leaf surfaces [unlike 'Pixy' plum (5)]. The contribution of the hydathodes to adaxial water loss in detached micropropagated 'Silvan' leaves was clearly shown. Reduced epithem and open water pores of cultured plantlet leaves likely promote water loss from the hydathodes.

Literature Cited

1. Burgerstein, A. 1904. Die Transpiration de Pflanzen. Gustav Fisher Verlag, Vienna.
2. Curtis, J.D. and N.R. Lersten. 1987. Hydathode anatomy in *Potentilla palustris* (Rosaceae: Rosoideae). Nordic J. Bot. (In Press).
3. Donnelly, D.J., F.E. Skelton, and H.A. Daubeny. 1986. External leaf features of tissue-cultured 'Silvan' blackberry. HortScience 21:306–308.
4. Fahn, A. 1979. Secretory tissues in plants. Academic, London.
5. Fuchigami, L.H., T.Y. Cheng, and A. Soeldner. 1981. Abaxial transpiration and water loss in aseptically cultured plum. J. Amer. Soc. Hort. Sci. 106:519–522.
6. Juniper, B.E. and C.E. Jeffree. 1983. Plant surfaces. Edward Arnold, London. p. 58–59.
7. Lersten, N.R. and J.D. Curtis. 1982. Hydathodes in *Physocarpus* (Rosaceae:Spiraeoideae). Can. J. Bot. 60:850–855.
8. Linsmaier, E.M. and F. Skoog. 1965. Organic growth factor requirements of tobacco tissue cultures. Physiol. Plant. 18:100–127.
9. Lippmann, E. 1925. Uber das Vorkommen der verschiedenen Arten der Guttation und einige physiologische und ökologische Beziehungen. Bot. Arch. 11:361–464.
10. Murashige, T. and F. Skoog 1962. A revised medium for rapid growth and bioassays with tobacco tissue cultures. Physiol. Plant. 18:100–127.
11. Sato, T. and M. Shamoto. 1973. A simple rapid polychrome stain for epoxy-embedded tissue. Stain Tech. 48:223–227.

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Distribution, Storage, and Remobilization of ^{14}C-labeled Assimilate in Easter Lily

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Abstract. **Whole shoots of Easter lily (*Lilium longiflorum* Thunb. cv. Nellie White) were exposed to $^{14}CO_2$ at 25, 37, and 51 days after full bloom of the commercial crop. Seven days after each exposure, 20% of the total recovered ^{14}C remained in the shoot, which included stem roots, 10–25% in stem bulblets, 11–20% in mother scales, and 34–44% in daughter scales. Sink activity increased sharply from the outer mother scales to the inner daughter scales. The fraction of total ^{14}C in the main bulb decreased, while that in the stem bulblets increased at successive exposures. Another group of plants was labeled repeatedly by dosing with $^{14}CO_2$ on the three previous occasions and, also, at 65 days after full bloom. Bulbs were harvested 7 days after the final exposure, stored at 18°C for 14 weeks, and then replanted, At bulb digging, 50%, 30%, and 20% of the total ^{14}C recovered were in the main bulb, stem bulblets, and shoot, respectively. Mother scales lost dry weight and ^{14}C during storage and were nearly depleted when flower buds were visible the next season. Specific ^{14}C activity in the emerging flowering shoot was high but decreased dramatically as the leaf number rapidly increased. The shoot and new daughter scales were the principal recipients of mobilized scale reserves, although only 28% of the ^{14}C lost from mother scales were recovered in other plant parts. A majority of the carbon originally in mother scales was likely lost in respiration between fall harvest and 3 weeks after anthesis the following year. The daughter bulb contained 64% of the ^{14}C in the bulb at fall harvest, and lost very little ^{14}C during regrowth the following year.**

