Clonal Variability among Grower Bulb Lots of Easter Lily ‘Nellie White’

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ABSTRACT. Potted Easter lily (*Lilium longiflorum* Thunb.) ranks among the top five potted flowering plants in the United States in economic value. One clone (‘Nellie White’) dominates the North American market. It is grown by less than 10 bulb producers, each maintaining their own propagation stock and practicing intracloonal strain selection. Greenhouse forcers attest to forcing differences depending on the bulb grower. The objective of this study was to determine the extent and sources of morphological variability among bulb growers. Bulb lots were obtained in 2002 (S1) and 2003 (S2) (n = 11 and n = 12 lots respectively) with 12 or 15 bulbs/lot. Grower’s identification was confidential but kept consistent across shipment years. Bulbs were obtained as the 20.3 to 22.9-cm circumference commercial class, and S1 and S2 shipments were control temperature forced over two forcing cycles (FC1, FC2). Data collection included initial bulb weight and circumference; days to stem emergence (SEM), visible flower bud (VFB), and anthesis (AN); plant and inflorescence height; number of stems, leaves, flowers, and ovules per first flower/stem reaching AN; percentage of ovules forming viable seeds; leaf length and width; major lily viruses (presence/absence, relative optical density); leaf length-to-width ratios; AN-SEM, AN-VFB, and VFB-SEM. Significant differences were found among bulb lots for every trait except AN-VFB. Variability among bulb lots can be attributed to variation in initial bulb size, previous forcing cycle environment, variable lily symptomless virus (LSV) titer, and underlying genetic/epigenetic differences. Bulb circumference had the highest standardized canonical coefficient for canonical variable one in S2-FC1 and was a significant covariate in analysis of covariance; larger bulbs tended to produce larger plants. Forcing over two cycles allowed for less phenotypic variability among bulb lots in FC2 because of a common FC1 environment. All lilies were positive for LSV and negative for four other viruses tested. Significant negative correlations in S2 between relative optical density and plant height (FC1), initial bulb weight (FC2), and initial bulb circumference (FC2) indicate an effect of relative LSV titer on plant morphology. The role of LSV titer and genetic/epigenetic intergrower variability in ‘Nellie White’ warrants further investigation. Likewise, a lack of breeder/producer companies and the corollary independent grower strain selection has significant genetic consequences and complicates identification of superior ‘Nellie White’ clones.

Flowering, potted Easter lilies ranked among the top five potted flowering plants for economic value in the United States in 2004, with more than 9.3 million pots produced and a wholesale value of about \$38.5 million (U.S. Department of Agriculture, 2005). Current Easter lily bulb propagation and field production for the North American market relies on one cultivar, Nellie White (>60-year-old clone), produced by less than 10 growers in a small coastal region between Smith River, Calif., and Brookings, Ore. (Dole and Wilkins, 1999; Zlesak and Anderson, 2003). Easter lily bulbs are 2 or 3 years old when field bulb producers ship them to greenhouse finishers. Bulbs are graded and sold according to bulb circumference: 17.8 to 20.3 cm, 20.3 to 22.9 cm, 22.9 to 25.4 cm, and more than 25.4 cm (Dole and Wilkins, 1999).

Although one clone predominates, greenhouse forcers recognize differences in forcing quality across grower bulb lots and years (Zlesak and Anderson, 2003). Forcers react by typically purchasing bulbs from multiple growers annually to ensure a salable crop during the narrow U.S. Easter lily marketing window, which is the 2 weeks before Easter (Zlesak and Anderson, 2003). Variability in forced plants [e.g., days to stem emergence (SEM), leaf number, flower number, internode length] can be attributed to factors such as variable temperatures during shipping and rooting, and variable bulb maturity and dormancy across bulb lots and years (Erwin and Engelen-Eigles, 1998). In addition, production duration and schedules change annually because the date of Easter is variable (22 Mar. to 25 Apr.), whereas greenhouse finishers consistently obtain harvested bulbs at the same time each year (weeks 42–44). To have salable, flowering plants within the 2 weeks before Easter, greenhouse finishers manipulate vernalization treatments, long-day photoperiod treatments after vernalization, and production temperatures. These production factors can alter plant morphology and therefore plant quality (Dole and Wilkins, 1999). Key traits that command a higher market price include high flower bud number, short plant stature (30–46 cm), and developmental milestones occurring in a timely manner to have the first flower opening within 2 weeks before Easter (Dole and Wilkins, 1999; Lange and Heins, 1990; Pi Alpha Xi, 1986; Wilkins and Roh, 1976).

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There is the potential for mutation and other genetic changes within and across grower stocks of clonally propagated crops that can lead to variability in morphology (Veilleux and Johnson, 1998). 'Nellie White' is more than 60 years old and has emerged as the primary U.S. cultivar, almost to the exclusion of all others (Zlesak and Anderson, 2003). To minimize phenotypic variability during bulb production, Easter lily field growers independently select and propagate their own intracultural strains (Zlesak and Anderson, 2003). Periodically (≈ 10 years), growers identify superior-performing lilies within the field with desirable production traits such as late stem emergence from the soil to avoid spring hail storms, quick growth to compensate for late emergence, high flower bud number, compact plants, and lack of premature daughter bulb sprouting (summer sprouting) before harvest (Zlesak and Anderson, 2003). Each grower prioritizes phenotypic characteristics during intracultural selection according to their production needs and phenotypic preferences. Propagules from each intracultural selection are kept distinct, and eventually those selections that are uniform and continue to perform well are propagated for commercial production (Zlesak and Anderson, 2003). As variability accumulates among ramets over clonal cycles, intracultural selection is repeated.

