measure of control over stem elongation. The fact that the shortest lilies were associated with larger leaf complements is consistent with greenhouse studies mentioned, where basal leaf removal increased plant height (Roberts and Blaney 1968). Also, the shortest greenhouse lilies are often those "rooted down" in coldframes or CTF (controlled temperature forcing) facilities, which results in large, well-developed basal leaves.

*Flower development.* Lily bulbs require a period of cold under moist conditions for rapid elongation of the shoot axis and for rapid flower induction and initiation. Exposure to temperatures below 21° and above 1.5°C (Wilkins

Table 10. Seasonal differences in leaf number, stem length, and bulb harvest weight as related to heat accumulation[1] during spring months (1974-1982)

| Year | Total degree-days in April-May-June | Stem length (June) | Total no. of leaves/plant | Daughter bulb weight (June) |
|---|---|---|---|---|
| | | (cm) | | (g) |
| | | 'Ace' | | |
| 1974 | 1,005 | 43.7 | 71 | 9.4 |
| 1979 | 839 | 40.1 | 78 | 14.9 |
| 1976 | 1,076 | 38.9 | 68 | 10.9 |
| 1975 | 1,014 | 38.6 | 61 | 9.0 |
| 1977 | 1,030 | 38.2 | 73 | 6.9 |
| 1978 | 930 | 37.1 | 72 | 13.2 |
| 1981 | 810 | 34.7 | 86 | 20.3 |
| 1982 | 890 | 34.1 | 72 | 14.7 |
| 1980 | 910 | 33.2 | 75 | 11.1 |
| | | 'Nellie White' | | |
| 1975 | 1,014 | 35.1 | 62 | 7.2 |
| 1977 | 1,030 | 34.2 | 69 | 7.0 |
| 1974 | 1,005 | 34.1 | 64 | 8.3 |
| 1976 | 1,076 | 33.6 | 69 | 9.5 |
| 1979 | 839 | 31.5 | 65 | 14.2 |
| 1982 | 890 | 30.6 | 82 | 14.5 |
| 1980 | 910 | 30.3 | 74 | 12.2 |
| 1981 | 810 | 28.8 | 87 | 19.2 |
| 1978 | 930 | 28.7 | 78 | 14.8 |

[1]Heat accumulation: total degree-days for April-May-June. Quarterly degree-day totals are the sum of the negative departures of average daily temperatures from 65°F. Therefore, the smaller the figure, the warmer the season.

1980, Matsuo 1975) is effective in inducing flowering, the duration depending on how near the exposure is to the optimum temperature (5° to 7°C) and the physiological condition of the bulb. The optimum temperature for flower induction shifts from 10°C for bulbs dug in July and August to 5°C for bulbs dug in September and October (Roberts and others 1978). When mature Easter lily plants from nonvernalized bulbs are subjected to short days (SD) during acquisition of their cold requirement, they are induced to flower more rapidly than when receiving cold treatment under long days (LD) (Roberts and Fuchiami 1972b).

Long-day treatment to shoots from nonvernalized bulbs can substitute for vernalization on a day-for-day basis in cold treatment to induce rapid flowering. The LD's must be at temperatures below 21°C. Shoots from bulbs harvested early (July-August) are more responsive to LD flower induction at 22°C than those harvested later. This suggests that different mechanisms are involved for cold and photoperiodic induction (Roh and Wilkins 1977a).

Lily bulbs are programmed for greenhouse forcing under numerous conditions and by a variety of methods. Bulbs are programmed naturally in the field under straw, in coldframes outdoors, case-cooled in refrigerated storages, or under controlled temperature forcing (CTF). Wilkins (1980) and DeHertogh (1974) outlined methods that control the time of flower induction and initiation in the greenhouse rather precisely.

DeHertogh and others (1976) found the average date of flower initiation in 'Ace' lilies after controlled temperature forcing to be January 21, and one week later if bulbs had been precooled (case-cooled). Under West Coast field conditions, flower initiation commences naturally sometime in March, depending on seasonal temperatures (Table 11). When the first flower bud is approximately 0.50 mm in diameter, we can distinguish buds as a separate entity on the apical dome under the binocular microscope.

As found under controlled environments in greenhouse and growth chambers (Roberts and others 1983, Wang and Roberts 1983), leaf unfolding rate, flower initiation and development, and secondary axis initiation were equally sensitive to temperature fluctuations and could be used in monitoring crop status (Table 11). Early flower initiation and development in the field in response to warm springs (1978-1981) were evident in April in advanced flower bud size and in June with early anthesis, which was accompanied by more rapid leaf unfolding and advanced daughter bulb development.

The relationship between leaf number and speed of flowering in lilies often has been misunderstood. The conversion of the shoot from the vegetative to the reproductive state depends on temperatures between 21° and 1.5°C (Langhans and Weiler 1967, Roh and Wilkins 1977a, Wilkins 1980). The rapidity of this conversion depends on the physiological condition (maturity) of the bulb, how near the temperature treatment is to the optimum, and the duration of the temperature treatment (Roberts and others 1978). How quickly this transition from leaf making to flower bud formation occurs depends on a combination of factors.

In both the field and the greenhouse, leaf number on the lily plant is related either directly or indirectly to date of flower induction. The number of leaves becomes fixed when the shoot apex is converted from the vegetative to reproductive state. The number of leaf primordia on the apex at the time flower-inducing temperatures are imposed has a bearing on the final leaf number. How rapidly vernalization is accomplished will determine how quickly leaf initiation ceases and flower initiation commences. Data in Table 12, extracted from an earlier paper, indicate that floral induction and initiation occurred most rapidly in 'Nellie White' shoots from bulbs harvested in October and given 8 weeks storage at 5°C. These plants also had the lowest leaf number, which is consistent with numerous other studies. In general, late-harvested (October) bulbs with 52 leaf primordia at harvest were much more responsive to optimum flower-inducing cold treatments than early-harvested (August or September) bulbs. This was reflected in low numbers of leaves being initiated during storage and during early forcing before flower bud formation in the late-harvested bulbs (Table 12). However, the total number of leaves at flowering was not significantly different, nor was the number of days required to

Table 11. Seasonal differences in primary and secondary axis development in 'Ace' and 'Nellie White' Easter lilies in West Coast fields (1974-1982)[1]

| Crop year | Primary axis (mother): No. of leaves unfolded (April) | Flower bud diameter[2] (March) | Flower bud diameter[2] (April) | Stem length (June) | Date full bloom | Mother bulb weight (June) | Secondary axis: Daughter bulb weight (June) | No. of daughter primordia (June) | Total bulb weight (June) |
|---|---|---|---|---|---|---|---|---|---|
| | | (mm) | (mm) | (cm) | | (g) | (g) | | (g) |
| | | | | | 'Ace' | | | | |
| 1975 | 44 | 0.50 | 1.8 | 38.6 | Jul 15 | 29.6 | 9.0 | 43 | 38.6 |
| 1974 | 49 | 0.51 | 1.8 | 43.7 | Jul 15 | 27.2 | 9.4 | 42 | 36.6 |
| 1982 | 48 | ..... | 2.0 | 34.1 | Jul 13 | 37.0 | 14.7 | 53 | 51.7 |
| 1976 | 45 | 0.58 | 2.1 | 38.9 | Jul 8 | 31.7 | 10.9 | 49 | 42.6 |
| 1977 | 60 | 0.71 | 3.2 | 38.2 | Jul 3 | 31.2 | 6.9 | 42 | 38.1 |
| 1979 | 66 | 0.86 | 3.1 | 40.1 | Jul 5 | 34.3 | 14.9 | 56 | 49.1 |
| 1980 | 63 | 0.85 | 3.8 | 33.2 | Jul 2 | 37.1 | 11.1 | 54 | 48.2 |
| 1981 | 83 | ..... | 6.0 | 34.7 | Jun 23 | 31.6 | 20.3 | 62 | 51.9 |
| 1978 | 72 | 1.75 | 6.7 | 37.1 | Jun 25 | 40.6 | 13.2 | 50 | 53.8 |
| | | | | | 'Nellie White' | | | | |
| 1975 | 40 | 0.50 | 1.8 | 35.1 | Jul 15 | 29.6 | 7.2 | 44 | 36.8 |
| 1974 | 45 | 0.62 | 2.2 | 34.1 | Jul 15 | 28.6 | 8.3 | 44 | 36.9 |
| 1982 | 56 | ..... | 2.3 | 30.6 | Jul 13 | 44.2 | 14.5 | 60 | 58.7 |
| 1976 | 40 | 0.66 | 2.0 | 33.6 | Jul 8 | 32.2 | 9.5 | 50 | 41.7 |
| 1977 | 51 | 0.64 | 3.1 | 34.2 | Jul 3 | 32.9 | 7.0 | 47 | 39.9 |
| 1979 | 57 | 1.14 | 3.3 | 31.5 | Jul 2 | 32.7 | 14.2 | 58 | 46.9 |
| 1980 | 63 | 1.03 | 4.0 | 30.3 | Jul 2 | 34.7 | 12.2 | 57 | 46.9 |
| 1981 | 83 | ..... | 5.7 | 28.8 | Jun 23 | 57.0 | 19.2 | 68 | 76.2 |
| 1978 | 80 | 1.73 | 6.7 | 28.7 | Jun 25 | 46.2 | 14.8 | 56 | 61.0 |

[1]Based on averages of field samples from five grower fields including Pacific Bulb Growers' Research and Development Station, Harbor, Oregon.

[2]Widest diameter of largest developing bud in last week of month.

Table 12. Effectiveness of various vernalization (temperature/duration) on flower induction in 'Nellie White' Easter lily bulbs harvested at various stages of maturity

| Treatment | Date of bulb harvest[1] August (24 leaves) Final leaf number | August Days to flower[2] | September (33 leaves) Final leaf number | September Days to flower[2] | October (52 leaves) Final leaf number | October Days to flower[2] |
|---|---|---|---|---|---|---|
| 22°C ± 5 | | | | | | |
| Continuous | 230 | X | 193 | X | 255 | 297 |
| 15°C ± 1 | | | | | | |
| 8 weeks | 212 | X | 246 | X | 260 | X |
| 10 weeks | 209 | X | 243 | X | 250 | X |
| 12 weeks | 232 | X | 258 | 294 | 230 | X |
| 10°C ± 1 | | | | | | |
| 6 weeks | 118 | 102 | 104 | 87 | 110 | 93 |
| 8 weeks | 103 | 89 | 92 | 78 | 100 | 81 |
| 10 weeks | 89 | 87 | 99 | 77 | 102 | 81 |
| 5°C ± 1 | | | | | | |
| 4 weeks | 233 | X | 315 | 319 | 119 | 110 |
| 6 weeks | 178 | 119 | 92 | 77 | 89 | 76 |
| 8 weeks | 105 | 90 | 86 | 74 | 73 | 69 |

[1]Number of leaves in parentheses refers to leaf primordia on secondary (daughter) axis at time of harvest.

[2]X = Plants had not flowered at termination of experiment.

Data taken from A. N. Roberts and others, 1978, lily bulb harvest maturity indices predict forcing response. Journal of the American Society for Horticultural Science, 103(6):827-833.

flower (the larger number of leaf primordia with late harvest were offset by lower numbers of leaves being initiated subsequent to harvest). As has been well established (Roberts and others 1978), 15°C is the inductive temperature most conducive to leaf initiation and least conducive to flowering, and 12 weeks storage at 15°C was required to bring about flowering in September-harvested bulbs (294 days to flower).

The above principles would apply to lilies grown under field conditions, so it was not surprising to find that during the warm growing seasons (1978-1982), especially those with warm spring temperatures, flower initiation and anthesis were rapid and leaf numbers were relatively high. When bulbs are planted in the field early, they would have a relatively long growing season with soil temperatures near 15°C. This would favor leaf-making before soil temperatures drop or sufficient 5 to 10°C temperatures accumulate to bring about rapid flower induction and initiation in late February and March.

*Deflowering studies.* Plantings of commercial Easter lilies seldom are allowed to reach full bloom or anthesis. Flower buds are snapped off by hand or cut off some days or weeks before to reduce the spread of "fire," *Botrytis elliptica*, from the flowers dropped down onto the foliage. Early bud removal also tends to shorten the plant, which is an advantage in cultivation. If buds are removed as soon as they appear, bulb size can even be enhanced (Roberts and Fuchiami 1972a).

Neil Stuart of the U.S. Department of Agriculture, Beltsville, Maryland, working with 'Georgia' lilies, and Larry Blaney of Oregon State University, using 'Ace' and 'Croft' lilies, several years ago tested various chemical sprays for deflowering lilies at very early stages of flower development. They found CIPC (chlorprophan) sprays to be very effective if applied at the right time in proper concentration. A 1,500 parts per million (ppm) CIPC spray, applied with a 235 ppm Triton B1956 spreader, when the flower buds were the size of peas (7 to 10 mm), prevented flowering and reduced plant height by half. Also, bulb weights were significantly increased without reducing subsequent forcing performance in any way. The only detrimental effect of the spray was some spotting and necrosis of the terminal leaves directly under the remaining bud scars. These necrotic spots were thought to be a possible point for *Botrytis* invasion, so the chemicals were not considered entirely safe for commercial use. A reliable deflowering spray would be of considerable economic value to the bulb grower.

Roberts and Fuchigami (1972a) compared a new compound (Atlox 3404F/ Tween 20) with the best CIPC treatment for deflowering lilies in 1970-1971. When applied on May 23, all sprays were more effective on 'Nellie White' than on 'Ace.' When properly timed, Atlox/Tween sprays were as effective as CIPC on 'Nellie White' but not on 'Ace.' There was some increase in bulb weight as a result of the deflowering treatments, with the Atlox 3404F treatment being as effective as CIPC in both height control and weight increase but only about half as good in complete removal of flowers.