Easter lily bulbs are composed of modified leaves, referred to as scales, which are filled with food reserves during the last few months of a growing season (5, 15, 17, 20). A mature lily bulb has two kinds of scales: mother scales from the previous year and daughter scales that develop during the current growing season. Since both mother and daughter scales are initiated and develop over a long period (5), scales at different nodal positions are likely filled at different rates and the filling pattern may change with time (7, 18). Bulblets, which develop along the underground stem, grow rapidly after anthesis (5, 17) and potentially can divert a large fraction of current assimilate away from the bulb and lower its final weight (5). A previous study showed that after anthesis the majority of the ^{14}C-labeled assimilate translocated out of a single source leaf in 24 hr was in the scales (20). However, the distribution of current assimilate from the entire lily shoot to various sink organs during the active filling period has not been determined.

Following bulb planting, dry weight of a lily plant decreases to a minimum before it increases again. Reserves in the old scales of an Easter lily bulb are depleted gradually during the development of the flowering shoot and formation of a new daughter bulb (17, 18). These scale reserves may be an important carbon source for new growth. Jefford and Edelman (10) reported that much of the dry matter removed from the Jerusalem artichoke tuber was used by the growing daughter shoots. Growth of the daughter bulb in tulip is partially dependent upon the reserves in the mother scales (1). The importance of scale reserves to new growth and the redistribution of reserves among new organs in Easter lily are not known.

The objectives of this study were to determine the long-term

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distribution of current assimilate from the entire shoot during active scale filling and to follow the mobilization and redistribution of scale reserves during the next growing cycle.

Materials and Methods

Field-grown 'Nellie White' Easter lily plants from yearling bulbs 15 cm in circumference were dug intact on 9 July 1982 at the Dr. A.N. Roberts Easter Lily Research Center, Harbor, Ore., and placed in individual 4-liter plastic containers. Plants were transported to Corvallis, Ore. and grown in a shaded place for 10 days before being exposed to full sun. Flower buds had been removed by hand on 18 June. Full bloom of the commercial crop occurred on 27 June.

To prepare ^{14}C-labeled bulbs for the reserve mobilization study, plants were exposed to $^{14}CO_2$ four times at 2-week intervals between 2 July and 2 Sept., which were 25, 39, 51, and 65 days after full bloom of the commercial crop. At each exposure, 80 µCi (1 Ci = 37 GBq) of $^{14}CO_2$ was generated from NaH^{14}CO$_3$ (6.5 µCi·µmol^{-1}) in each of four polyethylene chambers enclosing nine plants. A fan mixed the atmosphere during the course of labeling. Plants were allowed to photosynthesize in the chambers for 1 hr in a 50% shade lathhouse, then returned to the growing site. Five plants that had received four $^{14}CO_2$ exposures were harvested 1 week after the last exposure to analyze for ^{14}C partitioning after multiple labeling.

Five previously unlabeled plants also were exposed to $^{14}CO_2$ on each of the first three dates. These plants were harvested a week after labeling to analyze for ^{14}C distribution after a single exposure. No attempt was made to estimate the initial ^{14}C uptake and ^{14}C losses before harvest of plants.

At harvest, plants were washed free of soil and separated into shoot, with stem roots; the inner 10, middle 10, and outer mother scales; the outer 10, middle 10, and remaining daughter scales; stem bulblets with their roots; basal plate; and basal roots.

Bulbs from plants that received multiple exposure to $^{14}CO_2$ were harvested on 9 Sept., placed in polyethylene bags (4 mil), and stored at 18°C. Bulbs were replanted, one per 4-liter plastic pot, on 18 Dec. and placed in a cold frame. Five plants were harvested on each of the five dates, i.e., at planting; on 15 Mar., when 12 leaves had unfolded and a new daughter bulb was present; on 16 May, when flower buds were just visible; on 17 June, when the first flower buds were 4 cm in length; and on 29 July, which was 3 weeks after full bloom. The shoot was divided into one to three sections depending upon the date of harvest: lower, stem base to the 12th node; middle, the 13th to 30th node; and upper, everything above the 30th node. Basal and stem roots were combined due to difficulties in separating them. Plants produced an average of 60 leaves. The new daughter bulb, which was large enough to be separated easily from the rest of the bulb only on 16 May or later, was treated as a single part irrespective of the number of scales formed. Stem bulblets were present at the last two harvests and were handled as a separate fraction.