As growers independently perform intracultural selection and more cycles of intracultural selection accrue, there is a greater possibility for genetic divergence among grower stocks of 'Nellie White'. A survey of the relative performance of Easter lily bulb lots across the major growers has not been reported before. The objectives of this research were to determine 1) the extent of morphological variability of *L. longiflorum* 'Nellie White' among bulb lots from different growers across forcing cycles and years, and 2) the sources of the morphological variability.

Materials and Methods

PLANT MATERIAL. Bulb lots of *L. longiflorum* 'Nellie White' were obtained 24 Oct. 2002 [$n = 11$ bulb lots; $n = 15$ bulbs/lot; shipment number 1 (S1)] and 22 Oct. 2003 [$n = 12$ bulb lots; $n = 12$ or 15 bulbs/lot; shipment number 2 (S2)] of the 20.3 to 22.9-cm circumference commercial class. A third party, O. Hoffman (Fred C. Gloeckner Co., Harrison, N.Y.), collected freshly dug and graded bulbs directly from the major Easter lily bulb growers in Smith River, Calif., and Brookings, Ore., assigned a numeric code referencing each grower/bulb lot, and shipped the bulbs to us. The numeric code remained confidential. The bulb lot source from each grower was numbered identically across shipment years (S1, S2). One additional source/grower (bulb lot number 9) was represented in the 2003 shipment (S2) compared with the 2002 shipment (S1). Up to seven different growers are represented among the 12 bulb lot designations. The same bulbs were forced into flower in the greenhouse over two forcing cycles.

FORCING CYCLE ONE (FC1). Bulbs of S1 and S2 were individually potted 25 Oct. 2002 and 23 Oct. 2003 respectively, into 15-cm-diameter round plastic pots (1.84 L) using SB300 Universal Professional Growing Mix (Sun Gro Horticulture, Pine Bluff, Ark.). The bulbs were control temperature forced (CTF) (Dole and Wilkins, 1999). The CTF treatment was administered by allowing bulbs to root into media before vernalization treatment in a greenhouse maintained at 21 ± 2.0 °C (St. Paul, Minn., lat. 45°N) for 18 d. Potted bulbs were

subsequently vernalized in a cooler (4 °C) for 6 weeks (1000 h) and were then forced in the greenhouse. Pots were arranged in a randomized complete block design (S1 = five blocks; S2 = three blocks), with blocks being different benches at different distances from the greenhouse fans. Greenhouse temperatures for S1 bulbs were 24.2 ± 3.1 °C/ 18.2 ± 2.0 °C (day/night) and 24.6 ± 3.8 °C/ 20.5 ± 1.5 °C for S2 bulbs. For both S1 and S2 bulbs, day extension lighting (400-W metal halide lamps; 16 h, 0600–2200 HR; ≈ 150 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant level) was used. During active growth, plants were fertilized weekly (300 mg·L⁻¹ N) using Miracle-Gro Professional Peat-Lite Special 20N–4.4P–16.6K (The Scotts Co., Marysville, Ohio).

ENVIRONMENTAL CONDITIONS AFTER FC1. The S1 plants were allowed to senesce naturally under the FC1 forcing conditions. Bulbs were harvested and repotted in square plastic pots (15 × 15 × 16.5 cm; 2.75 L) using new soil medium as that used for FC1 on 7 July 2003. Potted bulbs were watered and placed in the greenhouse (24.0 ± 2.0 °C) for 1 week, vernalized (4 °C) for 6 weeks in a cooler, and returned to the greenhouse for forcing cycle two (FC2).

For S2 bulbs, the growing conditions after flowering were modified relative to S1. The photoperiod was reduced weekly during the final 8 weeks of FC1 growth (weeks 18–26) before bulb harvest to mimic the decreasing photoperiod (13 h 52 min daylight to 11 h 18 min daylight) during the final 8 weeks before bulb harvest under commercial production conditions (weeks 34–42) in Brookings, Ore. (lat. 42°N) (U.S. Naval Observatory, 2000). Bulbs were subsequently harvested and repotted in square plastic pots on 22 June 2004 as noted earlier using new soil medium as that used for FC1. Potted bulbs were placed in a greenhouse for 2 weeks of CTF ($\approx 21 \pm 2.0$ °C) before an 8-week vernalization treatment (4 °C). After the vernalization treatment, bulbs were held at 21 °C for 9 d to prevent devernization before returning to the greenhouse for forcing. Temperatures higher than 21 °C can lead to devernization (Miller and Kiplinger, 1966), and greenhouse temperatures can be difficult to maintain at or below 21 °C in late summer, when bulbs are returned to the greenhouse for the second forcing cycle.

FORCING CYCLE TWO. Vernalized plants were brought to the greenhouse and arranged in a randomized complete block design (S1 = five blocks; S2 = three blocks). Greenhouse temperatures during FC2 of S1 bulbs were 28.8 ± 3.7 °C/ 19.4 ± 3.0 °C (day/night) and 25.8 ± 4.4 °C/ 19.3 ± 2.3 °C for S2. For both S1 and S2 bulbs, day extension lighting (400-W metal halide lamps; 16 h, 0600–2200 HR; ≈ 150 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant level) was used.