Lee Riddle of the Pacific Bulb Growers' Research and Development Station, Harbor, Oregon, has completed a three-year study in the field to determine proper timing and yield gain potential for deflowering lilies. He concludes that CIPC sprays should be applied when the largest flower bud is no larger than 7 to 10 mm to reduce plant height and to increase bulb size. Manual disbudding, if done early enough, also increases bulb yields. Five to ten percent increases in yield have been obtained from chemical disbudding.

### *Postbloom factors*

*Primary axis senescence.* Seasonal changes in leaf canopy appearance during the growing season are evident in survey samples taken of 'Croft' lily growers' fields during 1955 and 1956 (Fig. 4). Dry weights of leaves showed that growth was greatest between May 15 and July 15 (Roberts and others 1964). At the May 15 sampling, the yearling plants were 4 to 5 inches tall with 45 to 55 leaves fully expanded. By June 15, all their leaves were fully expanded and the flower buds were 2.5-3.5 cm long and still upright. Most yearling plants in the five fields were in full bloom by July 15. In the better yearlings, the leaves continued to increase in weight until August, when they lost dry weight, indicating a translocation of certain materials out of the tops or loss of basal leaves from senescence.

A similar study with the 'Ace' cultivar in 1964 (unpub.) provided data on the partitioning of dry matter to various above- and below-ground organs in the lily during the growing season (Fig. 7). Again, maximum dry weight of leaves

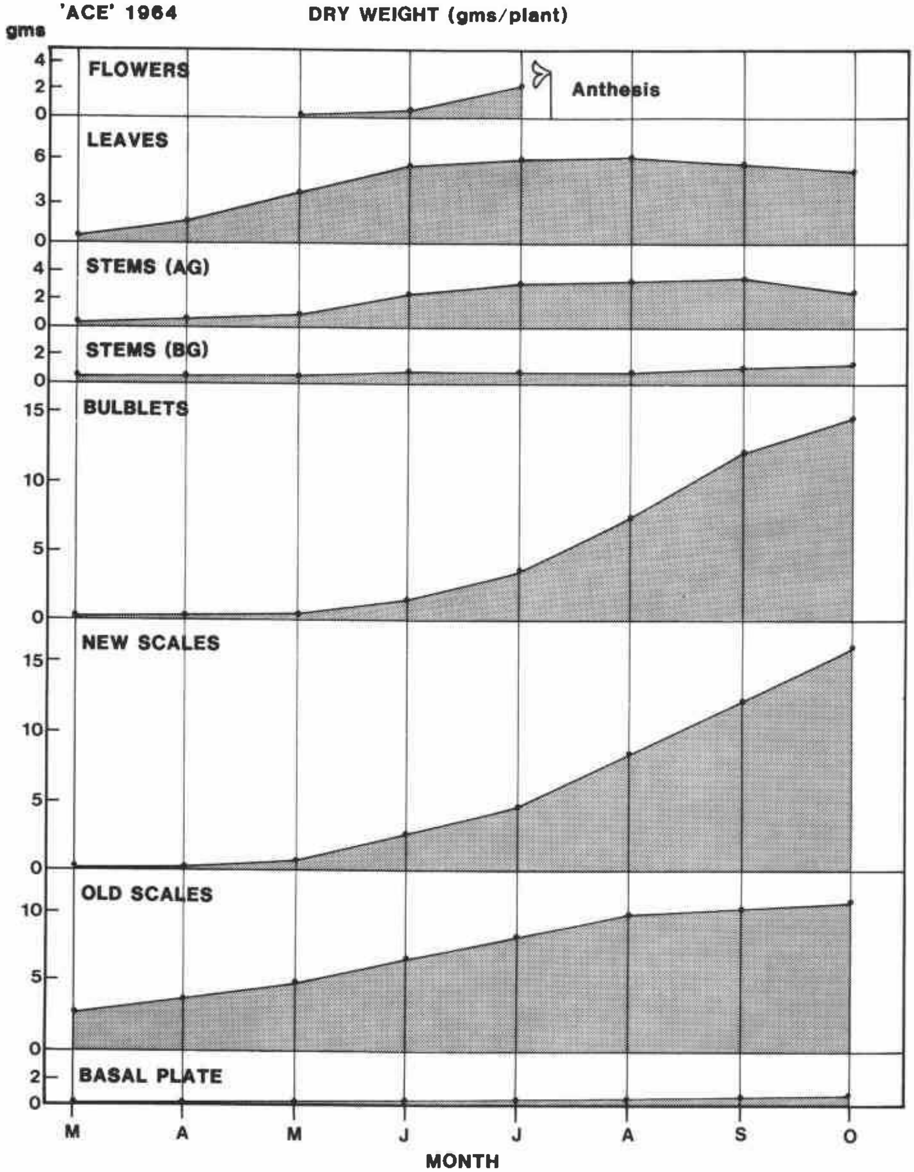


Figure 7a. Distribution of dry weight in organs of 'Ace' lily during the growing season in coastal fields of Oregon and California, 1964.

was achieved in August with some losses thereafter. Weather conditions are such in the West Coast lily-growing areas (California-Oregon) that the foliage remains green and intact until harvest in September and October. Leaf-yellowing,

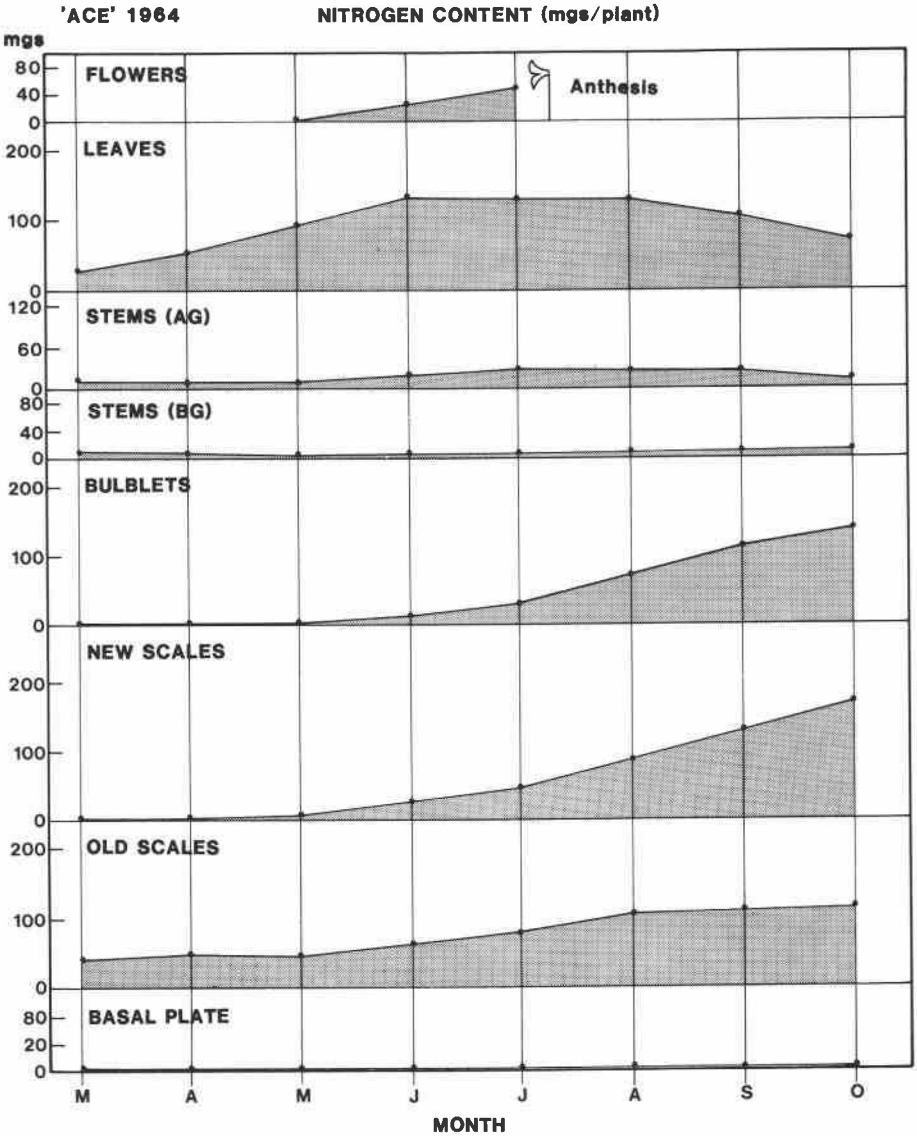


**Figure 7b. Seasonal distribution of nitrogen in organs of 'Ace' lily in West Coast (Oregon-California) fields during 1964.**

necrosis, and senescence often are the result of *Botrytis* infections, mechanical damage, or chemical injury.

Leaf-yellowing and senescence are assumed to be associated with the development of bulb maturity. However, Roberts and others (1983), using growth chamber studies, found leaf senescence (yellowing and loss of leaf weight) to be associated with advanced age and high temperatures. Leaf-

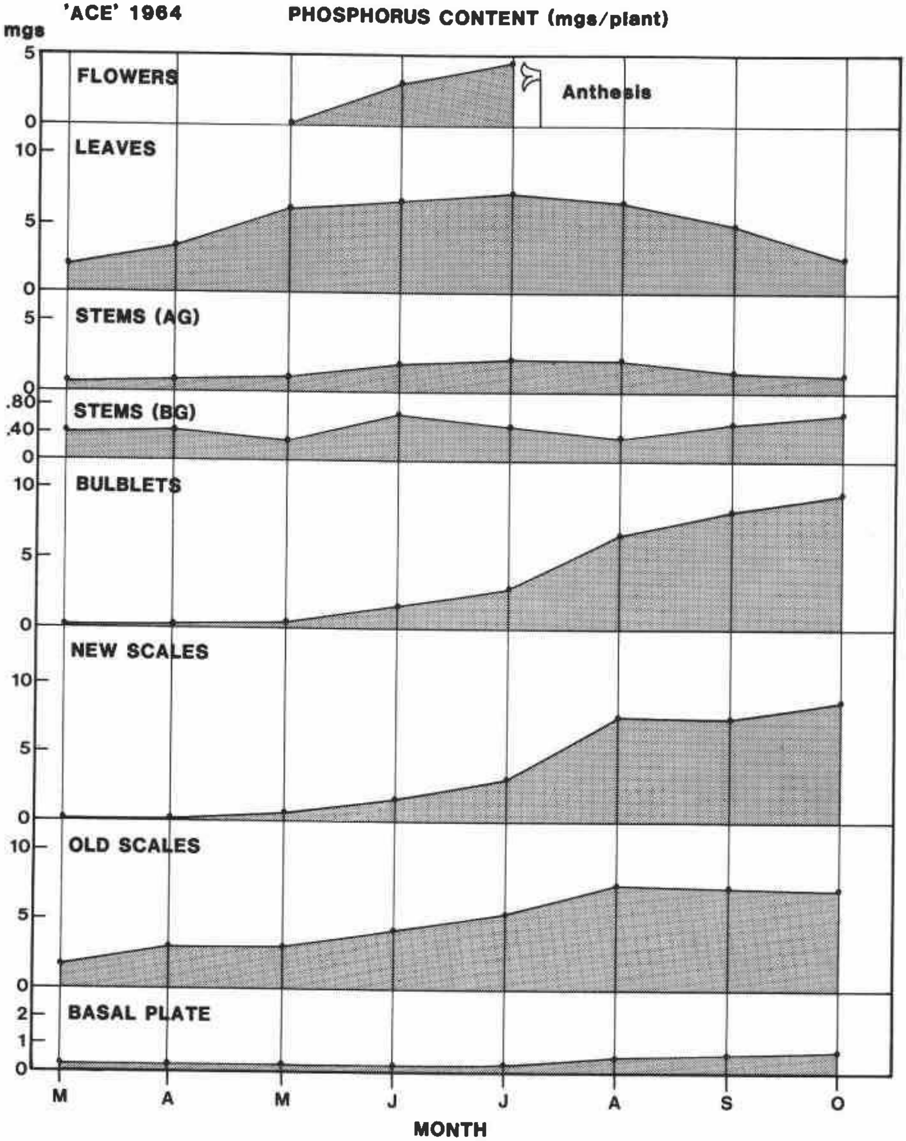


Figure 7c. Seasonal distribution of phosphorus, in organs of 'Ace' lily in West Coast (Oregon-California) fields during 1964.

yellowing was evident for the first time 50 days after flower anthesis at 24°C. At lower temperatures, no leaf senescence was observed. Eighty days after anthesis, plants at all temperatures showed some loss of green color, but at 24°C the plants turned yellow and withered. These temperatures are seldom achieved in late summer along the Oregon coast. After 110 days from anthesis, all leaves