Plant parts were weighed after being dried at 65°C for 72 hr. The combustion and liquid scintillation counting procedures used to estimate ^{14}C activity are described elsewhere (20).

Results

Distribution of ^{14}C-labeled assimilate during scale filling. Total amount of ^{14}C activity recovered in plants was relatively low at the second and third harvests (Fig. 1A). The low recovery probably reflected reduced uptake of $^{14}CO_2$ because of overcast skies on the two exposure dates in August. Seven days after single exposure, only about 20% of the recovered ^{14}C remained in the shoot (including stem roots), over half was in the main bulb, and 10–20% was in stem bulblets (Fig. 1B). In multiple-labeled plants harvested in Sept., 20%, 30%, and 50% of the total recovered ^{14}C were in the shoot, stem bulblets, and main bulb, respectively. The decreased proportions of ^{14}C in the main bulb at successive harvests were accounted for by the increased fractions in stem bulblets (Fig. 1B).

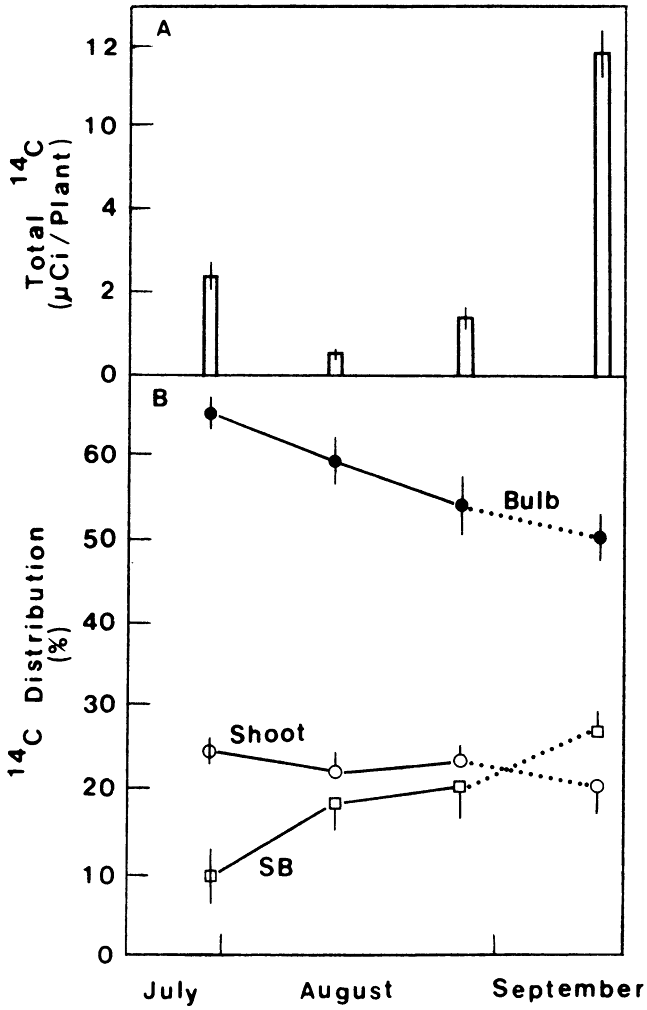

Fig. 1. Total ^{14}C recovered (**A**) and distribution of ^{14}C activity among bulb, shoot (including stem roots), and stem bulblets (**B**) of Easter lily plants 7 days after exposing the whole shoots to $^{14}CO_2$. Plants at the first three harvests were exposed only once. The September-harvested plants had been labeled four times. Vertical bars represent SE of the mean.

