Reduced Irradiance Affects Dry Weight Partitioning in Easter Lily

William B. Miller¹ and Robert W. Langhans²
Department of Floriculture and Ornamental Horticulture, Cornell University, Ithaca, NY 14853

Additional index words. Lilium longiflorum, flower bulbs, greenhouse crop physiology

Abstract. The effects of reduced irradiance on dry weight partitioning in Easter lilies was examined by forcing vernalized bulbs of Lilium longiflorum Thumb. 'Nellie White' during two growing seasons. Forcing commenced in a glasshouse under standard growing conditions; immediately following flower bud initiation (FBI), plants were transferred to a range of irradiance reduction treatments (0%, 20%, 50%, or 85% reduction) in the greenhouse or to complete darkness in a growth chamber. Greenhouse irradiance reduction treatments resulted in alterations in whole-plant source-sink relationships. Total plant dry weight and overall plant quality were reduced in shaded plants. The depletion rate of mother bulb dry matter was not affected by reduced irradiance, whereas daughter bulb reserve loss was increased by irradiance reduction treatments. There was no daughter bulb reserve remobilization in plants grown in complete darkness after FBI. Flower bud and open flower dry weights were progressively reduced as irradiance was reduced. With an 85% irradiance reduction, plants forced from 17.5-cm bulbs had 63% bud abortion, whereas, with 20.0-cm bulbs, only 12% of the buds aborted. Plants grown in complete darkness after FBI became etiolated, and flowers failed to open. These results demonstrate differences in the ability of various morphological regions of the bulb to respond to reductions in greenhouse irradiance. Since the daughter bulb response to reduced irradiance was relatively slow, additional remobilization of dry matter from the daughter bulb is probably of minimal benefit during short periods of reduced irradiance in commercial greenhouses.

Due to its popularity with consumers for the Easter holiday, the Easter lily is widely grown in commercial greenhouses in the United States. Flowering plants are grown from bulbs during the low-irradiance period of mid-winter to early spring.

Previous research has led to commercial recommendations emphasizing the importance of maximizing greenhouse irradiance for the production of highest-quality Easter lilies (Boodley et al., 1984; Einert and Box, 1967; Heins et al., 1982; Kohl, 1967; Kohl and Nelson, 1963; Weiler, 1978), although lilies have been reported to grow and flower under extremely low-irradiance environments (Wilkins et al., 1986). It is not certain how whole-plant source-sink relationships are affected by reduced irradiance. While earlier work established yearly dry weight partitioning cycles for field-grown plants (Blaney and Roberts, 1966), to the best of our knowledge no work has been published on dry weight partitioning in greenhouse forced Easter lilies. Low irradiance could result in lowered leaf carbohydrate levels, which might induce increased bulb reserve remobilization and export to the growing shoot. The purpose of the present work was to determine whole-plant source-sink responses of greenhouse-forced Easter lilies to reduced irradiance environments.

Materials and Methods

Cultural practices. ‘Nellie White’ Easter lily plants were grown according to recommended commercial practice (Boodley et al., 1984). After a 6-week 4.5C cold treatment, bulbs were planted into 15-cm-diameter clay containers (1.8 liter volume) using a 1 soil : 1 peat : 1 perlite (by volume) medium with the following amendments (kg·m⁻³): CaCO₃, 2.97; CaMg(CO₃)₂, 1.78; CaSO₄, 1.19; and Ca(H₂PO₄), 0.40. Plants were irrigated with a fertilizer solution containing 200 mg N and K/liter supplied from 540 mg KNO₃ and 759 mg Ca(NO₃)₂/liter. All plants were grown at 22.0/15.5C (venting/night) in a glass greenhouse, until the flower bud initiation stage in late January, when uniform plants of similar height and unfolded leaf number were selected for experimentation. Irradiance reduction treatments were commenced at floral initiation and continued to anthesis.

1984 Experiment. Bulbs (18 to 20 cm in circumference) were received 2 Nov. 1983, vernalized, and then potted 5 Dec. 1983. The four levels of irradiance reduction used were: 1) natural irradiance (0% reduction), 2) 50% reduction (one layer of 50%
shade cloth over the greenhouse bench), 3) 85% reduction (two layers of 50% cloth plus one layer of cheese cloth), and 4) complete darkness (100% reduction), where plants were grown in a 15.5°C constant-temperature growth chamber.

1985 Experiment: Bulbs (20 to 23 cm in circumference) were received 27 Oct. 1984, vernalized, and potted 2 Dec. 1984. The five levels of irradiance reduction used were: 1) natural irradiance (0% reduction), 2) 20% reduction (one layer of cheesecloth), 3) 50% reduction (one layer of 50% shade cloth), 4) 85% reduction (three 50% shade cloth layers), and 5) complete darkness (100% reduction) in a 15.5°C constant-temperature growth chamber.