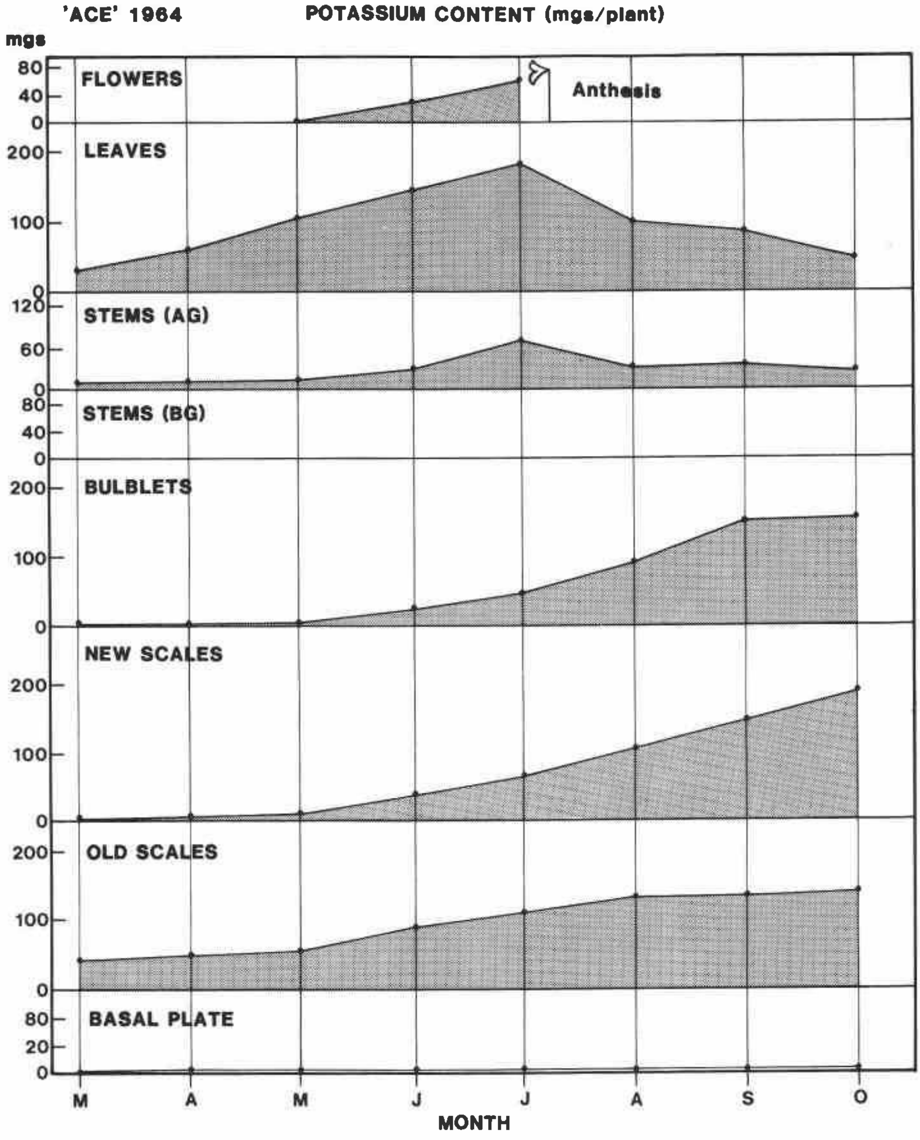


**Figure 7d. Seasonal distribution of potassium in organs of 'Ace' lily in West Coast (Oregon-California) fields during 1964.**

showed yellowing and withering except a few plants under 6° and 12°C treatment. The early leaf senescence associated with high temperature (24°C) did not favor increased bulb size, daughter leaf primordia count, daughter apex diameter, or sprouting tendency, so leaf senescence must be considered a poor index of harvest maturity and, therefore, unfavorable to bulb forcing potential as well.

Although leaf dry weight is maintained for some time after flower anthesis, the content of nitrogen, phosphorus, and potassium progressively decreases (Table 7). There is a compensatory increase of these nutrients in the storage organs of the bulb (scales and bulblets). There is a striking drop in the amount of potassium in the leaf and stem after flowering and a noticeable increase in the new daughter bulb and stem bulblets. Phosphorus increases rapidly in these organs at the same time, with only a slight change in the leaves, indicating entrance of new phosphorus into the system and redistribution of the phosphorus in above-ground parts.

The percentage (dry weight basis) of calcium in the foliage increases steadily during the growing season until time of bulb harvest (Roberts and others 1964). Leaf magnesium increases rapidly and uniformly from June till harvest. The differences among plantings were greater than for any other element. Bulb magnesium, like bulb calcium, was always very low and tended to decrease as the season progressed. Chaplin and Roberts (1981) have more recently cataloged the seasonal nutrient element distribution in leaves of 'Ace' and 'Nellie White' cultivars.

## Secondary Axis Development

### *Daughter bulb formation and development (initiatory activity)*

The shoot from a replanted yearling bulb emerges sooner in the autumn than does the shoot fron a replanted stem-bulblet. The new secondary axis (daughter meristem) first appears in the field near mid-December for the bulblet daughter (Blaney and Roberts 1966a). As in the stem-bulblet to yearling phases, the scale complement of the yearling daughter is determined at about flower anthesis in the yearling to commercial plant; primordia initiated later are destined to be leaves on the flower stem as the commercial bulb is forced into flower in the florists' greenhouses. At harvest, more than 30 percent of the total scale complement in commercial size bulbs was contributed during the bulblet to yearling phase; the remainder was contributed during the yearling to commercial phase. At harvest of a commercial bulb, it is not possible to determine between the innermost scales and the leaves until the shoot elongates off the basal plate.

Although scale initiation ceases sometime in July or near anthesis, recent studies have shown that the cessation of scale initiation and the beginning of leaf initiation on the secondary axis meristem are linked to temperature as much as the reproductive state of the primary axis. Blaney and Roberts (1966a) showed daughter or secondary primordia to be morphologically plastic at anthesis, and for several more weeks. When bulbs harvested in July and early August were precooled for 6 weeks at 5°C, the daughter-scale complement was reduced and the leaf primordia complement was higher than those of bulbs harvested at the same time but immediately replanted without vernalization. This vernalization resulted in some of the scale primordia becoming leaves on the flowering shoot when it finally elongated. When harvest was delayed until the early part of September or later, however, precooling did not alter the scale complement.

Recent growth chamber studies (Roberts and others 1983) have substantiated these earlier assumptions that the primordia being initiated by the secondary axis meristem during and for some time after anthesis are morphologically more plastic and can become leaves at lower temperatures or scales if subjected to warm enough growing conditions. High temperatures in the spring during the 1979 and 1981 growing seasons in the vicinity of Brookings, Oregon, and Smith River, California, resulted in bulb crops with 15 to 25 percent more daughter scales than average (Table 13). Regardless of harvest bulb weight, both 'Ace' and 'Nellie White' crops have had more daughter bulb scales after seasons with warm springs and early summers than those with lower temperatures.

The rate of scale initiation of the secondary axis meristem during the prebloom period is more or less related to growing temperature, reaching a maximum in 'Ace' at 18°C (Roberts and others 1983). 'Nellie White' has a lower temperature optimum. During primary axis development, the secondary axis of

Table 13. Relation of heat unit accumulation and bulb harvest weight (September) to daughter scale, leaf initiation, and meristem diameter at harvest in 'Ace' and 'Nellie White' bulbs (1974-1982)[1]

| Year | Degree-days[2] Spring A-M-J | Degree-days[2] Summer J-A-S | Average bulb weight | No. of scale primordia | No. of leaf primordia | Meristem diameter |
|---|---|---|---|---|---|---|
| | | | (g) | | | (mm) |
| | | | 'Ace' | | | |
| 1979 | 839 | 292 | 101 | 61 | 27 | 0.53 |
| 1981 | 810 | 474 | 109 | 57 | 47 | 0.63 |
| 1980 | 910 | 449 | 104 | 55 | 36 | 0.63 |
| 1976 | 1,076 | 514 | 88 | 53 | 33 | 0.65 |
| 1977 | 1,030 | 579 | 101 | 51 | 35 | 0.67 |
| 1974 | 1,005 | 573 | 94 | 49 | 32 | 0.57 |
| 1975 | 1,014 | 581 | 86 | 47 | 40 | 0.71 |
| 1978 | 930 | 505 | 115 | 45 | 42 | 0.68 |
| 1982 | 890 | 419 | 106 | 43 | 53 | 0.60 |
| | | | 'Nellie White' | | | |
| 1981 | 810 | 474 | 159 | 64 | 45 | 0.61 |
| 1979 | 839 | 292 | 114 | 62 | 24 | 0.49 |
| 1982 | 890 | 419 | 143 | 56 | 47 | 0.62 |
| 1980 | 910 | 449 | 107 | 57 | 34 | 0.56 |
| 1977 | 1,030 | 579 | 98 | 54 | 30 | 0.62 |
| 1976 | 1,076 | 514 | 103 | 53 | 30 | 0.61 |
| 1978 | 930 | 505 | 125 | 49 | 42 | 0.63 |
| 1974 | 1,005 | 573 | 82 | 49 | 36 | 0.53 |
| 1975 | 1,014 | 581 | 93 | 47 | 31 | 0.64 |

[1]From grower fields at Harbor, Oregon, and Smith River, California.

[2]Quarterly degree-day totals are the sums of the negative departures of average daily temperatures from 65°F. Therefore, the smaller the figure, the warmer the season (prebloom A-M-J, or postbloom J-A-S).

'Nellie White' produced as many scale primordia at 12°C as 'Ace' did at 18°C. This higher temperature optimum in 'Ace' also has been observed in the field, where the cultivar shows better performance during warm springs (Table 13). The tolerance of 'Nellie White' to lower temperatures may account for it having consistently higher yields than 'Ace' in the cool coastal climate of Oregon and northern California.

The shift in initiatory activity of the secondary axis from scale to leaf primordia at or near anthesis is accompanied by a shift in temperature optimum for organ initiation from 18° to 12°C in both cultivars, and a significant reduction in the rate of initiation at 24°C (Roberts and others 1983).

There has been no apparent relationship between daughter scale number and bulb size at harvest. However, the three largest crops (on basis of average bulb weight) produced during the 1974-1982 period (1978, 1981, and 1982) had significantly more leaf primordia per bulb (Table 13). This is consistent with Kohl and Nelson's (1963) observation that a high correlation exists between bulb size and leaf potential when the secondary axis elongates. Bulbs with the greatest number of scales and the least number of leaf primordia were produced in 1979 in both 'Ace' and 'Nellie White.' This, no doubt, was the result of a combination of one of the warmest springs on record with the warmest summer. This combination would be conducive to larger numbers of scale at the expense of leaf primordia. The higher numbers of scale and leaf found in bulbs produced in 1978, 1981, and 1982 were associated with warmer springs and summers, respectively. It is apparent that soil and air temperatures were not above the optimum for leaf initiation (Table 13).

Soil temperatures near 24°C are most conducive to initiation of scale primordia on the new secondary axis during the prebloom period (Wang and Roberts 1983). The acceleration in scale formation with warm (24°C) soil temperatures is most evident when air temperatures are low. These responses to warm soil temperatures are most evident during leaf unfolding and before flower buds are visible. The rate of secondary scale initiation decreases progressively during the prebloom period regardless of growing temperature (Roberts and others 1983, Wang and Roberts 1983).

### *Meristem (apex) diameter*

The relationship among leaf primordia number, daughter meristem diameter, and subsequent bulb-forcing performance has been the subject of considerable speculation as to their usefulness in developing harvest maturity indices (Roberts and others 1978). Likewise, the relation between bulb size and the number of leaf primordia and daughter meristem diameter at harvest has been confusing. Grower samples taken during the growing season and at harvest have not shown close relationships between these morphological characters (Table 13). Our results are not consistent with those of DeHertogh and others (1976) and Kolh (1967), who found that meristem diameter increased with bulb size. However, they were working with the new primary or flowering axis during greenhouse forcing, whereas our interest has been in the early stages of development of this axis in the field before bulb harvest. There has not been a consistent difference between secondary meristem diameter and growing temperature during prebloom phases, but after flower anthesis and in all phases of the postbloom period, large meristem size has been associated with 12°C or lower growing temperatures (Roberts and others 1983). As with leaf initiation, 12 to 18°C tended to increase apex diameter as well as the number of leaf primordia and 24°C significantly reduced both, especially in 'Nellie White.' Wang and Roberts (1983) found the diameter of secondary axis apical meristem decreased progressively with the approach of anthesis in the primary axis, but increased afterward.

During stem elongation and leaf unfolding, if the air temperatures were high and soil temperatures were below 24°C, dome size was increased in bulbs previously vernalized. When air temperatures were low and soil temperatures near or below 24°C, the size of the secondary axis meristem was increased. Wang and others (1970) found a negative correlation between apex size and length of bulb vernalization, concluding that the question still remains whether dome size or cessation of initiatory activity limits flower number in Easter lily, an indeterminate plant.

DeHertogh and others (1976) found that numbers of initial primary flowers on the flowering primary axis were correlated with large meristem diameter and bulb size with 'Ace,' and that a greenhouse temperature of 13°C promoted the formation of raised secondary flowers, while 21°C promoted the formation of tertiary flowers. Roh and Wilkins (1977b) found that with 'Nellie White' these temperatures are 7.2° and 15.6°C, respectively.

Growth chamber studies (Roberts and others 1983, Wang and Roberts 1983) and field observations (Table 13) have shown that in warm seasons (1979 and 1974) it is possible to produce large bulbs that have comparatively small secondary meristems with low leaf-primordia numbers at harvest, thus requiring modification of forcing programs to increase leaf numbers and meristem diameter before inducing flowering. An example of such modification is bulb vernalization at 10° rather than 5°C. This increases leaf and flower numbers without sacrificing speed of flowering (Roberts and others 1978). The more rapid emergence of bulbs given 10°C storage appears to offset the time required to unfold the increased leaf complement.

## BULB SIZE DEVELOPMENT

### Bulb Weight Increase

Early anthesis usually has been associated with above-average yields because the scale-filling period of development is longer. Yield potential is greater, provided the foliage remains functional (Rees 1972, Roberts and Tomasovich 1975). From shoot emergence to visible buds, and sometimes beyond (Wang and Roberts 1983), there is a decrease in bulb dry weight, primarily as a result of complete utilization of reserves in older scales and partial depletion of younger scales on the primary axis (Roberts and others 1983). It is difficult to determine the significance of dry weight changes in individual organs, especially old primary scales, during growth and development. The failure of scale weight to increase during a growth phase can be the result of reserves being moved out of older scales for canopy formation at the same rate that they are being stored in the younger scales, or there may be no reserves available for storage as a result of excessive respiration or reduced net assimilation.