Date of exposure to $^{14}CO_2$ had little effect on the partitioning of ^{14}C within the bulb (Table 1). About two-thirds of the ^{14}C in the main bulb was present in daughter scales, with the middle scales (scales 11–20) receiving the largest share. The outer mother scales accumulated the least proportion of ^{14}C. The basal roots and basal plate had similarly low ^{14}C activity. Specific ^{14}C activity (dpm per mg dry weight) was highest in inner daughter scales and lowest in outer mother scales (Table 1). It was relatively high in roots and basal plate.

Dry weight changes and redistribution of ^{14}C after bulb harvest and during regrowth. Mother bulb dry weight declined by 25% during the 14 weeks in storage, with most of the loss

Table 1. The distribution and specific ^{14}C activity of labeled assimilate in various parts of the Easter lily bulb (including basal roots) after exposing the whole shoot to $^{14}CO_2$.

	^{14}C distribution (%)[z]				Specific ^{14}C activity (dpm/mg dry wt)			
	Harvest date				Harvest date			
Bulb	29 July[y]	12 Aug.[y]	26 Aug.[y]	9 Sept.[x]	29 July[y]	12 Aug.[y]	26 Aug.[y]	9 Sept.[x]
Mother scales								
Outer	4.2 c[w]	1.2 d	1.2 e	3.2 d	55 e	6 c	10 e	84 d
Middle	14.3 b	6.5 cd	9.3 cd	10.3 c	96 de	17 c	42 de	233 de
Inner	12.6 b	10.7 c	13.5 bd	13.1 bc	149 de	33 c	95 de	464 c
Daughter scales								
Outer	18.6 b	18.7 b	17.1 b	15.3 b	226 cd	64 c	133 d	479 c
Middle	27.0 a	30.4 a	24.9 a	24.0 a	441 b	125 b	229 c	671 bc
Inner	17.5 b	22.5 b	20.4 b	23.8 a	1040 a	284 a	462 a	1339 a
Basal plate	3.4 c	5.5 cd	6.1 d	4.4 d	357 bc	144 b	324 b	924 b
Roots	2.4 c	4.5 cd	7.5 d	5.9 d	219 cd	164 b	458 a	788 b

[z] ^{14}C activity of the entire bulb is equivalent to 100%.

[y] Plants exposed to $^{14}CO_2$ once.

[x] Plants exposed to $^{14}CO_2$ four times.

[w] Mean separation within columns by Duncan's multiple range test, 5% level.

Table 2. Dry weight distribution in Easter lily plants from bulb digging (9 Sept.) until 3 weeks after full bloom (29 July) the following year.

	Dry weight (g)																
Date of harvest	Mother scales				Daughter scales				Basal plate	Root[z]	Shoot				New daughter bulb	Stem bulblets	Whole plant
	Outer	Middle	Inner	Total	Outer	Middle	Inner	Total			Bottom	Middle	Top	Total			
1982																	
9 Sept.	3.8 a[y]	6.3 a	4.1 a	14.2 a	4.3 a	4.2 a	2.5 a	11.0 a	0.8 a	0.7 a	---	---	---	---	---	26.7 c	
18 Dec.	2.5 b	4.8 b	3.7 a	11.0 b	4.3 a	3.9 a	3.8 ab	12.0 a	0.8 a	0.5 a	0.1 a	---	---	0.1 a	---	---	24.4 b
1983																	
15 Mar.	1.1 c	4.4 b	3.4 a	8.9 c	4.0 a	4.1 a	3.8 ab	11.9 a	0.8 a	0.7 a	0.4 b	0.1 a	---	0.5 b	---	---	22.8 a
16 May	---[x]	0.7 c	1.0 b	1.7 d	3.9 a	5.1 ab	4.7 b	13.7 b	0.8 a	3.2 b	1.2 c	1.7 b	2.1 a	5.0 c	0.13 a	---	25.5 bc
17 June	---[x]	---[x]	---[x]	---[x]	---[w]	---[w]	---[w]	13.1 ab	0.7 a	5.4 c	1.5 d	2.0 c	8.3 b	11.8 d	1.3 b	0.1 a	32.4 d
29 July	---[x]	---[x]	---[x]	---[x]	4.6 a	6.1 b	7.3 b	18.0 c	0.8 a	6.5 d	1.6 d	2.7 d	12.5 c	16.8 e	6.0 c	1.2 b	49.3 e

[z] Combination of stem and basal roots in May and later harvests.