DATA COLLECTED. For FC1 and FC2, initial bulb weight and circumference (except for S1-FC1 bulbs because of the assumption bulbs were uniform in size and within the designated commercial size class), days to SEM above the soil, visible flower buds (VFB), and anthesis (AN); plant height (in centimeters) at flower, inflorescence height (in centimeters; uppermost node of the main stem to the top of the longest pedicel), number of emerging stems, number of leaves, number of flowers, leaf length (in millimeters; $n = 3$ central stem leaves), and leaf width (in millimeters; $n = 3$ central stem leaves) were measured. Other variables were calculated: the number of days from SEM to VFB (VFB-SEM), the number of days from SEM to AN (AN-SEM), the number of days from VFB to AN (AN-VFB), and the mean leaf length-to-width ratio. In S2-FC2, the first flower/stem reaching AN was pollinated

with pollen of *L. longiflorum* 'Europa' to assess female fertility. Pollen of 'Europa' was obtained from cut flowers imported from the Netherlands (Koehler & Dramm, Minneapolis, Minn.). Anthers were dried for 24 h and stored at -20°C . Plastic film canisters containing dried anthers (≈ 12) of 'Europa' were capped and frozen (-20°C) until use. One canister was acclimated to room temperature (21°C)/day for pollination and was discarded after use. After capsules were harvested from 'Nellie White' plants, the number of viable seeds and the number of undeveloped ovules were recorded. Seeds scored as viable had a visible embryo when observed over a light board (McRae, 1998).

One mature leaf from three plants/bulb lot for each S1 and S2 bulbs were harvested to screen for the presence of viruses using enzyme-linked immunosorbent assay (ELISA) testing. Weekly scouting throughout production in the greenhouse and pest control was used to minimize viral transmission through insect vectors. The S1 bulbs were sampled in FC1 (three plants/bulb lot were from the same block) and S2 bulbs were sampled in FC2 (one plant/bulb lot sampled per block). Virus testing was performed by Agdia (Elkhart, Ind.). The standard lily virus screen was performed, testing for the presence/absence (+/-) of cucumber mosaic virus, lily symptomless virus (LSV), tobacco ringspot virus, tomato aspermy virus, and the potyvirus group. Relative optical density (ROD) values were calculated for lilies testing positive for virus by dividing the OD value for each lily by 4.0, the upper limit of the reported OD range among samples and the value reported for each positive control.

STATISTICAL ANALYSIS. Univariate analysis of variance (ANOVA) or univariate analysis of covariance (ANCOVA) was calculated for each dependent variable for S1-FC1, S2-FC1, and S2-FC2, and Tukey's honestly significant difference (HSD; $\alpha = 0.05$) was used for mean separations. Data transformations were explored when necessary to meet the normality and homogeneity of variance assumptions for ANOVA and were assessed using the Wilk-Shapiro and Levene tests respectively. Analyses of variance are not reported for S1-FC2 data as a result of poor and erratic stem emergence. Initial bulb weight (recorded before the commencement of S2-FC1 and S2-FC2) and stem number (S2-FC2 bulbs) were tested in the ANCOVAs as covariates. For traits with significant covariates, adjusted means are reported and LSD ($\alpha = 0.05$) was used for mean separations instead of HSD because of computer software limitations. For ease of analysis, only data from plants with one stem in S2-FC1 were used to calculate bulb lot means, generate correlations, and calculate univariate ANOVAs. Pearson's correlation was used to correlate traits on a per-stem or mean-bulb-lot basis. Multivariate analysis of variance (MANOVA) and canonical variables were used to explore trends among bulb lots. Analyses of variance, ANCOVAs, HSDs, and LSDs were performed using SPSS (version 11.0 for Windows; SPSS, Chicago, Ill.). Multivariate analyses of variance (and canonical variables were generated using Mac-Anova (version 5.05; University of Minnesota, St. Paul, Minn.).

Results

Lilium longiflorum 'Nellie White' bulbs obtained for this study were labeled as the commercial 20.3 to 22.9-cm circumference class. However, for S2-FC1, for which initial bulb circumference was measured (these data were not recorded for S1-FC1), only the mean of bulb lot 14 (22.7 cm) fell within the

designated range (Table 1). Seven of the bulb lots had bulbs with mean circumferences (23.4–25.4 cm) within the next larger commercial class (22.9–25.4 cm circumference). The remaining four bulb lots had mean bulb circumferences (25.6–26.2 cm) that were in the largest commercial class (>25.4 cm; Table 1). Mean initial bulb weight in S2-FC1 also varied among bulb lots (130.4–202.8 g), and bulb lots with relatively greater mean initial bulb circumference also tended to have relatively greater mean initial bulb weight (Table 1).