During the prebloom period, there are net losses in dry weight of mother scales (Roberts and others 1983). However, if air temperatures are relatively cool (18° day and 13°C night) with warm (24°C) soil temperatures, some dry weight accumulation will occur during canopy formation. Generally, higher temperatures (24°C) will increase scale dry weight loss during the prebloom period, as a result of increased growth rate of the flowering axis.

### Scale Filling (Bulbing)

From the time the flower buds tipped downward until the flowers reached anthesis, the new secondary scales significantly increase in dry weight at an optimum temperature range between 18 and 24°C (Roberts and others 1983). The greatest gains in secondary scale weight were made 50 to 80 days after flower anthesis, as contrasted with the primary scales that appeared to have the strongest sink 20 to 50 days after anthesis. Secondary scale filling appears strongest somewhat later in time and to be favored by higher temperatures (18-24°C) than filling for the primary scales. This has been observed in the field as well as in growth chamber experiments. Forty percent of bulb weight increase (1974 example) occurred the month before harvest (August 15-September 15) and principally in these secondary scales.

A five-year cycle (1978-1982) of above-average spring and summer temperatures has produced the five largest 'Ace' and 'Nellie White' crops harvested in the last 10 years on the Oregon-California lily sites (Table 14).

### Substrate Partitioning

Air and soil temperatures significantly influence carbohydrate utilization in above- and below-ground organs (Wang and Roberts 1983). High temperatures result in a more rapid initiation of secondary scales, thus providing a longer duration for scale filling. Consequently, this increases the potential for larger and earlier maturing bulbs. The partitioning pattern for organic and mineral constituents in above- and below-ground organs in Easter lily are shown in Figure 7. The distribution of monthly gains or losses in dry weight of various organs of 'Nellie White' Easter lily during various phases of growth at near optimum (18°C) temperature for growth is found in Figure 6.

## BULB DORMANCY DEVELOPMENT AND REMOVAL

### Secondary Axis Elongation

#### *Autumn sprouting*

Initiatory activity (scales and leaves) is a continuous process for the secondary axis meristem. This process in the daughter bulb continues until flower initiation, which follows shoot elongation. Elongation of this secondary axis (leaves and internodes) off the basal plate normally is inhibited in the field until autumn (Wang and Roberts 1970). Inhibition of secondary axis elongation is high during the spring before anthesis of the mother, but progressively decreases following anthesis and normally disappears completely by autumn. The period

Table 14. Apparent relationship between seasonal weather conditions based on degree-day accumulations and bulb development (scale filling) in 'Ace' and 'Nellie White' lilies, 1974-1982[1]

| Year | No. of degree-days[2] in spring (A-M-J) | Bulb weight in June | | | |
|---|---|---|---|---|---|
| | | 'Ace' | | 'Nellie White' | |
| | | Daughter | Total | Daughter | Total |
| | | (g) | (g) | (g) | (g) |
| 1981 | 810 | 20.3 | 51.9 | 19.2 | 76.2 |
| 1978 | 930 | 13.2 | 53.8 | 14.8 | 61.0 |
| 1982 | 890 | 14.7 | 51.7 | 14.5 | 58.7 |
| 1979 | 839 | 14.9 | 49.1 | 14.2 | 46.9 |
| 1980 | 910 | 11.1 | 48.2 | 12.2 | 46.9 |
| 1976 | 1,076 | 10.9 | 42.6 | 9.5 | 41.7 |
| 1977 | 1,030 | 6.9 | 38.1 | 7.0 | 39.9 |
| 1974 | 1,005 | 9.4 | 36.6 | 8.3 | 36.9 |
| 1975 | 1,014 | 9.0 | 38.6 | 7.2 | 36.8 |

| Year | No. of degree-days[2] in summer (J-A-S) | Bulb weight in September | | | | | |
|---|---|---|---|---|---|---|---|
| | | Mother | | Daughter | | Total | |
| | | Ace | Nellie W. | Ace | Nellie W. | Ace | Nellie W. |
| | | (g) | (g) | (g) | (g) | (g) | (g) |
| 1981 | 474 | 55 | 81 | 54 | 78 | 109 | 159 |
| 1982 | 419 | 54 | 70 | 53 | 73 | 106 | 143 |
| 1978 | 505 | 62 | 63 | 52 | 62 | 115 | 125 |
| 1979 | 292 | 52 | 55 | 48 | 59 | 101 | 114 |
| 1980 | 449 | 57 | 56 | 47 | 51 | 104 | 107 |
| 1976 | 514 | 42 | 49 | 45 | 54 | 88 | 103 |
| 1977 | 579 | 57 | 56 | 45 | 42 | 101 | 98 |
| 1975 | 581 | 54 | 54 | 33 | 39 | 86 | 93 |
| 1974 | 573 | 49 | 40 | 44 | 42 | 94 | 82 |

[1]Spring (April-May-June) degree-day totals as compared with average June bulb weights and summer (July-August-September) totals compared with September bulb weights.

[2]Quarterly degree-day totals are the sums of the negative departures of average daily temperatures from 65°F. Therefore, the smaller the figure, the warmer the season.

of dormancy in the daughter portion of the lily bulb is of the correlated type and involves scale inhibition of axis elongation rather than initiatory activity in the apex (Lin and Roberts 1970). Daughter scales are the principal source of inhibitors.

The existence of a summer dormancy of the secondary axis of the Easter lily (Wang and Roberts 1970) and the storage temperature/duration requirements for its removal with successive bulb harvest dates have been established (Roberts and others 1978). Studies have shown that lily bulbs become progressively more responsive to sprout-inducing cold storage with increasing age and later harvest. Four weeks is not sufficient exposure to remove dormancy, regardless of temperature, until plants are 50 days beyond anthesis (Roberts and others 1983). This is approximately when the secondary axis would start to elongate in the field in an average season (September 15 for 'Ace' and October 15 for 'Nellie White'). The earlier response of 'Ace' is also evident in growth chamber experiments. It is significant that temperatures of 12° and 18°C are almost equally effective in removing the dormancy in 'Ace' bulbs 50 days after anthesis of the primary axis; 12°C is more effective with 'Nellie White,' thus explaining its slow sprouting in the field. One month later, temperatures from 6 to 18°C produced 100 percent sprouting, although sprout length was longest at the higher temperature. Temperatures above 24°C are sufficient to inhibit sprouting of both 'Ace' and 'Nellie White.' Prematurely sprouted bulbs harvested in October 1973 and stored at 27°C for 6 to 8 weeks developed modified leaves with thickened bases at the sprouted terminal and eventually filled out sufficiently to form small, compact bulbs.

The excessive sprouting of bulbs in West Coast (Oregon-California) fields and in common storage sheds in late September and early October 1973 was associated with average (12°C) or above-average spring (April-June) temperatures followed by below average (15°C) summer (July-September) temperatures. Field data indicate that early daughter (secondary axis) bulb development in warm springs accompanied by cool summers is conducive to sprouting in early autumn. Conversely, when daughter bulb development is slowed by excessively cool srpings followed by relatively hot summers, summer dormancy is prolonged into the autumn and shoot emergence is delayed (Table 15). Wang and Roberts (1970) found that when bulbs were given soil heat treatments before flowering of the primary axis, the secondary axis would elongate prematurely in the field, while daughter bulbs without heat treatment continued to be correlatively inhibited (summer dormancy). When the bulbs were warmed in the field after flowering, the secondary axes emerged later than the controls.

There is increasing evidence that the effectiveness of dormancy-removing treatments in lily (cold/moist treatment, hot water treatment, or red light irradiation) are dependent in great measure on temperature sequences during development (Stimart and others 1982). Tuyl van (1983) found *L. longiflorum* bulblet production to be greater at higher temperatures and to be associated with occurrence of many bolting plants and fewer dormant bulblets.

Results obtained by Roberts and others (1983) from growth chamber experiments indicate that fairly short periods of chilling (12°-18°C) are sufficient for hastening sprouting of bulbs of advanced maturity (80 days after anthesis). The bulbs were on intact plants. These bulbs would be comparable in maturity to field plants in late September.

Roh and Wilkins (1977c) have proposed two types of dormancy in *L. longiflorum*—an *innate* dormancy in the mother scales of early harvested bulbs and an *imposed* dormancy in the outer daughter scales. They found that dormancy in lily could be induced under both long and short photoperiods, and both types of dormancy could be removed by exposing bulb scales to light. Shoot emergence of the daughter axis was hastened by delaying induction of flowering of the mother axis by exposure to a temperature of 21.1°C or by short-day (SD) treatment. After anthesis of the mother axis, SD treatment

Table 15. Degree of autumn-sprouting in 'Ace' and 'Nellie White' lilies related to spring and summer temperatures on West Coast (Oregon-California) lily fields (1974-1982)

| | Degree-day totals[1] | | Autumn-sprouting[2] | | |
|---|---|---|---|---|---|
| | Spring | Summer | Percent | | |
| Year | A-M-J | J-A-S | September | October | Length |
| | | | (%) | (%) | (mm) |
| | | 'Ace' | | | |
| 1973 | 926 (average) | 633 (cold) | ..... | ..... | ..... |
| 1981 | 810 (warm) | 474 (average) | 92 | 100 | 23 |
| 1980 | 910 (average) | 449 (warm) | 32 | 100 | 15 |
| 1982 | 890 (warm) | 419 (warm) | 28 | ..... | ..... |
| 1975 | 1,014 (cool) | 573 (cool) | 20 | 100 | 21 |
| 1974 | 1,005 (average) | 581 (cool) | 10 | 100 | 24 |
| 1977 | 1,030 (cool) | 579 (cool) | 20 | 88 | 18 |
| 1976 | 1,076 (cool) | 514 (average) | 0 | 100 | 8 |
| 1978 | 930 (average) | 505 (average) | 6 | 60 | 25 |
| 1979 | 839 (warm) | 292 (warm) | 0 | 93 | 3 |
| | | 'Nellie White' | | | |
| 1973 | 926 (average) | 633 (cold) | ..... | ..... | ..... |
| 1981 | 810 (warm) | 474 (average) | 16 | 100 | 7 |
| 1974 | 1,005 (average) | 581 (cool) | 0 | 100 | 11 |
| 1975 | 1,014 (cool) | 573 (cool) | 0 | 100 | 8 |
| 1982 | 890 (warm) | 419 (warm) | 0 | ..... | ..... |
| 1980 | 910 (average) | 449 (warm) | 0 | 94 | 5 |
| 1979 | 839 (warm) | 292 (warm) | 0 | 69 | 2 |
| 1977 | 1,030 (cool) | 579 (cool) | 0 | 20 | 12 |
| 1978 | 930 (average) | 505 (average) | 0 | 10 | 6 |
| 1976 | 1,076 (cool) | 514 (average) | 0 | 6 | 5 |

[1]Quarterly degree-day totals are the sums of the negative departures of average daily temperatures from 65°F. Therefore, the smaller the figure, the warmer the season. Words in parentheses indicate type of season.

[2]Not sampled in regular series in 1973.

(exposure to cool, white fluorescent light for 30 days as an 8-hour extension to the mother plant) hastened shoot emergence from the daughter bulb. In contrast, Roberts and Fuchigami (1972b) concluded that daylength effects in lily are primarily on flowering, and only indirectly through flowering do they affect daughter sprouting. They also showed SD treatment of the mother axis after anthesis hastened flowering in the daughter axis without significantly changing rate of axis elongation.

Roberts (1980) has suggested that because harvested bulbs readily respond each year to a standard commercial dormancy-removing treatment (6-8 weeks at 4.5° to 10°C), that future researchers should drop "degree of daughter dormancy remaining" from their list of harvest maturity indices (HMI). However, the 1976, 1977, 1978, and 1982 crops were slow to emerge in greenhouse tests

(Table 18). Whether this was because of bulb immaturity or lack of natural cooling in the coldframes was not clear. It is significant that in years when the bulbs were slow to emerge in the greenhouse, they were also late in flowering. This is not always the case in the field, and there is increasing evidence that daughter speed of emergence and speed of flower induction are independent phenomena subject to different temperature optimums and other stimuli.

It has been suggested that leaf removal (or losses in leaf surface during the growing season from disease or insects) delays subsequent sprouting and flowering of the daughter axis. The study of leaf removal with 'Croft' (p. 30) provided samples for greenhouse forcing and evaluation of this question (Table 16). These data show that a considerable amount of leaf surface can be removed after the canopy is complete (buds visible) without adversely affecting the bulb in forcing. There was no significant effect of leaf removal on subsequent speed of daughter shoot emergence or flowering. The most notable carryover effect was on leaf numbers in the greenhouse. It is surprising that the number of flowers was not more adversely affected. The number of primordia (scale and leaf) present in the daughter bulb at harvest had been reduced appreciably by removing leaves on the mother axis in the field and could account in great measure for the reduced number of leaves on the secondary axis when forced. These bulbs had received natural chilling in coldframes. Removing the younger upper leaves in the field appeared to shorten the forced plant as well, in

Table 16. Effects of leaf removal in field on forcing performance of 'Croft' Easter lily in the greenhouse (1964-1965)[1]

| Treatments | | Days to emerge | Days to flower | Plant height | No. of leaves | No. of flowers |
|---|---|---|---|---|---|---|
| | | | | (cm) | | |
| Basal leaves retained | Leaves removed[2] | | | | | |
| L 10 | 55 | 17 | 103 | 41.7 | 54 | 3.3 |
| L 20 | 45 | 19 | 102 | 45.5 | 61 | 4.0 |
| L 30 | 35 | 20 | 102 | 47.1 | 60 | 4.2 |
| L 40 | 25 | 19 | 103 | 49.6 | 67 | 4.3 |
| Basal leaves removed | Leaves retained[3] | | | | | |
| R 10 | 55 | 20 | 102 | 49.8 | 76 | 4.5 |
| R 20 | 45 | 19 | 99 | 49.2 | 76 | 4.5 |
| R 30 | 35 | 20 | 106 | 55.0 | 80 | 4.5 |
| R 40 | 25 | 18 | 104 | 51.4 | 79 | 4.3 |

[1]Potted and coldframed September 29, 1964; to greenhouse bench on December 1, 1964, and forced at 21.1° day and 18.3°C night temperatures. Leaf removal treatments of plants in field were made on May 21, when buds were visible when terminal leaves were separated.