[y] Mean separation within columns by Duncan's multiple range test, 5% level.

[x] Scales decomposed.

[w] Daughter scales not separated.

Table 3. Amounts of ^{14}C in various Easter lily plant parts from bulb harvest (9 Sept.) until 3 weeks after full bloom (29 July) the following years.

	^{14}C activity (nCi)															
Date of harvest	Whole plant	Mother scales				Daughter scales				Basal plate	Root[z]	Shoot				New daughter	Stem bublets
		Outer	Middle	Inner	Total	Outer	Middle	Inner	Total			Lower	Middle	Upper	Total		
1982																	
9 Sept.	6179 a[y]	198 a	636 a	810 a	1644 a	945 ab	1483 a	1471 a	3899 a	272 a	364 a	---	---	---	---	---	---
18 Dec.	6379 a	172 a	478 ab	581 ab	1231 b	1142 a	1633 a	1933 a	4708 a	287 a	134 b	19 a	---	---	19 a	---	---
1983																	
15 Mar.	5519 b	28 b	331 b	475 b	834 b	861 ab	1501 a	1860 a	4222 a	265 a	99 b	88 b	11 a	---	99 b	---	---
16 May	4639 c	---[x]	46 c	158 c	204 c	677 b	1408 a	1680 a	3877 a	181 ab	172 b	97 b	74 b	60 a	231 c	14 a	---
17 June	4785 c	---[x]	---[x]	---[x]	---[x]	---[w]	---[w]	---[w]	4090 a	140 b	171 b	128 b	80 b	119 b	327 c	57 b	---
29 July	4590 c	---[x]	---[x]	---[x]	---[x]	1037 a	1629 a	1313 a	3979 a	92 b	128 b	101 b	69 b	92 ab	262 c	124 c	9

[z] Combination of basal and stem roots in May and later harvests.

[y] Mean separation within rows by Duncan's multiple range test, 5% level.

[x] Scales decomposed.

[w] Daughter scales not separated into three groups.

occurring in the outer and middle mother scales (Table 2). The combined mother scales also lost a similar fraction of total ^{14}C during storage (Table 3). Total plant ^{14}C did not decrease significantly until rapid shoot growth took place in spring. Loss of reserves during this period occurred most rapidly in outer mother scales, and their complete depletion was followed by that of middle and inner scales (Tables 2 and 3). The decline in total plant ^{14}C activity ceased in mid-May, at which time mother scales were nearly depleted of dry matter and had lost 89% of the ^{14}C they contained at bulb harvest the previous autumn. Mother scale reserves apparently were uniformly labeled, since the specific ^{14}C activity of the scales showed little change during depletion (Fig. 2).

Dry weight of the combined daughter scales increased during bulb storage because of a 50% increase in the weight of inner scales, although the increase was not statistically significant (Table 2). After replanting, total dry weight of daughter scales remained stable for several months, then increased markedly in mid-June as shoot elongation approached completion. The gain in dry weight was not associated with increasing labeling (Table 3); therefore, the specific ^{14}C activity of daughter scales declined sharply (Fig. 2). The amount of ^{14}C in all three groups of daughter scales remained unchanged during the 11 months following bulb digging. When harvested in late July, 60% of the dry matter in the daughter (now mother) scales was likely accumulated the year before.