In S1-FC1 bulbs, 100% of the bulbs produced an emerging stem, 99% (163 of 165) of the pots with emerged stems flowered (one nonflowering plant died), whereas 98% (159 of 163) of the flowering containers produced one flowering stem (the remainder produced two flowering stems). Emergence and plant growth, however, were erratic during S1-FC2. Only 78% of the pots (128 of 164) had one or more emerged stem after returning to the greenhouse and, of those with emerged stems, only 52% (66 of 128) had one or more flowering stem. In addition, some stems with a high leaf number developed a bulb at the apical meristem. Leaf number/stem was quite variable in S1-FC2 ($n = 76$ –198) compared with S1-FC1 ($n = 74$ –120). In S1-FC2, some of the stems continually produced leaves without initiating flower buds. Because of erratic stem emergence and flowering, morphological data are not presented for bulb lots in S1-FC2. During the time period between S2-FC1 and S2-FC2, the combination of decreasing photoperiod, 8 weeks of vernalization (4°C), and 9 d at 21°C postvernalization, before greenhouse forcing, improved the rate of bulb emergence to 99% (166 of 168) from 78% (128 of 164) in S1-FC2. Likewise, the frequency of one or more flowering stem/bulb with emerged stems also increased to 100% (166 of 166) in S2-FC2 from 52% (66 of 128) in S1-FC2.

Significant differences in bulb weight and circumference were found among bulb lots upon receipt (S2-FC1 bulbs; Tables 1 and 2), and initial bulb weight and circumference were highly and positively correlated (Table 3). Therefore, initial bulb weight was tested as a covariate (with highly correlated traits typically only one is chosen as a covariate) in ANOVAs for S2-FC1 and S2-FC2. Stem number was also included as a covariate for S2-FC2 (Tables 2 and 4). Covariates were not significant for SEM (Tables 2 and 4). Although initial bulb weight was not available for S1-FC1 bulbs, the lack of bulb weight as a significant covariate for S2-FC1 and S2-FC2 supports direct bulb lot comparisons for SEM data between shipments. Because initial bulb weight was not a significant covariate for SEM in S2-FC1, it is assumed that initial bulb weight was not a significant covariate in S1-FC1 either. In addition, a single data point for SEM/pot allows comparisons to be made on a per-pot basis across S2-FC1 and S2-FC2. Greater variability across bulb lots for SEM was found in S1-FC1 and S2-FC1 bulbs (range of 19.0 and 15.7 d respectively) relative to S2-FC2 bulbs (7.7-d range). In addition, the mean SEM for the S2-FC2 bulbs (20.1 d) is almost twice that of S2-FC1 (11.1 d; Table 1). On a per-pot basis for the S2 bulbs, there is a significant, positive correlation across FC1 and FC2 for SEM ($r = 0.30$, $P < 0.01$; Table 3).

In S2-FC1 bulbs, 99% (167 of 168) of the bulbs produced one or more emerged stem; of those that emerged, 93% (155 of 167) produced one flowering stem/bulb (the remainder produced two stems/bulb across bulb lots). Variable stem numbers/pot (one to four stems, as a result of one to four daughter bulbs) in S2-FC2 was a significant covariate for 12 of 15 traits

Table 1. Descriptive statistics for bulb circumference (in centimeters), bulb weight (in grams), and days to stem emergence (SEM) for *Lilium longiflorum* ‘Nellie White’ bulb lots from different growers obtained in shipment 1 (S1), forcing cycle 1 (FC1), S2-FC1, and S2-FC2.

	Bulb lot no.												Pooled		
	1	2	3	4	5	6	7	9	11	12	13	14	Mean	Range ^z	MSE ^y
Bulb circumference (cm)															
S1-FC2	29.9 ab ^x	30.7 a	29.0 bcd	29.4 abc	28.8 bcd	29.2 abc	30.3 ab	—	27.5 de	27.0 e	28.0 cde	29.5 abc	29.0	3.7	2.1
S2-FC1 ^w	25.7 a ^x	23.5 bc	25.6 a	23.5 bc	24.8 ab	25.4 a	26.0 a	26.2 a	23.4 bc	23.4 c	23.4 bc	22.7 c	25.0	3.5	6.6 × 10 ³
S2-FC2 ^v	28.7 ab	27.4 c	28.0 bc	27.4 c	27.5 c	28.6 ab	27.1 c	28.9 a	27.5 c	27.5 c	28.2 abc	28.1 abc	27.9	1.8	
Bulb wt (g)															
S1-FC2	254.7 abc ^x	281.2 a	221.0 cde	266.3 ab	235.6 bc	235.5 bc	272.7 ab	—	191.1 de	179.9 e	230.8 bcd	240.3 abc	237.2	101.3	1.1 × 10 ³
S2-FC1 ^u	202.8 a ^x	148.9 def	179.7 abc	150.4 def	170.8 bcd	173.9 cd	199.9 ab	190.8 abc	151.8 de	132.0 f	145.9 ef	130.4 f	167.0	72.4	2.3 × 10 ⁹
S2-FC2 ^v	204.1 abcd	189.2 bcd	206.9 ab	199.1 bcd	188.5 cd	206.1 abc	193.6 bcd	221.9 a	192.4 bcd	183.1 d	204.4 abc	188.2 cd	198.1	38.7	
SEM															
S1-FC1	10.4 abcd ^x	15.9 de	5.3 a	7.5 ab	5.7 a	9.8 abc	17.4 e	—	11.5 bcd	24.3 f	13.7 cde	18.6 e	12.7	19.0	31.3
S2-FC1 ^t	11.5 ab ^x	10.5 ab	4.4 a	7.1 ab	2.2 a	17.9 ab	16.3 ab	11.9 ab	17.3 b	11.3 ab	8.2 a	14.7 ab	11.1	15.7	328.0
S2-FC2 ^s	24.0 b ^x	20.0 ab	20.3 ab	16.3 a	18.5 ab	21.2 ab	18.4 ab	23.5 ab	20.8 ab	18.8 ab	19.4 ab	19.3 ab	20.1	7.7	3.3 × 10 ³

^zRange was calculated by subtracting the lowest bulb lot mean from the highest bulb lot mean.