Percentage irradiance reduction was determined by periodic measurements of photosynthetic photon flux (400 to 700 nm) using a LI-COR LI-185A meter equipped with a quantum sensor. Data are expressed as percent reduction from the natural irradiance control treatment. Deviations of ±5% were noted during the experiment. Seasonal irradiance data were provided by the Cornell Agronomy Dept.

At 14-day intervals, five plants were harvested from each treatment and dissected into the component parts: stem (including below-ground stem portions and pedicels), leaves, flower buds, mother (mature, outer) scales, daughter (encompassing the current emerged shoot) scales, and new daughter (developing) scales. Fresh and dry weights of the above and leaf area were recorded for each plant. Dry weights were determined after tissues were in a 70°C forced-air oven for 72 hr. Bud length was measured from the tip of the bud to the point of attachment to the pedicel.

All data were analyzed in a completely randomized design using CoStat (Cohort Software, Berkeley, Calif.).

Results

The 1984 and 1985 data were similar and in most cases 1985 data are presented. The Ithaca, N.Y. area received 927 mol photons/m² (400 to 700 nm) during the period from shoot emergence to flowering in 1985. Outdoor irradiance was 6% greater during the 1984 experiment.

Overall plant quality was reduced when plants were grown under shaded conditions. As previously described (Einert and Box, 1967), plants grown under reduced irradiance environments were taller due to elongated internodes, developed thinner leaves, and flowered 3 to 5 days earlier than normal. Reducing the experiment averaged 180 mg dry weight/day. About 4 weeks after planting, mother scales were developing wrinkles, providing a visual indication of the mobilization events in progress.

The rate of daughter bulb reserve mobilization and final daughter bulb weight at anthesis depended on the irradiance

Table 1. Dry weight characteristics of plants, bulbs, stems, and leaves at anthesis, 10 weeks after irradiance reduction treatments began. Data are the means of five plants per treatment (1985 experiment).

<table>
<thead>
<tr>
<th>Irradiance reduction (%)</th>
<th>Shoot and bulb*</th>
<th>Bulb*</th>
<th>Stem</th>
<th>Leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>30.9</td>
<td>12.1</td>
<td>7.6</td>
<td>11.3</td>
</tr>
<tr>
<td>20</td>
<td>23.9</td>
<td>10.3</td>
<td>5.4</td>
<td>8.1</td>
</tr>
<tr>
<td>50</td>
<td>18.6</td>
<td>6.9</td>
<td>4.9</td>
<td>6.7</td>
</tr>
<tr>
<td>85</td>
<td>16.9</td>
<td>6.3</td>
<td>5.1</td>
<td>5.5</td>
</tr>
<tr>
<td>100</td>
<td>20.3</td>
<td>15.2</td>
<td>4.4</td>
<td>0.7</td>
</tr>
<tr>
<td>LSD 0.05 level</td>
<td>4.6</td>
<td>4.1</td>
<td>1.1</td>
<td>1.7</td>
</tr>
</tbody>
</table>

*Excluding flowers and root system.

Table 1 shows dry weight characteristics of plants, bulbs, stems, and leaves at anthesis, 10 weeks after irradiance reduction treatments began. Data are the means of five plants per treatment (1985 experiment).

Fig. 1. Time course of mother bulb dry weight depletion during 10 weeks of irradiance reduction. Irradiance reduction treatments were continuously imposed after the flower bud initiation stage (week 0). Visible buds were present and anthesis occurred 3.5 and 10 weeks later, respectively. Each point is the mean of five plants. Data from 1985 experiment.

Available to the plant. Daughter bulb depletion was not influenced by irradiance reduction until 4 weeks after treatments began. Therefore, the daughter bulb dry matter depletion rate was related to the irradiance reduction regime imposed; i.e., daughter bulb dry matter depletion increased as greenhouse irradiance was reduced (Fig. 2). At anthesis (week 10), 50% to 85% irradiance reduction resulted in daughter bulbs that were 40% smaller than daughter bulbs from non-shaded plants (Fig. 2). The conclusion of the experiment, daughter bulbs of dark-grown plants had retained essentially all of the dry matter that was present at the start of the experiment (Fig. 2). At anthesis, dark-grown plants had a significantly greater daughter bulb dry weight than plants grown under any of the greenhouse irradiance reduction treatments (Fig. 2). Total bulb dry matter (mother plus daughter portions) was significantly affected by irradiance reduction (Table 1).

Reductions in irradiance resulted in decreased stem dry weight at anthesis (Table 1). Stems in all treatments gained dry matter after imposition of irradiance reduction treatments, although dark-grown plants had etiolated and spindly stems. At anthesis, leaf dry weight was significantly reduced as a result of irradiance reduction (Table 1). Leaves from plants in the dark treatment slowly lost dry matter, whereas leaf dry weight continued to increase (at different rates) in each of the other treatments.