[2]Number of leaves removed from upper part of plant was difference between average number of leaves on the plant (65) and those retained on basal portion of plant.

[3]Number of leaves retained on the upper part of the plant was difference between the average number of leaves on the plant (65) and those removed from the basal portion of the plant.

proportion to number of leaves previously removed on mother axis. This is a reflection of bulb size (weight) and primordia count at harvest (Table 9). The more young leaves removed at the top of plant, the smaller the bulb produced and the fewer the primordia at harvest.

*Summer-sprouting*

The secondary axis (daughter meristem) normally does not elongate until September or October with the advent of short days and low temperatures (Blaney and Roberts 1966b). This is almost a year after its first appearance at the base of the old primary axis. The correlated inhibition of the daughter axis by the mother axis in non-cooled or only partially cooled plants appears to depend in great measure on the ability of the young expanding leaves to supply the necessary inhibitors (Roberts and Blaney 1968). Lin and Roberts (1970) found dormancy in the lily bulb daughter axis increased with progressive development of the inner daughter scales, and a chilling requirement developed in the spring that decreased in early summer in connection with events leading to anthesis in July.

The term "summer-sprouting" has been used to describe the premature elongation of the secondary axis (daughter) in the field in spring or early summer brought about by loss of correlative inhibition. Examination of large numbers of sprouted bulbs over the years supports the conclusion that there is a critical daughter bulb size or scale number above which the secondary axis can be "triggered" if climatic factors favor premature daughter shoot elongation. Such summer-sprouted bulbs are, of course, useless for greenhouse forcing because there is not sufficient time and substance to form a new secondary axis. Often two or three new axes that are weak in developing will form.

Thirty- to forty-gram planting stock (yearlings) ordinarily will not summer-sprout until the daughter axis has initiated 30-35 scale primordia. This number, of course, varies with size of planting stock. Weather conditions, primarily warm temperatures in early spring, also determine how quickly the bulb will reach this critical stage (Fig. 8). Once the bulb reaches this stage, premature sprouting can occur if temperatures favorable to removing dormancy (correlative inhibition) occur. Bulbs receiving soil heating (cables) before flowering of the mother axis had daughter axes which elongated (summer-sprouts); those without this treatment were still dormant (Wang and Roberts 1970). Bulbs warmed in the field after bloom tended to emerge later than the controls.

Greenhouse studies (Roberts and others 1955) established a high correlation between temperature sequence and shoot emergence in 'Croft' lily bulbs. This was true for all stages of growth subjected to temperatures in the 5° to 10°C (41-50°F) range. No secondary axes elongation occurred from bulbs grown continuously at 16°C (60°F). Except for plants held continuously at 16°C and one lot moved from 16° to 10°C temperature at an early stage, all lots sprouted 100 percent. The results of this research suggest that at early stages of secondary axis development, temperatures above 10°C or somewhere between 10° and 16°C do not induce summer sprouting.

None of the bulbs emerged prematurely in these greenhouse tests if the plants were grown under a sequence of gradually rising air temperatures. Such

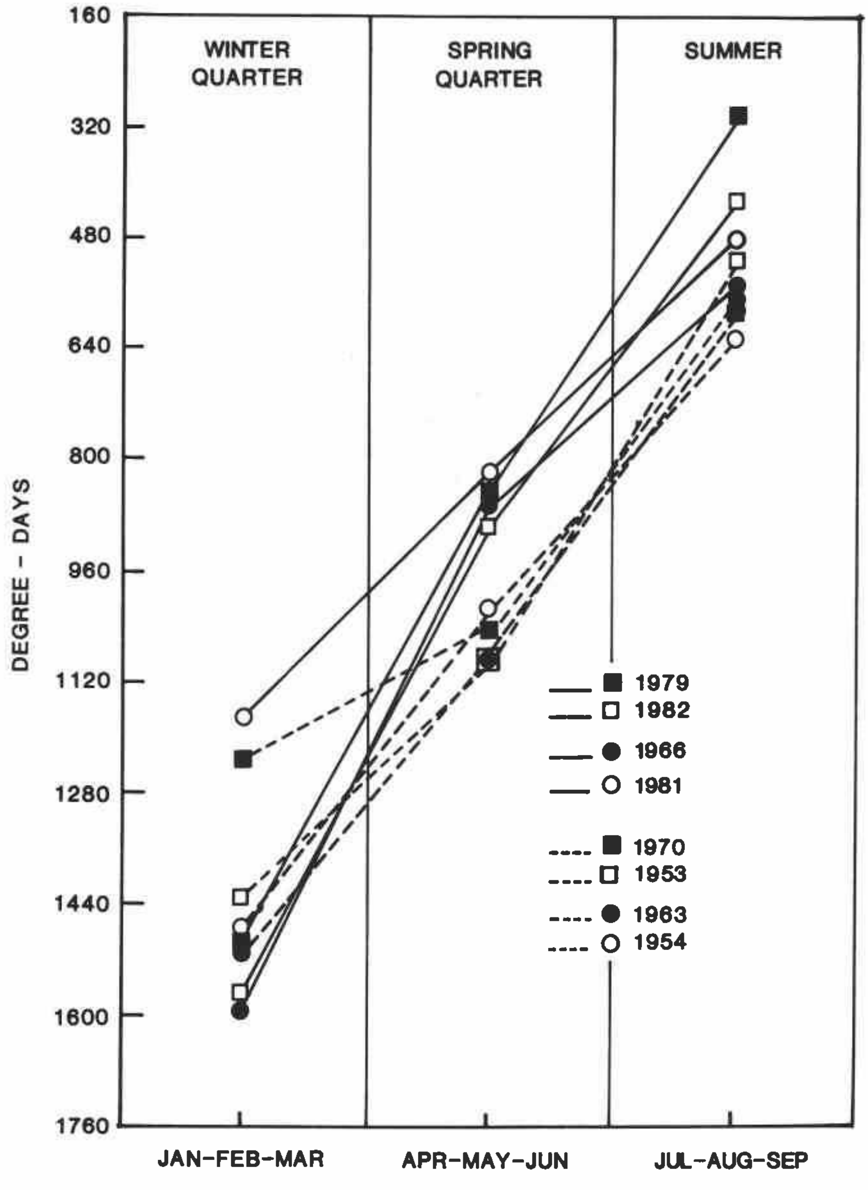


Figure 8. Seasonal weather patterns at Brookings, Oregon, responsible for four largest crops (1966, 1979, 1981, and 1982) and for high percentage of "summer-sprouting" (1953, 1954, 1963, and 1970), based on quarterly degree-day totals. Quarterly degree-day totals are the sums of the negative departures of average daily temperatures from 65°F. Therefore, the smaller the figure, the warmer the season.

a temperature pattern is comparable to that experienced in normal years from early spring until the following autumn. Sensitivity to cool temperatures during this early formation of scales around the secondary axis varied somewhat with the height of the plants at the time they were first exposed to such temperatures. Ten days of exposure to critical temperatures was as effective as longer periods in inducing premature sprouting.

In a 1956-1957 experiment, bulbs exposed to 16°C or lower temperatures for 15 days "summer-sprouted" if the plants continued growth in a 16°C greenhouse after such cool temperatures. No bulbs summer-sprouted after the 16°C temperature treatments if the plants were moved to a greenhouse with a temperature of 21°C or above (Blaney 1957).

A comparison was made between four outstanding crop seasons in the Oregon-California production area (Table 17) when summer-sprouting was a minor problem (1966, 1979, 1981, and 1982) and four seasons when yields were less than desirable and summer-sprouting was epidemic (1953, 1954, 1963, and

Table 17. Apparent relations of spring temperatures to date of flowering, daughter scale, number of leaf primordia in July, and final bulb harvest weight in 'Ace' and 'Nellie White' Easter lilies[1]

| Year[2] | Total degree-days[3] (Apr-May-June) | Date full bloom | 'Ace' No. of scale primordia (late July) | 'Ace' No. of leaf primordia (late July) | 'Ace' Bulb weight at harvest (Sept.) | 'Nellie White' No. of scale primordia (late July) | 'Nellie White' No. of leaf primordia (late July) | 'Nellie White' Bulb weight at harvest (Sept.) |
|---|---|---|---|---|---|---|---|---|
| | | | | | (g/bulb) | | | (g/bulb) |
| 1981* | 810 | June 23 | 57 | 14 | 109 | 64 | 14 | 159 |
| 1979* | 839 | July 3 | 61 | 8 | 101 | 62 | 11 | 114 |
| 1966 | 851 | July 12 | 47 | 18 | 172 | 48 | 20 | 191 |
| 1982* | 890 | July 13 | 44 | 35 | 106 | 56 | 31 | 143 |
| 1980* | 910 | July 2 | 55 | 17 | 104 | 57 | 14 | 107 |
| 1973 | 926 | July 9 | 47 | 0 | 74 | 49 | 0 | 100 |
| 1978* | 930 | June 25 | 50 | 13 | 115 | 50 | 21 | 125 |
| 1969 | 951 | July 16 | 44 | 17 | 124 | 45 | 23 | 125 |
| 1968 | 986 | July 4 | 47 | 17 | 103 | 50 | 15 | 150 |
| 1972 | 992 | July 17 | 50 | 6 | 103 | 50 | 8 | 163 |
| 1974* | 1,005 | July 15 | 49 | 0 | 94 | 48 | 8 | 82 |
| 1975* | 1,014 | July 15 | 49 | 4 | 86 | 48 | 5 | 93 |
| 1977* | 1,045 | July 4 | 44 | 29 | 112 | 41 | 34 | 138 |
| 1976* | 1,076 | July 12 | 53 | 8 | 88 | 54 | 6 | 103 |
| 1971 | 1,137 | July 28 | 46 | 6 | 92 | 47 | 2 | 113 |

[1]Grown in the Brookings-Smith River (Oregon-California) area from 1966-1982.

[2]In years marked with asterisk, bulbs are average of five growers' samples; other years are based on Station sample only.

[3]Degree-day totals for spring quarter are the sums of the negative departures of average daily temperatures from 65°F. Therefore, the smaller the figure, the warmer the spring season.

1970). These field data illustrate the importance of seasonal temperature patterns in maintaining correlative inhibition of the daughter axis and thus preventing summer-sprouting (Fig. 8). Serious summer-sprouting always has occurred when the seasonal pattern is one where above average winter temperature is followed by lower than average spring temperatures. High yields, without summer-sprouting, are related to above-average warm springs and summers regardless of winter temperatures.

The 1973 season provided an interesting study of influence of seasonal weather pattern on dormancy removal. After near-average winter temperatures, the 1973 crop was subjected to above-average spring temperatures and then to one of the coolest summers on record (Fig. 8). This brought about early fall sprouting of the crop, causing much difficulty in harvesting and storing the crop successfully.

## CROP MATURITY AND QUALITY

On the basis of detailed studies of weather records, crop responses, and greenhouse forcing performances during the last several years (1974-1982), we are now in a better position to define bulb maturity and evaluate forcing potential. The precision required in programming Easter lilies with vernalization or light treatments before and during greenhouse forcing, respectively, requires bulbs of known quality. Lily bulbs are mature when they force rapidly and predictably after low-temperature storage (Blaney and Roberts 1967), but the bulbs must also be pathogen-free and a reliable cultivar.

Evaluation of bulb maturity has been proposed (Roberts and Moeller 1971, Roberts and Tomasovic 1975) on the basis of the following:

- ✓ bulb weight or extent of scale filling;
- ✓ nature and extent of initiatory activity of apical meristems;
- ✓ degree of summer dormancy remaining; and
- ✓ responsiveness to flower-inducing cold or light treatments.

### Bulb Weight

Large bulb sizes (weight or diameter) and crops are associated with long, warm, growing seasons starting in early March and continuing until early October. There is no substitute for early daughter axis development, when scale numbers are being determined, and early flowering (mother axis). When daughter scale initiation ceases, daughter leaf initiation starts (if temperatures are favorable) and scale filling increases in intensity. In West Coast fields, flowering in late June is indicative of large bulb potential. The presence of large numbers of daughter scales and scale initials at this time is also indicative of large bulb potential. Continued warm air and soil temperatures (18° to 24°C) (Roberts 1980), coupled with maintenance of a healthy leaf canopy into late September and early October, facilitate attaining full bulb potential. Scale filling continues as long as the daughter axis remains dormant and the foliage remains functional. When the daughter axis starts to lift (elongate) off the basal plate, scale filling drops off rapidly.

## Degree of Summer Dormancy

There does not appear to be any consistent relationship between bulb size attained and degree of dormancy remaining in the bulbs at harvest (Table 2). The 1976 and 1978 'Ace' and 'Nellie White' crops appeared more dormant than others as evidenced in both field emergence (Table 2) and greenhouse forcing (Table 18). The 1976 bulbs were relatively small; the 1978 bulbs were above average in size. The 1982 crop also produced above-average bulb sizes but these bulbs were significantly slow in emerging. Bulbs showing little or no dormancy at harvest (1974, 1975, 1980, and 1981) also varied in size, the 1974 and 1975 bulbs being relatively small compared to those of 1980 and 1981. But neither size showed any degree of dormancy remaining at October harvest. This suggests that we can have very large and very mature bulbs that are also quite dormant as far as daughter shoot elongation is concerned (1978 and 1982) (Table 2).