^yEstimate of mean square error used to calculate Tukey's HSD at $P \leq 0.05$ for mean separation.

^xMeans within row followed by the same letter do not differ significantly using Tukey's HSD ($\alpha = 0.05$).

^wData were transformed with the inverse of the square.

^vAdjusted means are presented because of a significant covariate. Means within row followed by the same letter do not differ significantly using LSD ($\alpha = 0.05$).

^uData were transformed with the inverse of the square root.

^tData were transformed with squaring.

^sData were transformed with the inverse.

FC1, forcing cycle 1; FC2, forcing cycle 2; S1, shipment 1; S2, shipment 2; SEM, stem emergence.

Table 2. Mean squares and significance from analyses of variance for morphological traits measured on bulb lots of *L. longiflorum* 'Nellie White' from different growers in shipment 2, forcing cycle 1 (S2-FC1).

Traits	Covariate	Independent factors		
	Initial bulb wt ^z	Bulb lot (L) (<i>df</i> = 11)	Block (B) (<i>df</i> = 2)	L × B (<i>df</i> = 22)
Initial bulb wt (g)	na ^x	4.5 × 10 ^{-4**}	na ^w	na ^w
Initial bulb circumference ^v (cm)	na ^x	3.7 × 10 ^{-7**}	na ^w	na ^w
SEM (d) ^u		290975.6*	126604.8 NS	100785.6 NS
VFB (d) ^t		0.8**	<0.1 NS	0.1 NS
AN (d)		117.4**	6.7 NS	25.1 NS
VFB-SEM	89.6*	37.1 NS	11.7 NS	25.1 NS
AN-SEM		48.1*	38.9 NS	18.9 NS
AN-VFB		15.8 NS	7.4 NS	7.1 NS
Flower no.	23.2**	13.0**	0.4 NS	1.7 NS
Plant ht (cm)		418.7**	117.8 NS	36.9 NS
Inflorescence ht (cm)		48.3**	2.7 NS	5.2 NS
Leaf no.	560.8*	177.1**	128.4 NS	47.7 NS
Leaf length (m)	627.2*	658.6**	216.8 NS	217.1**
Leaf width (m)		9.8 NS	5.7 NS	6.8 NS
Leaf length-to-width ratio		1.7**	1.4 NS	0.4 NS

^zInitial bulb weight before FC1 was tested as a covariate. The mean squares are included in the model and reported only for traits when the covariate is significant ($P \leq 0.05$).

^vData were transformed with one over the square root.

^xInitial bulb weight as a covariate was not applicable for these traits.

^wBlock was not applicable because initial bulb circumference and weight were measured before bulbs were assigned to blocks.

^yData were transformed with one over the square.

^uData were transformed with squaring.

^tData were transformed with square root.

NS,*,** Nonsignificant and significant at $P < 0.05$ and 0.01 respectively.

AN, anthesis; SEM, stem emergence; VFB, visible flower bud.

(Table 4). Stem number/pot (varying numbers of daughter bulbs) in S2-FC2 influenced individual stem architecture. Significant ($P \leq 0.05$) correlations between stem number and other traits were found; greater stem number/pot was generally associated with larger bulbs before S2-FC2, as were fewer numbers of leaves, flowers, and ovules; shorter stems; and a longer duration to reach most flowering milestones (Table 3). In fact, only correlations between stem number and SEM, percentage of ovules forming viable seeds, and ROD were not significant ($P > 0.05$; Table 3).

All 'Nellie White' samples tested from both S1 and S2 bulbs were positive for LSV, but negative for the other screened viruses. Relative optical density for LSV varied significantly among bulb lots for S2 (Table 4), but not S1 (Table 5). Correlations between ROD and all other morphological traits were not significant in the S1 bulbs (Table 6). However, in S2-FC1, significant correlations were observed between ROD and bulb weight ($r = 0.42$), bulb circumference ($r = 0.42$), and plant height ($r = -0.51$; Table 3). In S2-FC2, significant correlations also occurred between ROD and bulb weight ($r = -0.40$), bulb circumference ($r = -0.40$), SEM ($r = 0.45$), VFB ($r = 0.41$), and AN ($r = 0.39$; Table 3). The correlation between mean bulb lot ROD between S1 and S2 was not significant after the removal of an outlier (bulb lot number 12; Table 7).