Irradiance reduction throughout the forcing period resulted in decreased flower bud dry weight, regardless of bud length (Fig. 1).
In all cases, irradiance reduction reduced flower quality, as judged by visual flower appearance and decreased flower longevity on the plant.

Incidence of bud abortion (blasting) was similar between the 1984 and 1985 experiments. The exception was the 85% irradiance reduction treatment, which resulted in 63% bud abortion in 1984 but only 12% abortion in 1985 (Table 3). In both years, 50% irradiance reduction resulted in <10% bud abortion. Plants grown in darkness after flower bud initiation exhibited nearly 100% abortion (Table 3).

### Discussion

As a first step in studying dry weight partitioning in the forced Easter lily, we have used reduced irradiance environments to alter whole-plant source-sink relationships. Irradiance was chosen as the experimental factor because of its obvious role in photosynthate formation and because of its importance in the production of high-quality commercial crops (Kohl, 1967; Boodley et al., 1984). The current research has demonstrated differences in the physiological ability of mother and daughter bulb tissues to respond to ambient irradiance. The rate of dry weight loss from mother scales was unchanged as a result of irradiance reduction, suggesting that, once initiated, remobilization events leading to carbohydrate export from mother scales are insensitive to ambient irradiance. At anthesis, daughter bulbs from shaded plants had lost greater amounts of dry matter than daughter bulbs of non-shaded plants; we infer these reserves were exported to the shoot. This inference is supported by earlier work reporting that daughter scales did not lose 14C activity during shoot growth and flowering in non-shaded conditions (Wang and Breen, 1987). The mechanism of this differential irradiance response between scale types is unknown; however, the response is slow, since more than 4 weeks of reduced irradiance treatment were necessary to induce significantly different daughter bulb dry weights (Fig. 2).

Daughter bulbs were not fully depleted at anthesis, even under the 85% irradiance reduction treatment (Fig. 2), whereas mother bulb scales were fully depleted at this time. After anthesis, a major shift in partitioning of current photosynthate occurs, with the initiation of a strong basipetal movement of assimilate into the bulb (Wang and Breen, 1986 and 1987). The mechanism of this differential irradiance response between scale types is unknown; however, the response is slow, since more than 4 weeks of reduced irradiance treatment were necessary to induce significantly different daughter bulb dry weights (Fig. 2).

Developing buds and leaves are strong sinks in natural or reduced irradiance, but not in complete darkness (Tables 1 and 3; Fig. 2). The demand for assimilate by the developing buds and leaves influences daughter bulb export activity. Reducing shoot source activity by progressively removing mature leaves starting 1 week after the visible bud stage resulted in reduced daughter bulb dry weight (Roberts and Blaney, 1968; W.B.M., unpublished data). During prolonged periods of reduced photosynthetic activity, these developing leaves and buds constitute a sink capable of attracting assimilates from the daughter bulb (Fig. 2). Our work suggests that daughter bulb reserve export was critical for adequate shoot and floral growth in experiments where lilies were forced for long time periods under minimal irradiance regimes (Wilkins et al., 1986). Conversely, due to the 4-week lag period (Fig. 2), remobilization and export of daughter bulb reserves is probably of minimal benefit to the shoot system during short-term irradiance reduction events during forcing.
Table 3. Flower bud abortion as a function of irradiance reduction within the greenhouse. Data are from two experiments conducted over 2 years.

<table>
<thead>
<tr>
<th>Year</th>
<th>Bulb circumference (cm)</th>
<th>Irradiance reduction (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>20</td>
</tr>
<tr>
<td>1984</td>
<td>18–20</td>
<td>7.1 (4.2)*</td>
</tr>
<tr>
<td>1985</td>
<td>20–23</td>
<td>4.4 (1.4)</td>
</tr>
</tbody>
</table>

*Means ± (se) of 20 plants.

It has long been thought that low greenhouse irradiance is a main factor controlling lily bud blast, based on work with 'Croft' lilies (Mastalerz, 1965). However, subsequent reports using 'Ace', 'Georgia', and 'Nellie White' indicated irradiance reduction at 50% to 85% (applied at various stages, or throughout the forcing period) did not significantly increase flower bud blast (Table 3) (Einert and Box, 1967; Heins et al., 1982; Weiler, 1978). The present results do indicate flower bud dry weight is significantly reduced as a result of reduced irradiance conditions during forcing (Table 2), a finding not previously reported. While it is difficult to directly compare past results, all available evidence suggests that greenhouse irradiance plays only a minor role in Easter lily bud abortion. Interactions of other environmental factors known to cause bud abortion, including ethylene (Rhoades et al., 1973), calcium nutrition (Seeley, 1950), elevated day or night temperatures (Smith and Langhans, 1962), and excessive moisture (Miller and Langhans, 1986) should be investigated.

Literature Cited