All bulbs had sprouted at replanting and the emerging shoot slowly accumulated dry matter until mid-Mach, thereafter the increase was rapid and linear (Table 2). The specific ^{14}C activity of the young shoot was relatively high and stable for the 3 months following replanting, but then declined sharply (Fig. 2). The shoot ceased to gain radioactivity after mid-June (Table 3). At this time, the whole shoot had only 7% of the total plant ^{14}C, which accounted for only 20% of the radioactivity lost from mother scales.

The new daughter bulb, which originated after replanting, was visible on 15 Mar. but did not start to actively accumulate dry matter and radioactivity until after mid-May (Tables 2 and 3). Initially, the specific ^{14}C activity in the new daughter bulb was identical to that of the mother scales (Fig. 2), suggesting that they were the major sources of carbon for early growth of the new bulb. The increase in the amount of ^{14}C in the new daughter bulb between the last two harvests might have been from the redistribution of ^{14}C in the shoot. Final radioactivity in the new daughter bulb represented 8% of the ^{14}C lost from mother scales. Stem bulblets grew rapidly after mid-June, but they were essentially unlabeled (Tables 2 and 3) and, therefore, were not dependent on scale reserves (Fig. 1A).

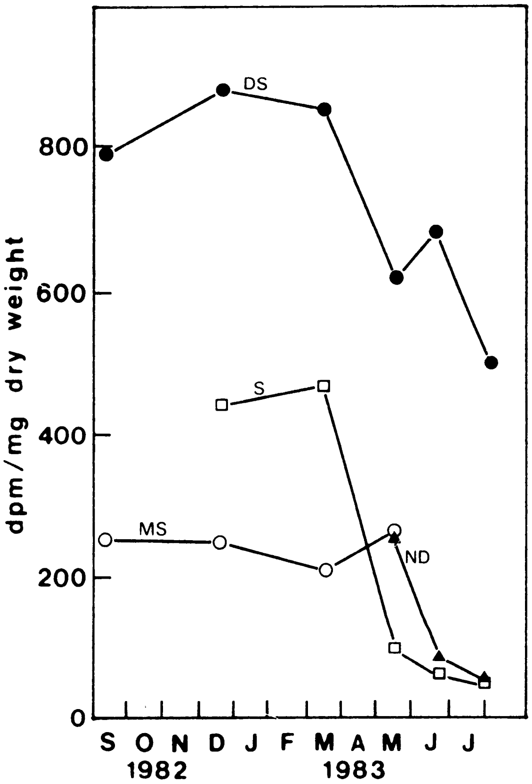

Fig. 2. Specific ^{14}C activity in selected plant parts from bulb harvest (Sept. 1982) until 3 weeks after full bloom the following year (1983). MS, mother scales; DS, daughter scales; ND, new daughter bulb; S, shoot.

The root system rapidly accumulated dry matter after mid-March (Table 2), with much of the gain resulting from extensive growth of stem roots. Both the roots and basal plate lost ^{14}C activity (Table 3). The decline in ^{14}C in the roots occurred during bulb storage and may represent respirational losses. Decomposition of the portion of mother scales attached to the basal plate (4) likely contributed to the loss of ^{14}C activity from this organ.

By the time of the final harvest, 3 weeks after anthesis, one-quarter of the radioactivity and half of the dry weight present in the bulb harvested the year before was lost.

Discussion

This study agrees with previous reports that storage organs in bulbous plants are the major sinks for current photoassimilate after all flowers have bloomed (7, 20). The fraction (80%) of ^{14}C partitioned to storage organs was similar to that reported previously (20). However, in the previous study, the storage organ received 80% of the "translocated" ^{14}C only, and the amount of ^{14}C that remained in the exposed leaf was unaccounted for. Therefore, the distribution of assimilate from a single leaf 24 hr after labeling only revealed the sites of major carbon sinks. It may not represent the partitioning pattern of carbon from the entire shoot over periods of days or weeks after exposure to $^{14}CO_2$.