Significant differences among bulb lots for S1 (FC1) and S2 bulbs (FC1 and FC2) were found using ANOVA for all traits measured except AN-VFB (S1-FC1, S2-FC1, S2-FC2), leaf width (S2-FC1, S2-FC2), and inflorescence height (S1-FC1; Tables 2, 4, and 5). For S1-FC1, variability attributed to bulb lots may be inflated relative to S2-FC1, because of the lack of initial bulb weights to test as a covariate (Table 5). Bulb lot

means for each trait are reported for S1-FC1 (Table 8) and S2-FC1 (Table 9) bulbs. S2-FC2 bulb lot means are not reported, with the exception of SEM, initial bulb circumference and weight, ovule number, and percentage of ovules forming viable seeds, because of variable stem number/pot values, which alters plant architecture and the generation of bulb lot means adjusted according to significant covariates. Variability for high-priority forcing traits among bulb lots were found in S1-FC1: 6.2 to 9.5 flowers, 50.4 to 63.5 d VFB, 84.3 to 100.5 d AN, and 47.5 to 56.7 cm in plant height (Table 8). For bulb lot means in S2-FC1, 5.9 to 9.1 flowers occurred, and 88.5 to 100.2 d AN, 55.7 to 68.9 d VFB, and 65.7 to 81.9 cm in plant height were also found (Table 9). As a result of plant architecture alterations within and between FCs, correlations of adjusted S2-FC1 and S2-FC2 bulb lot means were predominantly nonsignificant for most traits (data not shown).

When considering the key commercial forcing traits examined (high flower bud number, short plant, and relatively quick emergence and flowering for especially early Easters) (Lange and Heins, 1990; Wilkins and Roh, 1976), some bulb lots performed better than others. For instance, bulb lot number 5 ranked among the top three bulb lots for all key traits in S2-FC1 (Tables 1 and 9), only SEM in S2-FC2 (Table 1), and all traits except plant height in S1-FC1 (Table 8). Bulb lot number 3 also ranked high and was among the top three bulb lots for these traits, with the exception of SEM in S2-FC2 and plant height in S1-FC1 and S2-FC1 (Tables 1, 8, and 9).

Because of the complications imposed by variable stem number in S2-FC2 relative to S2-FC1, each S2-FC is treated separately for MANOVA analysis and generation of canonical variables. Eigenvalues for the ordered canonical variables are

Table 3. Pearson correlation values on a per-stem basis and significance between morphological traits in *L. longiflorum* 'Nellie White' bulbs for shipment 2, forcing cycle 1 (S2-FC1; lower left) and shipment 2, forcing cycle 2 (S2-FC2; upper right).

	S2-FC2																		
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
A	0.62**	0.78**	0.07 NS	0.06 NS	0.07 NS	0.05 NS	0.09 NS	0.03 NS	0.02 NS	-0.08 NS	0.09 NS	-0.04 NS	-0.05 NS	-0.08 NS	0.06 NS	0.34**	-0.08 NS	0.15 NS	-0.40*
B	0.90**	0.61**	0.16*	0.19*	0.21**	0.16*	0.21**	0.00 NS	0.12 NS	-0.24**	0.01 NS	-0.18*	-0.16*	-0.24**	0.14 NS	0.44**	-0.08 NS	0.13 NS	-0.40*
C	0.01 NS	0.04 NS	0.30**	0.79**	0.81**	0.49**	0.46**	-0.11 NS	0.15**	-0.29**	0.19**	-0.33**	0.12*	0.04 NS	-0.04 NS	0.05 NS	0.25**	0.03 NS	0.45**
D	-0.10 NS	-0.05 NS	0.85**	—	0.90**	0.86**	0.71**	-0.22**	-0.09 NS	-0.55**	0.14*	-0.61**	0.02 NS	-0.21**	0.20**	0.26**	0.25**	0.04 NS	0.41**
E	-0.05 NS	-0.02 NS	0.84**	0.88**	—	0.74**	0.85**	-0.05 NS	0.28**	-0.40**	0.21**	-0.47**	0.13*	-0.10 NS	0.21**	0.14*	0.16**	-0.04 NS	0.39**
F	-0.12 NS	-0.10 NS	-0.63**	-0.11 NS	-0.28**	—	0.83**	-0.28**	-0.01 NS	-0.61**	0.05 NS	-0.66**	-0.13*	-0.36**	0.32**	0.32**	0.10 NS	-0.16*	-0.23 NS
G	-0.14 NS	-0.13 NS	-0.77**	-0.44**	-0.35**	0.78**	—	0.14*	0.10 NS	-0.45**	0.14*	-0.51**	-0.03 NS	-0.29**	0.32**	0.21**	0.04 NS	-0.10 NS	-0.21 NS
H	0.01 NS	-0.02 NS	-0.25**	-0.51**	-0.08 NS	-0.26**	0.37**	—	0.25**	0.32**	0.25**	0.31**	0.18**	0.16**	-0.01 NS	-0.20**	-0.08 NS	0.06 NS	0.08 NS
I	0.41**	0.42**	0.41**	0.22**	0.29**	-0.37**	-0.43**	-0.08 NS	—	0.57**	0.62**	0.48**	0.70**	0.50**	0.05 NS	-0.47**	0.14*	0.28**	-0.23 NS
J	0.27**	0.24**	-0.31**	-0.41**	-0.35**	-0.05 NS	0.04 NS	0.19*	0.35**	—	0.40**	0.90**	0.51**	0.61**	-0.26**	-0.62**	-0.08 NS	0.23**	0.11 NS
K	0.53**	0.55**	0.35**	0.19*	0.26**	-0.34**	-0.35**	-0.05 NS	0.65**	0.21**	—	0.41**	0.40**	0.27**	0.02 NS	-0.45**	0.08 NS	0.28**	0.01 NS
L	0.43**	0.36**	-0.41**	-0.49**	-0.43**	0.05 NS	0.17*	0.23**	0.15 NS	0.54**	0.30**	—	0.47**	0.56**	-0.23**	-0.63**	-0.11 NS	0.26**	0.18 NS
M	-0.07 NS	-0.09 NS	0.43**	0.37**	0.33**	-0.26**	-0.43**	-0.30**	0.39**	-0.10 NS	0.12 NS	-0.24**	—	0.55**	0.19**	-0.44**	0.00 NS	0.19**	-0.05 NS
N	-0.01 NS	-0.10 NS	-0.12 NS	-0.08 NS	-0.07 NS	0.07 NS	0.05 NS	-0.02 NS	-0.09 NS	0.05 NS	-0.28**	0.09 NS	0.31**	—	-0.68**	-0.62**	-0.03 NS	0.19**	0.11 NS
O	-0.04 NS	0.03 NS	0.45**	0.36**	0.32**	-0.28**	-0.40**	-0.22**	0.40**	-0.12 NS	0.35**	-0.27**	0.53**	-0.63**	—	0.36**	0.00 NS	-0.08 NS	-0.12 NS
P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.03 NS	-0.26**	-0.18 NS
Q	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	-0.01 NS	-0.12 NS
R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	-0.19 NS
S	0.42*	0.42*	-0.02 NS	0.12 NS	0.19 NS	0.27 NS	0.33 NS	0.13 NS	-0.51**	-0.26 NS	-0.26 NS	-0.17 NS	-0.28 NS	-0.16 NS	-0.11 NS	—	-0.31 NS	-0.20 NS	—