Samples were taken annually from September 6 to October 10 to evaluate greenhouse forcing performance. The bulbs were given natural coldframe chilling, assuming that the cold requirement for flowering would be fully satisfied each year while the bulbs were "rooting down" in the pots. Samples for forcing were taken from the same five grower fields each year, but only the results from those taken from the Research and Development Station are presented (Table 18). These bulbs were taken from the same location each year, following the same cultural practices.

In 1979, when the bulbs were outstanding in size but had some degree of summer dormancy remaining following above-average summer temperatures, the bulbs responded sharply to standard cold treatment (6 weeks at 5°C) or coldframe chilling to emerge without delay in greenhouse forcing and flowering earlier than any crop during the 1974-1982 period. The 1979 crop responded more sharply than other somewhat dormant crops, such as the 1978 crop, possibly because it had received increasingly higher temperatures throughout the growing season. Although the 1978 crop produced above-average sized bulbs from above-average temperatures, the pattern was one of decreasing temperatures as the season progressed (Fig. 8).

Matsue (1975) found that bulblets formed on scales at a temperature of 25°C gave a high percentage of dormant bulbs (NLB's—no green leaf bulblet) when the high temperature was maintained after planting. Similarly, 'Ace' bulbs given heat treatment after blooming went into a deeper dormancy than bulbs not heat treated or treated before bloom (Wang and Roberts 1970). However, Tuyl van (1983) found that bulblets of *L. longiflorum* were more responsive to 17° and 5°C chilling treatment after higher starting temperatures (26° and 30°C).

There is increasing evidence that bulbs grown in warm seasons may be more dormant at harvest time but also more responsive to subsequent short days and cool nights that remove dormancy and induce flowering. This supports our present position that bulb dormancy is not indicative of immaturity and one can have large, dormant, mature bulbs (as were produced in 1979) or small, relatively immature, nondormant bulbs that sprout in the field (as were produced in 1973). Or, put in another way, the degree of daughter dormancy or

Table 18. Bulb qualities at harvest and forcing performance of 'Ace' and 'Nellie White' Easter lily bulbs (1974-1982)[1]

| Year | Average soil temperature 6" depth | | Harvest date | Bulb harvest weight | Daughter bulb weight | No. of daughter scale primordia at harvest | No. of leaf primordia at harvest | Daughter meristem diameter | Sprouting at harvest | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Spring A-M-J | Summer (J-A-S) | | | | | | | Percent | Length |
| | | | | (g) | (g) | | | (mm) | (%) | (mm) |
| | | | | | BULB QUALITIES 'Ace' | | | | | |
| 1980 | 59.6 | 69.7 | 9/30 | 149.4 | 69.6 | 57 | 50 | 0.67 | 70 | 2.9 |
| 1981 | 63.6 | 69.3 | 10/8 | 133.4 | 62.3 | 61 | 46 | 0.67 | 100 | 3.4 |
| 1974 | ..... | ..... | 9/17 | 123.2 | 62.7 | 49 | 40 | 0.59 | 0 | ..... |
| 1979 | 61.1 | 69.9 | 10/2 | 118.7 | 58.2 | 62 | 39 | 0.56 | 0 | ..... |
| 1978 | 58.6 | 67.9 | 9/28 | 108.7 | 45.9 | 46 | 36 | 0.66 | 10 | 3.0 |
| 1977 | 61.4 | 68.5 | 9/27 | 101.1 | 42.7 | 51 | 38 | 0.73 | 10 | 3.0 |
| 1975 | 58.1 | 62.8 | 9/19 | 93.8 | 35.8 | 46 | 29 | 0.69 | 10 | ..... |
| 1982 | 58.5 | 61.6 | 9/30 | 91.8 | 39.6 | 40 | 51 | 0.55 | 40 | 6.1 |
| 1976 | 56.4 | 64.4 | 9/10 | 89.2 | 40.5 | 53 | 28 | 0.63 | 0 | ..... |
| | | | | | 'Nellie White' | | | | | |
| 1981 | 63.6 | 69.3 | 10/8 | 202.4 | 96.3 | 70 | 48 | 0.61 | 50 | ..... |
| 1979 | 61.1 | 69.9 | 10/2 | 153.7 | 78.1 | 70 | 17 | 0.54 | 0 | ..... |
| 1980 | 59.6 | 69.7 | 9/30 | 141.2 | 72.6 | 74 | 35 | 0.60 | 0 | ..... |
| 1976 | 56.4 | 64.4 | 9/10 | 131.3 | 71.0 | 54 | 35 | 0.70 | 0 | ..... |
| 1978 | 58.6 | 67.9 | 9/28 | 119.9 | 59.8 | 48 | 44 | 0.63 | 0 | ..... |
| 1982 | 58.5 | 61.6 | 9/30 | 118.0 | 56.9 | 56 | 42 | 0.59 | 0 | ..... |
| 1977 | 61.4 | 68.5 | 9/27 | 106.3 | 44.5 | 54 | 33 | 0.64 | 0 | ..... |
| 1974 | ..... | ..... | 9/17 | 95.5 | 41.8 | 48 | 27 | 0.51 | 0 | ..... |
| 1975 | 58.1 | 62.8 | 9/19 | 94.9 | 35.7 | 44 | 30 | 0.64 | 0 | ..... |

Table 18. Bulb qualities at harvest and forcing performance of 'Ace' and 'Nellie White' Easter lily bulbs (1974-1982)[1] (Continued)

| Year | Bulb weight of forcing sample | Potting date (to coldframe) | Date of shoot emergence | Total leaves unfolded | Date of flowering | No. of flowers | Plant height | Forcing rank[2] |
|---|---|---|---|---|---|---|---|---|
| | (g) | | | | | | (cm) | |
| FORCING PERFORMANCE | | | | | | | | |
| 'Ace' | | | | | | | | |
| 1980 | 165.6 | 10/20 | 12/29 | 88 | 4/3 | 6.4 | 38.4 | 2 |
| 1981 | 154.4 | 10/21 | 12/29 | 90 | 4/2 | 5.8 | 53.8 | 3 |
| 1974 | 107.6 | 10/10 | 12/23 | 77 | 4/1 | 6.0 | 32.9 | 4 |
| 1979 | 145.8 | 10/19 | 1/4 | 81 | 3/24 | 8.0 | 36.4 | 1 |
| 1978 | 111.2 | 10/16 | 1/12 | 68 | 4/18 | 6.0 | 23.8 | 7 |
| 1977 | 108.4 | 10/20 | 1/5 | 78 | 4/14 | 5.2 | 50.0 | 6 |
| 1975 | 110.6 | 9/22 | 12/20 | 79 | 4/12 | 5.8 | 33.5 | 5 |
| 1982 | 120.4 | 11/7 | 1/9 | 75 | 5/7 | 3.2 | ..... | 8 |
| 1976 | 91.6 | 10/19 | 1/25 | 54 | 4/25 | 4.6 | 18.0 | 9 |
| 'Nellie White' | | | | | | | | |
| 1981 | 227.6 | 10/21 | 12/29 | 96 | 4/4 | 7.2 | 57.0 | 1 |
| 1979 | 163.2 | 10/19 | 1/1 | 81 | 3/20 | 6.6 | 37.1 | 2 |
| 1980 | 138.0 | 10/20 | 1/2 | 74 | 4/11 | 7.4 | 29.6 | 3 |
| 1976 | 104.8 | 10/19 | 1/22 | 51 | 4/19 | 5.8 | 17.1 | 9 |
| 1978 | 130.2 | 10/16 | 1/15 | 61 | 4/16 | 6.0 | 23.5 | 8 |
| 1982 | 164.0 | 11/7 | 1/15 | 83 | 5/6 | 4.6 | ..... | 6 |
| 1977 | 120.4 | 10/20 | 1/5 | 64 | 4/8 | 6.2 | 35.8 | 5 |
| 1974 | 93.6 | 10/10 | 12/24 | 61 | 3/30 | 5.0 | 31.0 | 7 |
| 1975 | 106.6 | 9/22 | 12/30 | 71 | 4/15 | 6.8 | 36.5 | 4 |

[1]Harvested from the Pacific Bulb Growers' Research and Development Station, Harbor, Oregon.

[2]Composite rank in forcing based on earliness, number of leaves, and flowers. Best = 1, poorest = 9.

elongation at harvest is not a valid criterion for bulb maturity any more than a green winter pear is necessarily immature at harvest. If the bulbs are capable of responding sharply to environmental stimuli as they proceed into their next phase of development, they are mature.

## Initiatory Activity

A leafy plant is desirable in a pot lily if it does not complicate forcing time. The leafy plant usually will present a better "plant picture" and has the potential for producing more flowers. Approximately half the leaf primordia that develop during greenhouse forcing are normally on the daughter axis at time of bulb harvest (Table 19). The remaining leaves are initiated during storage and early stages of greenhouse forcing, and their number is determined

Table 19. Relationship of initiatory activity in 'Ace' and 'Nellie White' Easter lilies to summer temperatures as reflected in number of scales, leaves, and flowers formed in field and greenhouse (1974-1982)[1]

| | | Number per 100 grams total bulb weight | | | | |
|---|---|---|---|---|---|---|
| Year | Degree-days in summer[2] (J-A-S) | Scale primordia at harvest | Leaf primordia at harvest | Leaf primordia during forcing | Total leaves unfolded | No. of flowers |
| | | | 'Ace' | | | |
| 1982 | 419 | 33 | 47 | 20 | 67 | 2.7 |
| 1974 | 573 | 46 | 37 | 34 | 72 | 5.6 |
| 1978 | 505 | 41 | 32 | 29 | 61 | 5.4 |
| 1976 | 514 | 58 | 31 | 28 | 59 | 5.0 |
| 1975 | 581 | 42 | 30 | 45 | 75 | 5.2 |
| 1977 | 579 | 47 | 30 | 37 | 68 | 4.8 |
| 1981 | 474 | 40 | 30 | 29 | 59 | 3.8 |
| 1979 | 292 | 43 | 27 | 29 | 56 | 5.5 |
| 1980 | 449 | 34 | 26 | 23 | 49 | 3.9 |
| | | | 'Nellie White' | | | |
| 1978 | 505 | 37 | 34 | 13 | 47 | 4.6 |
| 1976 | 514 | 52 | 33 | 15 | 49 | 5.5 |
| 1974 | 573 | 53 | 29 | 36 | 65 | 5.3 |
| 1975 | 581 | 41 | 28 | 39 | 67 | 6.4 |
| 1977 | 579 | 45 | 27 | 26 | 53 | 5.1 |
| 1982 | 419 | 34 | 26 | 25 | 51 | 2.8 |
| 1980 | 449 | 54 | 25 | 28 | 54 | 5.4 |
| 1981 | 474 | 31 | 21 | 21 | 42 | 3.2 |
| 1979 | 292 | 43 | 10 | 39 | 50 | 4.0 |

[1]Bulbs grown at Pacific Bulb Growers' Research and Development Station, Harbor, Oregon, and forced at Oregon State University.

[2]Degree-days (J-A-S). Summer quarter degree-day totals are the sums of the negative departures of average daily temperatures from 65°F. Therefore, the smaller the figure, the warmer the season.

by the flower-inducing cold treatment given and the *responsiveness* of the bulb to treatment.

The number of daughter scale primordia at harvest has been rather closely associated with both bulb size at harvest and greenhouse forcing performance, the latter evaluated on the basis of leafiness, early flowering, and number of flowers (Table 20). The warm seasons of 1979, 1980, and 1981 produced large bulbs with 20 to 40 percent more daughter scales than average, and these forced rapidly with greater numbers of leaves and flowers than the bulbs produced in 1976, 1977, and 1978 (Tables 18 and 21). These latter years produced smaller, more dormant bulbs with less daughter scales that forced slower and plants with significantly fewer leaves and flowers. The 1976 season, with below-average temperatures throughout, was one of the least favorable for bulb production.

The number of daughter leaf primordia at harvest has been an inconsistent indicator of bulb forcing quality. For instance, the 1979 'Nellie White' field crop produced one of our best greenhouse crops on record even though at harvest it had 18 daughter leaf primordia, the lowest number on record. The

Table 20. Annual evaluation of forcing performance of 'Ace' and 'Nellie White' Easter lilies at Oregon State University based on earliness, leafiness, and floriferousness[1]

| Year | Early flowering | Number leaves | Number flowers | Total | Forcing[2] rank |
|---|---|---|---|---|---|
| | | | 'Ace' | | |
| 1974 | 2 | 6 | 3 | 11 | 4 |
| 1975 | 5 | 4 | 6 | 15 | 5 |
| 1976 | 8 | 9 | 8 | 25 | 9 |
| 1977 | 6 | 5 | 7 | 18 | 6 |
| 1978 | 7 | 8 | 4 | 19 | 7 |
| 1979 | 1 | 3 | 1 | 5 | 1 |
| 1980 | 4 | 2 | 2 | 8 | 2 |
| 1981 | 3 | 1 | 5 | 9 | 3 |
| 1982 | 5 | 7 | 9 | 21 | 8 |
| | | | 'Nellie White' | | |
| 1974 | 2 | 8 | 8 | 18 | 7 |
| 1975 | 6 | 5 | 3 | 14 | 4 |
| 1976 | 8 | 9 | 7 | 24 | 9 |
| 1977 | 4 | 6 | 5 | 15 | 5 |
| 1978 | 7 | 7 | 6 | 20 | 8 |
| 1979 | 1 | 3 | 4 | 8 | 2 |
| 1980 | 5 | 4 | 1 | 10 | 3 |
| 1981 | 3 | 1 | 2 | 6 | 1 |
| 1982 | 5? | 2 | 9 | 16 | 6 |

[1]Bulbs from Pacific Bulb Growers' Research and Development Station, Harbor, Oregon, 1974-1982.