The results show that stem bulblets are strong carbon sinks that compete with the main bulb for current photosynthate (Table 2, Fig. 1). Since bulblets grow on underground nodes and are nearer to source leaves, they may have better access to the carbon supply from leaves than the more distant main bulb. Since growth of the Easter lily bulb is likely limited by the supply of current assimilate (19, 20), inhibiting the growth of stem bulblets may greatly enhance the partitioning of current photosynthate into the main bulb.

Within the bulb, the inner and middle daughter scales were the most efficient in acquiring labeled assimilates, as shown by the high specific ^{14}C activity and fraction of total ^{14}C in these young tissues. This increased sink activity may have been the result of a rapid conversion of sugars into stored material as reported for tulip (8) and potato (14). As is generally the case, reserves rapidly accumulated in daughter scales during the first year of their development are unavailable for shoot growth until the third growing season. However, these reserves can be remobilized when bulbs are forced in a greenhouse and rapid shoot growth creates a large carbon demand, or when low light levels or damage to the foliage severely limit photosynthate production (3, 16), or when outer scales are removed before planting (12).

Growth of inner daughter scales during bulb storage (Table 2) was apparently at the expense of mother scale reserves, since there was no other carbon source. Mobilization of reserves from older to younger lily scales during bulb storage was suggested by Matsuo et al. (13) after monitoring the ratio of dry to fresh weight of scales at various nodal positions. However, in the present study, only one-third of the dry matter loss from mother scales during storage is accounted for by the net gain in the weight of daughter scales. Studies of lily bulb respiration (ref. 9; unpublished data) suggest that a majority of the dry matter lost from month scales during storage is through respiration. Mother scales of tulip bulb lose a large fraction of dry matter (25–65%) during storage due to their high rates of respiration (2, 4, 6, 15).

Since removal of very young expanding Easter lily leaves was shown previously to prevent further depletion of scale reserves (16) and scale removal reduced shoot growth (12), most of the dry matter and ^{14}C removed from mother scales after replanting was likely translocated to the developing shoot. However, only 30% of the ^{14}C lost from the mother scales was recovered in the shoot and new daughter bulb (Table 3), presumably much of the remainder was lost through respiration (8). In Jerusalem artichoke, most of the dry matter removed from the mother tuber is translocated to the developing daughter shoots, where 25% of it is used in respiration (10, 11). In tulip plants pulsed with $^{14}CO_2$ prior to harvest, 80% of the ^{14}C activity in the bulb was lost during the first 3 weeks of forcing (8). Apparently, these rapidly growing shoots have large energy demands.

Since there were few small, fully expanded leaves before 15 Mar., shoot growth during this period was heavily dependent on scale reserves. However, the specific ^{14}C activity in the young shoot was higher than that in mother scales (Fig. 2). Since specific ^{14}C activity in the inner daughter scales was much higher than the other scales at fall harvest (Table 1), the concentration of ^{14}C in the growing point in the center of the daughter bulb also may have been high. This emerging shoot also could draw labeled assimilates of high specific ^{14}C activity from the inner daughter scales. As it continued to develop, ^{14}C was diluted by carbon from other sources. The decline of specific ^{14}C activity in all organs after 15 Mar. and the low recovery of label lost from the bulb suggest that current photosynthate is the major carbon source for structural materials in the shoot. This evidence supports a previous report (20) that growth of Easter lily flower buds relies heavily on leaf photosynthesis under normal field conditions.

This study shows that, after flowering, the bulb of an Easter lily plant is the major carbon sink, although as the season progresses, stem bulblets become increasingly competitive for available assimilate. In the following year, reserves in mother scales are remobilized to support the energy demands of the developing shoot, with only 28% of the carbon being incorporated into stable components. Reserves in daughter (now mother) scales are largely unused and presumably available for new growth during the next growing cycle. Growth of new daughter scales is initially dependent on reserves from mother scales but is soon supported by current photosynthesis.