S2-FC1

^aA, initial bulb weight before forcing; B, initial bulb circumference before forcing; C, days to stem emergence; D, days to visible flower bud; E, days to anthesis; F, difference in days between visible flower bud and stem emergence; G, difference in days between anthesis and stem emergence; H, difference in days between anthesis and visible flower bud; I, plant height; J, inflorescence height; K, leaf number; L, flower number; M, leaf length; N, leaf width; O, leaf length-to-width ratio; P, stem number; Q, percentage of ovules forming viable seeds; R, number of ovules of first flower reaching anthesis; S, relative optical density for lily symptomless virus tested during forcing cycle 2 (FC2) using enzyme-linked immunosorbent assay for three plants per bulb lot.

^bData were transformed with the inverse in FC2.

^cCorrelations are made on a per-bulb basis across FC1 and FC2.

NS, *, ** Nonsignificant and significant at $P \leq 0.05$ and 0.01 respectively.

S2-FC1, shipment 2, forcing cycle 1; S2-FC2, shipment 2, forcing cycle 2.

Table 4. Mean squares and significance from analysis of variance F-statistic for relative optical density (ROD) for lily symptomless virus (LSV) and morphological traits measured on bulb lots of *L. longiflorum* 'Nellie White' from different growers in shipment 2, forcing cycle 2 (S2-FC2).

Traits	Covariates ^z		Independent factors		
	Initial bulb wt (g)	Stem no. ^y	Bulb lot (L) (<i>df</i> = 11)	Block (B) (<i>df</i> = 2)	L × B (<i>df</i> = 22)
ROD	na ^x	na ^x	9.0×10^{-2} *	4.7×10^{-2} NS	^w
Initial bulb wt ^v (g)	9282.4**u	na ^x	1306.8*	1226.9 NS	625.1 NS
Initial bulb circumference (cm)	33.4**u	na ^x	5.2*	1.7 NS	1.8 NS
Stem no.	8.2**v	na ^x	1.1*	0.5 NS	0.4 NS
SEM (d) ^t			7.0×10^{-4} *	1.8×10^{-3} *	3.1×10^{-4} NS
VFB (d) ^s		2.5×10^{-8} **	1.6×10^{-8} *	1.6×10^{-9} NS	4.7×10^{-9} *
AN (d) ^s			1.7×10^{-9} **	1.2×10^{-10} NS	4.4×10^{-10} *
VFB-SEM	370.2**v	989.0**	216.6*	38.3 NS	71.9 NS
AN-SEM	258.1**v	361.0*	238.1*	76.8 NS	86.7*
AN-VFB		146.3**	27.6 NS	6.6 NS	13.0 NS
Flower no.	58.2**v	464.6**	14.6**	4.5 NS	2.9 NS
Plant ht (cm)		6589.9**	667.3**	222.5 NS	105.9*
Inflorescence ht (cm)	187.3**v	2868.5**	79.2*	15.6 NS	29.1*
Leaf no.		9003.8**	814.1**	539.2*	138.6*
Leaf length (mm)		13449.2**	855.8**	1488.3**	202.0 NS
Leaf width (mm)	37.7**v	843.1**	6.5 NS	53.2**	5.6 NS
Leaf length-to-width ratio	2.4**v	32.5**	2.5*	15.9**	1.1**
Ovule no.	41594.5**v	137643.6**	13759.6**	3697.5 NS	3861.9 NS
Ovules forming seeds (%)	322.5**v		195.7**	95.2 NS	50.3 NS

^zThe mean squares are included in the model and reported only for traits for which covariates were significant ($P \leq 0.05$).

^yStem number during FC2.

^xInitial bulb weight or stem number used as a covariate was not applicable for these traits.

^wBecause of insufficient *df*, interaction was removed from the model.