[2]Composite rank in forcing performance. Best = 1, poorest = 9.

Table 21. Characteristics of 'Ace' and 'Nellie White' bulbs in best and poorest forcing years[1]

| | Daughter bulb weight at harvest | Daughter scales at harvest | Daughter meristem diameter | Number per 100 grams total bulb weight: Daughter leaf primordia at harvest | Leaves initiated during forcing | Total leaves unfolded |
|---|---|---|---|---|---|---|
| | (g) | | (mm) | | | |
| | | | 'Ace' | | | |
| Best years | | | | | | |
| 1979 | 58.2 | 62 | 0.56 | 26.7 | 28.8 | 55.5 |
| 1980 | 69.6 | 57 | 0.67 | 26.0 | 22.9 | 48.9 |
| 1981 | 62.3 | 61 | 0.67 | 30.4 | 28.5 | 58.9 |
| Average | 63.4 | 60 | 0.63 | 27.7 | 26.7 | 54.4 |
| Poorest years | | | | | | |
| 1976 | 40.5 | 53 | 0.63 | 30.6 | 28.4 | 59.0 |
| 1978 | 45.9 | 46 | 0.66 | 32.4 | 28.8 | 61.2 |
| 1982 | 39.6 | 40 | 0.55 | 47.0 | 19.9 | 66.9 |
| Average | 42.0 | 46 | 0.61 | 36.7 | 25.7 | 62.4 |
| | | | 'Nellie White' | | | |
| Best years | | | | | | |
| 1979 | 78.1 | 70 | 0.54 | 10.4 | 39.2 | 49.6 |
| 1980 | 72.6 | 74 | 0.60 | 25.4 | 28.3 | 53.7 |
| 1981 | 96.3 | 70 | 0.61 | 21.1 | 21.1 | 42.2 |
| Average | 82.3 | 71 | 0.58 | 19.0 | 29.5 | 48.5 |
| Poorest years | | | | | | |
| 1976 | 71.0 | 54 | 0.70 | 33.4 | 15.3 | 48.7 |
| 1978 | 59.8 | 48 | 0.63 | 33.8 | 13.1 | 46.9 |
| 1982 | 56.9 | 56 | 0.59 | 25.6 | 25.0 | 50.6 |
| Average | 62.6 | 53 | 0.64 | 30.9 | 17.8 | 48.7 |

[1]Bulbs taken from Pacific Growers' Research and Development Station from 1974-1982 and forced in greenhouses at Oregon State University after coldframe chilling.

crop made up for this small number of daughter leaf primordia by initiating 64 leaf primordia during forcing (Tables 18 and 19). More significant is the number of leaves initiated during storage and forcing. In both cultivars ('Ace' and 'Nellie White'), the large bulbs produced in warm seasons have consistently initiated more leaves during vernalization treatment and forcing, and as a result have been leafier, earlier, and more floriferous.

There is no close correlation among bulb size, leaf primordia count at harvest, and degree of sprouting. However, large bulbs normally contain more daughter leaf initials at harvest or initiate and expand leaves more rapidly than smaller ones after dormancy-removing and flower-inducing cold treatments. In general, the larger the bulb, the higher the leaf initial count at harvest, the larger the daughter apical meristem, and the greater the flowering potential. However, exceptions spoil the best of generalizations. For instance, the 1979 crop produced the best forcing bulbs we have seen in our tests. Even though they were large bulbs (not as large as in 1981), they had the smallest number of daughter leaf primordia at harvest on record (18) and the smallest apical diameter (0.49 mm) (Table 2).

## Responsiveness to Flower-Inducing Cold Treatment

Probably the most significant factor in successful lily forcing is the responsiveness of the bulb to flower-inducing cold treatment. This quality in the bulb can influence the number of leaves and flowers produced and the speed of forcing. Growth rate is measured on the basis of leaf unfolding rate (Wang and others 1970). Speed of flowering, therefore, is determined by the number of leaf primordia at the time of flower initiation and the rate at which these leaves and flowers unfold and develop during forcing. Leaf number is determined by the rate and duration of leaf initiation before bulb harvest and rate and duration of leaf initiation during storage and forcing and before flower initiation. Growth rate, of course, can be influenced by a great number of factors during the forcing process, but the bulb itself can influence growth rate as a consequence of the way it responds to vernalization and greenhouse forcing stimuli. Its responses vary depending on cultivar, bulb size, disease incidence, and, as yet not clearly understood, physiological conditioning in the field before harvest. Breeding programs have demonstrated the differences in seedlings, cultivars, and cultivar variants (clones) in leaf and flower numbers and in speed of flowering. Kohl (1967) found not only a high positive correlation between bulb size and leaf count per unit of time, but also between bulb size and apex diameter. Wang and others (1970) measured growth rate on the basis of number of leaves unfolding per day. Vernalization for 6 weeks at 4.5°C (40°F) increased the growth rate of 'Ace' plants considerably (1.62 leaves per day as compared with 1.16 for nonvernalized controls) but reduced the number of leaves and flowers produced. Prolonging vernalization to 18 weeks, however, significantly reduced both growth rate (0.79 leaves per day) and initiatory activity. This could be an example of physiological conditioning processes taking place in the field before harvest that are compounded during vernalization storage. Data taken from lily bulb maturity studies in 1968-1969, similar to those published from data taken in 1969-1970 (Roberts and others 1978), showed that the later the bulbs were harvested the more responsive they were to vernalization treatment (Fig. 9). Late harvesting of bulbs has consistently increased their responsiveness to flower-inducing cold treatment and increased growth rate if treatment durations were optimum (Roberts and Mueller 1971). It is not known whether these increases in leaf number, growth rate, and earliness of flowering were the result of increased bulb size or some as yet undefined physiological condition. It is significant, however, that the large bulbs produced and forced in 1982-1983 were late in emerging, late in flowering, had average or above leaf numbers, but were lowest in bud count of a decade (Table 18).

On the basis of crop yield and bulb size, the warm years—1979, 1980, and 1981—were outstanding for both 'Ace' and 'Nellie White' (Table 18). These larger bulbs also had larger daughter bulbs with greater numbers of scales. Leaf

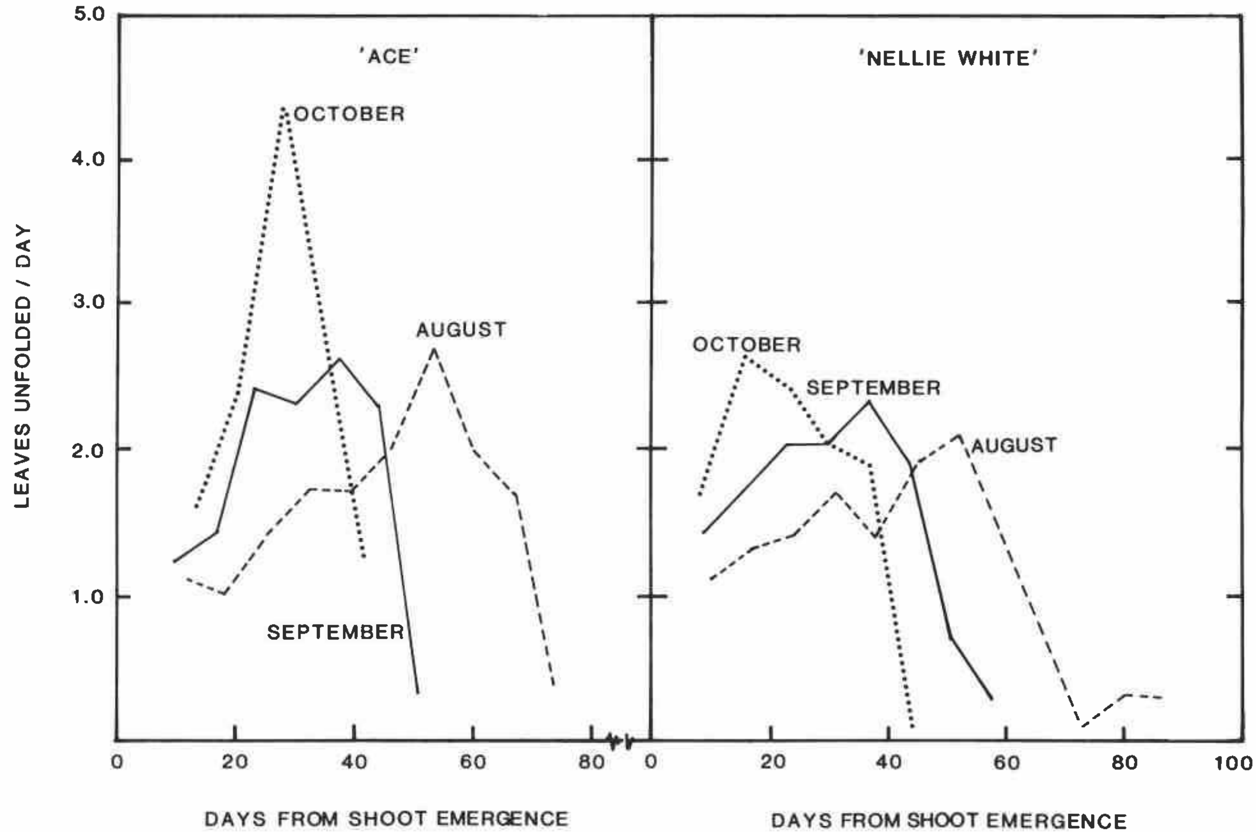


Figure 9. Growth rate (leaves unfolded per day) of 'Ace' and 'Nellie White' plants from bulbs harvested in August, September, and October. Bulbs were given six weeks vernalization storage at 5°C and forced at 21° and 15°C ±3 day and night temperatures, respectively, with natural daylengths (December to April) at Corvallis, Oregon, 1968-1969.

primordia numbers at harvest were not consistent with bulb size, nor was meristem diameter. Evidences of summer dormancy remaining in the bulb at harvest were not consistently related to bulb size at harvest.

## TERMINOLOGY

**apical dome** (shoot apex or apical meristem): terminal meristem of primary or secondary axis.

**autumn-sprouting:** commencement of daughter axis elongation at time of autumn bulb harvest as a normal consequence of developing bulb maturity, shortening days, and natural cooling temperatures.

**axis elongation** (sprouting, shoot elongation): elongation of axis internodes in response to dormancy-removing (inhibitors) treatments.

**basal plate:** perennial, shortened, modified stem which has a growing point and to which scales and roots are interjoined (see Fig. 10).

**basal root:** root which develops from the basal plate of the bulb (Fig. 10).

**bulb** (lily): a specialized plant organ consisting of a greatly reduced stem (basal plate) surrounded by fleshy, modified leaves called scales (Fig. 10).

**bulb dormancy:** a physiological state of a healthy bulb characterized by a temporary delay in the sprouting or elongation of the daughter stem axis (summer dormancy or correlative inhibition).

**bulb maturity:** measure of capacity of a healthy daughter stem axis to sprout without delay and to respond rapidly to flower-inducing treatments.

**bulb quality:** evidence that the bulb is pathogen-free, true-to-name, proper weight for size, and responsive to cold treatment.

**bulb size:** transverse circumference measurement of the bulb.

**bulblet:** small bulb produced either on the stem or base of an older bulb or by scale propagation. It is called bulblet until grown independently for one year. Called stem bulblet or scale bulblet (Fig. 14).

**case-cooling** or precooling (PC): a cold/moist treatment before planting that induces rapid growth (leaf initiation and unfolding) and flowering. Bulbs usually are packed in moist peat in cases during handling and storage.

**chemical deflowering:** use of chemicals at buds-visible stage to inhibit further development of buds and provide a compensatory shift of substrate to growth of the daughter bulb.

**cold requirement:** extension growth in bulbous plants frequently is caused by the enlargement of cells formed previously in the life history and requiring some external stimulus (such as cold) for their enlargement or is caused by the activity of subapical meristems. There is also a cold requirement (vernalization requirement) for flower induction in lilies and other bulbous plants.

**cold treatment:** portion of the forcing program in which bulbs are induced to flower. The methods used are precooling (case), controlled temperature forcing (CTF), natural cooling, and long-day treatments.

**commercial:** bulb of a size suitable for commercial forcing; usually 20 to 30 centimeters in circumference (Fig. 14).

**compensatory growth:** a special type of regeneration, characterized by the greater than normal growth of an organ or organs of the same type as the one which has been removed or lost from other causes.

**controlled temperature forcing** (CTF): procedure for forcing Easter lilies in which nonprecooled bulbs are potted, placed in a controlled temperature facility at 15.6° to 17.2°C (60-63°F) for 2 to 4 weeks and subsequently cooled at 1.7° to 4.4°C (35-40°F) for 6 to 7 weeks before being placed in the greenhouse.

**daughter bulb** (secondary axis): scales and leaves initiated by, and developing below and around, the new daughter apex. This apex arises from a meristem (bud) in the axil of a scale subtending the old or mother axis (Fig. 10).

**degree-days:** sum of the negative departures of average daily temperatures from 65°F. Therefore, the smaller the cumulative figure, the warmer the period.

**devernalization:** negation of a vernalizing stimulus by temperatures above a critical level.

**disbudding:** manual removal of developing flowers for various reasons, including disease control, to decrease plant height and enhance bulb development.

**dormancy-removing cold treatment:** optimum temperature for initiating leaf primordia is 16° to 18°C; a temperature of 10° to 12°C is optimum for internode elongation during the final stages of bulb maturity. Progressively lower temperatures are required for flower induction as the bulb matures, with 5°C being near optimum for bulbs harvested in September and October.