Literature Cited

1. Aung, L.H., F. Tognoni, and A.A. De Hertogh. 1973. Changes in the carbohydrates of tulip bulbs during development. HortScience 8:207–208.
2. Aung, L.H., R.D. Wright, and A.A. De Hertogh. 1976. Carbohydrate and dry matter changes in organs or *Tulipa gesneriana* L. during low temperature treatment. HortScience 11:37–39.
3. Bell, G.L., W.B. Miller, and R.W. Langhans. 1985. Effects of reduced light levels in growth and dry matter partitioning in Easter lily. HortScience 20:600. (Abstr.)
4. Benschop, M. 1980. Growth and development of tulip, cv. Apeldoorn, from planting until emergence. Acta Hort. 109:189–196.
5. Blaney, L.T. and A.N. Roberts. 1966. Growth and development of the Easter lily bulb. Proc. Amer. Soc. Hort. Sci. 89:643–650.
6. Hansen, H. 1976. [Analytical studies on the growth of tulip.] Vaekstanalytiske undersogelser i tulipener. Tidsskr. Planteavl. 80:869–892.
7. Ho, L.C. and A.R. Rees. 1975. Aspects of translocation of carbon in tulip. New Phytol. 74:421–429.
8. Ho, L.C. and A.R. Rees. 1976. Remobilization and redistribution of reserves in the tulip in relation to new growth until anthesis. New Phytol. 76:59–68.
9. Hosoki, T. 1984. Effect of hot water treatment on respiration, endogenous ethanol, and ethylene production from gladiolus corms and Easter lily bulbs. HortScience 19:700–701.
10. Jefford, T.G. and J. Edelman. 1960. Changes in content and composition of the fructose polymers of *Helianthus tuberosus* L. during growth of daughter plants. J. Expt. Bot. 12:177–187.
11. Jefford, T.G. and J. Edelman. 1963. The metabolism of fructose polymers in plants: II. Effect of temperature on the carbohydrate changes and morphology of stored tubers. J. Expt. Bot. 14:56–62.
12. Lin, P.C. and A.N. Roberts. 1970. Scale function in growth and flowering of *Lilium longiflorum* Thunb. 'Nellie White''. J. Amer. Soc. Hort. Sci. 95:559–561.
13. Matsuo, E., K. Arisumi, and N. Garran. 1980. Studies on growth and development of bulbs in the Easter lily (*Lilium longiflorum* Thunb.): IX. The ratio of dry to fresh weight of scales, with special reference to its variation in scale positions and its changes during bulb storage. J. Jpn. Soc. Hort. Sci. 48:483–487.
14. Moorby, J. 1970. The production, storage, and translocation of carbohydrates in developing potato plants. Ann. Bot. 34:297–308.
15. Rees, A.R. 1972. The growth of bulbs. Academic, New York.
16. Roberts, A.N. and L.T. Blaney. 1968. Effects of vernalization and partial defoliation on flowering and correlative relationships in *Lilium longiflorum* Thunb. 'Croft'. Proc. Amer. Soc. Hort. Sci. 92:646–663.
17. Roberts, A.N., Y.T. Wang, and F.W. Moeller. 1983. Effects of pre- and post-bloom temperature regimes on development of *Lilium longiflorum* Thunb. Scientia Hort. 18:363–379.
18. Wang, Y.T. and A.N. Roberts. 1983. Influence of air and soil temperatures on the growth and development of *Lilium longiflorum* Thunb. during different growth phases. J. Amer. Soc. Hort. Sci. 108:810–815.
19. Wang, Y.T. and P.J. Breen. 1986. Growth and photosynthesis of Easter lily in response to flower bud removal. J. Amer. Soc. Hort. Sci. 111:442–446.
20. Wang, Y.T. and P.J. Breen. 1986. Partitioning of ^{14}C-assimilate in Easter lily as affected by growth stage and flower removal. Scientia Hort. 29:273–281.