**double-nose bulb:** commercial with two daughter bulbs and stem axes with a common basal plate (Fig. 15).

**feathering:** condition which can occur during the period from late spring to harvest in which all or part of the scales developing around the daughter axis elongate faster than they are filled. They may project out of the top of the bulb and will appear papery. Often confused with *summer-sprouting*.

**filling** (bulbing): enlargement of the scales associated with storage of food reserves in the bulb; rate of filling varies with season, growth phase, and partitioning of dry matter.

**flower differentiation:** complete morphological development of the floral organs following initiation.

**flower induction:** an unobservable, preparatory step which occurs before visible flower bud initiation.

**flower initiation:** visible organization of flower primordia at the stem apex.

**flowering shoot:** primary (mother) axis.

**forcing:** acceleration of flowering by manipulation of environmental conditions. This manipulation is referred to as *programming*.

**foundation stock:** pathogen-free, true-to-name planting stock.

**full bloom:** when one-half of the plants have a fully open flower.

**growth phase:** period of growth and development marked by recognizable morphological events.

**growth rate:** rate of leaf unfolding on primary axis as measured in leaves per day. Leaf considered unfolded when it is extended at 45-degree angle from spindle.

**harvest maturity index** (HMI): harvest date, daughter bulb weight, and the number of scale and leaf primordia on the daughter axis, and responsiveness to dormancy-removing and flower-forcing treatments have been evaluated as indices.

**initiatory activity:** rate of scale, leaf, or flower initiation (primordia) by daughter meristem. Number over time.

**long-day treatment** (LDT): use of light (10 p.m. to 2 a.m.) at the time of shoot emergence to promote rapid flowering.

**morphologically plastic:** organ primordia have the capacity to change form and function over time as a result of external or internal stimulus. Daughter bulb primordia can produce scales or leaves or revert from bractlike leaves to thickened scales.

**mother bulb** (primary axis): portion of the bulb that is currently flowering and producing a daughter bulb in the axil of a scale subtending the mother axis. The *old mother scales* encompass the new daughter bulb (Fig. 10).

**mound height:** distance from wheel track (tractor) to top of the mound.

**natural cooling:** technique in which nonprecooled commercial bulbs are planted immediately on arrival and grown under cool, natural conditions but with frost protection, before being placed in the greenhouse.

**new scales** (daughter scales): scales initiated on new secondary axis which encompasses the daughter meristem.

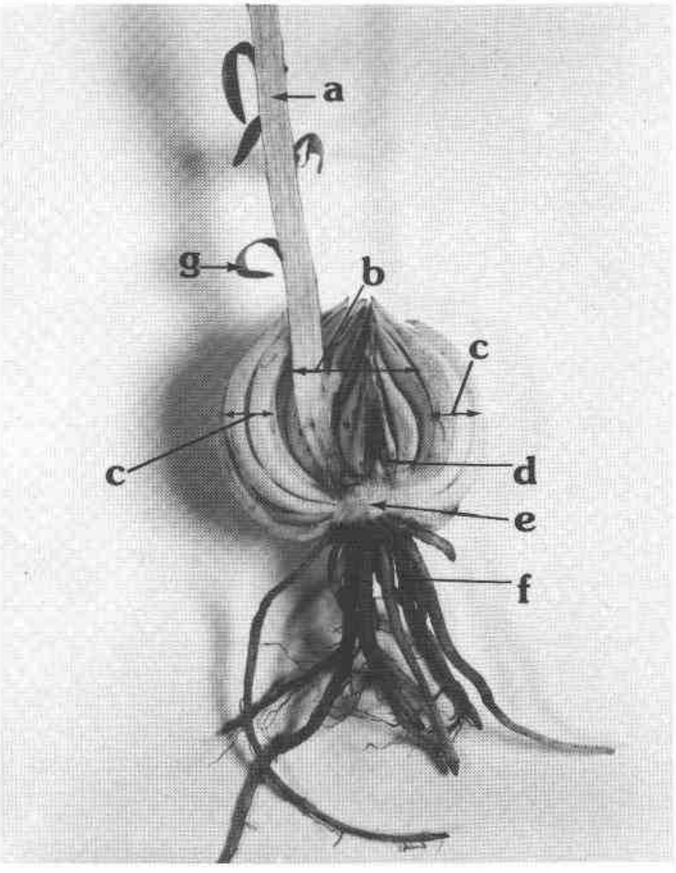


**Figure 10. Position of new scales, old scales, flowering shoot, daughter apex, and basal plate in a commercial bulb at time of harvest. a. flowering shoot of mother bulb; b. new scales (daughter scales); c. old scales (mother scales); d. daughter apex (next season's flowering plant); e. basal plate; f. basal roots; g. leaves.**

**Figure 11.** "Summer-sprout" at base of primary (mother) axis produced artificially in growth chambers by temperature manipulation.

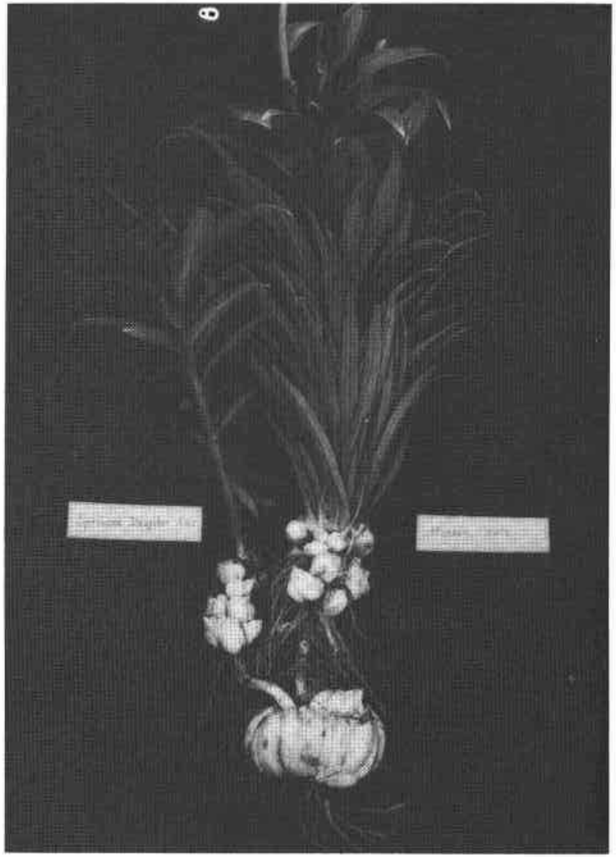

Figure 12. Appearance of "summer-sprout" in field after flowering and before harvest.

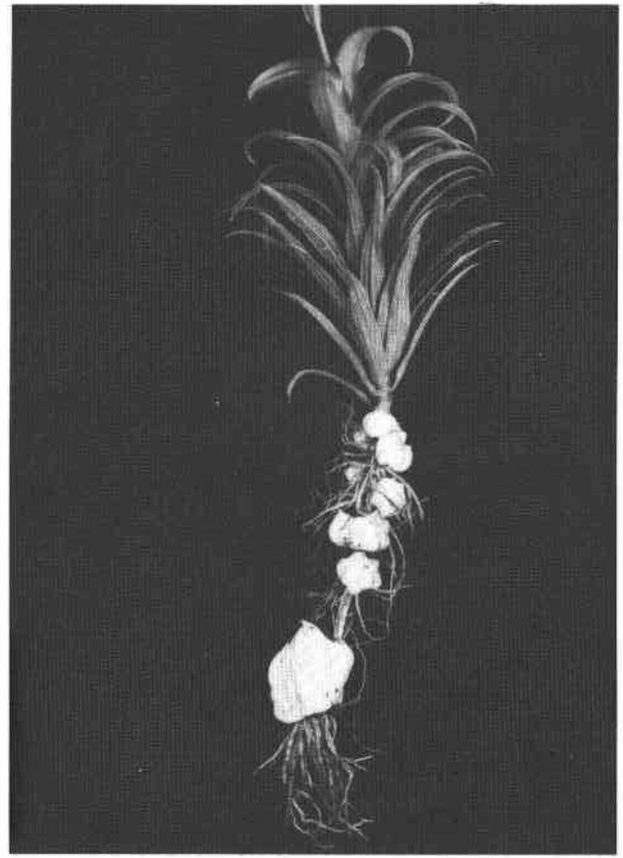

Figure 13. Yearling bulb at time of harvest.

**nonprecooled bulb** (NP): bulb that is delivered direct to the forcer and has not received a cold treatment. Also called nonvernalized.

**periodicity:** growth events in plant controlled by external (photoperiodicity, thermoperiodicity) and internal (correlative relationships) influences. Events such as emergence, flowering, senescence, and death are obvious, but others (initiation of scale, leaf, and flower primordia in bulb) are not.

**physiological conditioning:** some bulbous plants such as the lily require an external (cold) or internal (substrate level) stimulus to bring about physiological changes necessary for events in subsequent phases (phasic development).

**plant height:** distance from soil surface to base of first flower stalk.

**plant picture:** qualities of leafiness, plant height, and flower number and quality.

**plant quality:** based on speed of forcing, bud count, and plant picture.

**planting depth:** distance from top of bulb in ground to top of mound.

**planting stock:** bulblets and yearlings.

**prebloom period:** from shoot emergence to flower anthesis.

**precooling** (PC): a cold-moist treatment before planting which induces rapid shoot elongation and flowering. Usually bulbs are packed in moist peat (case cooling).

**pre-emergence period:** from planting to shoot emergence.

**preheating:** use of a 21.1°C (70°F) temperature either before planting of nonprecooled bulbs or before precooling treatment to prevent loss in leaf and flower numbers from excessive vernalization.

**postbloom period:** from flower anthesis to bulb harvest.

**primary scales** (mother scales): older scales encompassing the new daughter bulb (Fig. 10c).

**primordia:** first recognizable aggregation of cells that will form a distinct organ.

**secondary scales** (daughter scales): new scales formed by the daughter meristem during the current growing season and before leaf initiation commences.

**shoot emergence:** emergence of the primary axis above the soil surface.

**spindle:** tightly clasped leaves at shoot apex before they unfold.

**stem length:** distance from point of attachment to basal plate to first flower stalk.

**stem root:** adventitious root produced on the underground portion of the stem.

**summer-sprouting:** premature sprouting of the secondary (daughter) axis before normal scale complement and bulb size are achieved (Figs. 11 and 12).

**vernalization requirement: absolute** (abs): if plants are unable to flower without a cold/moist treatment; **quantitative** (quant): if flowering is accelerated by, although it will eventually occur without, cold treatment.

**yearlings:** plant stock at the end of the first growing season from a bulblet. Can be produced from either *stem* or *scale bulblets* (Figs. 13 and 14).

Definitions taken in part from: A. A. DeHertogh and others, A Guide to Terminology for the Easter Lily *(Lilium longiflorum* Thunb.), *HortScience*, 6:121-123.

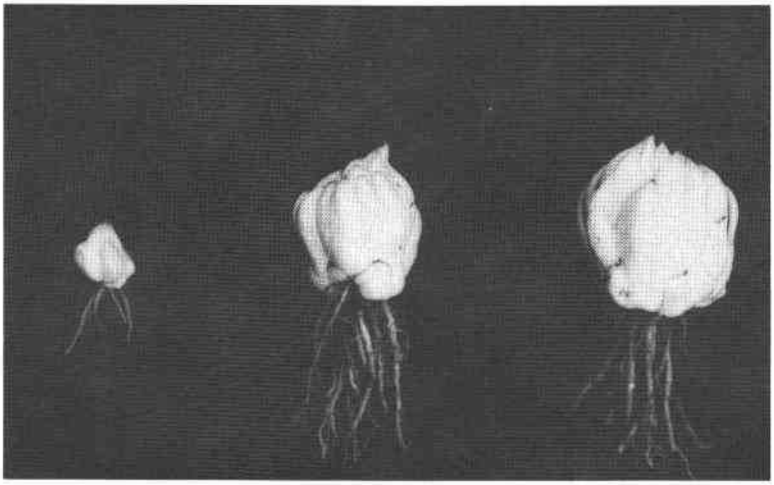

**Figure 14. Comparative size and appearance of stem bulblet, yearling, and commercial bulb.**

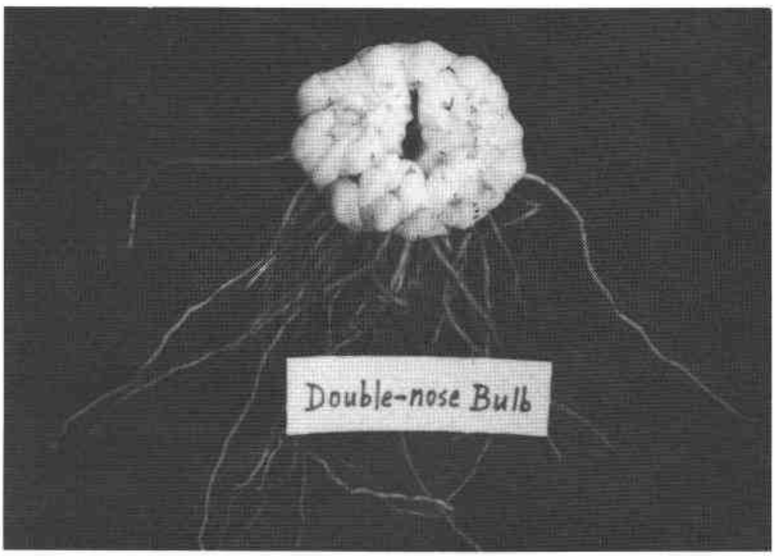


**Figure 15. Double-nose bulb at harvest.**

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