^vInitial bulb weight before FC2.

^tInitial bulb weight before FC1 transformed with one over the square root.

^sData were transformed with inverse.

^uData were transformed with inverse of the square.

NS,*,**Nonsignificant and significant at $P < 0.05$ and 0.01 respectively.

AN, anthesis; LSV, lily symptomless virus; ROD, relative optical density; SEM, stem emergence.

presented in Fig. 1. The standardized canonical coefficients for the first canonical variable (canonical variable one) in S2-FC1, S2-FC2 reveals that the most influential traits for maximizing the F-statistic and distinguishing between bulb lots in S2-FC1 were initial bulb circumference, initial bulb weight, VFB, and leaf length-to-width ratio (Table 10). Although, for S2-FC2, the most influential traits were AN, VFB, leaf length-to-width ratio, and SEM (Table 10). Because initial bulb size measurements (weight and circumference) highly influenced canonical coefficient values for S2-FC1, canonical analysis is not reported for S1-FC1 because these initial bulb size data were not recorded. Plotting the first two canonical variables in S2-F1 and S2-F2 reveals an overlap in distribution for flowering stems across bulb lots (Fig. 2). However, there are clustering trends for bulb lots. In addition, some bulb lots (e.g., bulb lots numbers 4 and 9) overlap considerably with other bulb lots in S2-FC1 (Fig. 2A). These bulb lots subsequently cluster in separate regions relative to the other bulb lots in S2-FC2 (Fig. 2B).

Many of the morphological traits are significantly correlated, but the strength and significance of the correlations differ across FCs (Table 3). Initial bulb weight and circumference were highly and positively correlated with each other in S2-FC1 ($r = 0.90$; Table 3), and significant correlations ($P \leq 0.05$) between each of these two bulb measurements with each of the other morphological traits displayed a similar trend (Table 3). For instance, larger bulb size (greater weight and circumference) was positively associated with overall plant size traits,

such as plant height, inflorescence height, number of leaves, and number of flowers (Table 3). In S2-FC2, bulb weight and circumference were also highly and positively correlated ($r = 0.78$; Table 3); however, the correlations between both bulb weight and circumference with the other morphological traits were inconsistent. Only bulb weight in S2-FC2 was significantly correlated with stem number ($r = 0.34$). Bulb circumference was significantly and positively correlated with stem number ($r = 0.44$) and most of the traits measuring the number of days to developmental milestones (SEM, VFB, and AN), but was significantly and negatively correlated with flower number ($r = -0.18$), inflorescence height ($r = -0.24$), leaf length ($r = -0.16$), leaf width ($r = -0.24$), and ROD ($r = -0.40$; Table 3). Longer time periods to SEM were associated with taller plants, longer leaves, and fewer flowers in S1-FC1, S2-FC1, and S2-FC2, and more leaves in S2-FC1 and S2-FC2 but not S1-FC1 (Tables 3 and 6). In S1-FC1, SEM was significantly and negatively correlated with AN-SEM ($r = -0.18$) and AN-VFB ($r = -0.20$), but not significantly correlated with VFB-SEM ($r = -0.14$; Table 6). In S2-FC1, SEM was negatively correlated with VFB-SEM ($r = -0.63$), AN-SEM ($r = -0.77$), and AN-VFB ($r = -0.25$), whereas, in S2-FC2, SEM was positively correlated with VFB-SEM ($r = 0.49$), AN-SEM ($r = 0.46$), and not significantly correlated with AN-VFB (Table 3).

Four of the 15 morphological traits compared across S1-FC1 and S2-FC1 were significantly and positively correlated (Table 7). Two of these traits were related to flowering milestones—namely,

Table 5. Mean squares and significance from analysis of variance F-statistic for relative optical density (ROD) for lily symptomless virus (LSV) and morphological traits measured on bulb lots of *L. longiflorum* 'Nellie White' from different growers in shipment 1, forcing cycle 1 (S1-FC1); initial bulb circumference and weight for shipment 1, forcing cycle 2 (S1-FC2).

Traits	Independent factors		
	Bulb lot (L) (<i>df</i> = 10)	Block (B) (<i>df</i> = 4)	L × B (<i>df</i> = 40)
S1-FC1			
ROD for LSV	5.0×10^{-3} NS	na ^z	na
SEM (d)	520.7**	13.1 NS	31.3 NS
VFB (d)	548.0**	16.4 NS	20.9 NS
AN (d)	402.8**	28.8 NS	22.8 NS
VFB-SEM	27.2*	11.7 NS	11.9 NS
AN-SEM	33.4**	6.7 NS	11.7 NS
AN-VFB	6.8 NS	13.0*	3.6 NS
Flower no.	13.4**	1.2 NS	1.5 NS
Plant ht ^y	$1.2 \times 10^{6**}$	$2.5 \times 10^{6**}$	2.3×10^5 NS
Inflorescence ht ^y (cm)	1.2×10^4 NS	1.9×10^4 NS	$1.0 \times 10^{4**}$
Leaf no.	327.2**	57.0 NS	41.8 NS
Leaf length ^y (mm)	$2.5 \times 10^{7**}$	$1.5 \times 10^{7**}$	3.4×10^6 NS
Leaf width (mm)	4.8**	8.0**	1.6 NS
Leaf length-to-width ratio	2.1**	0.1 NS	0.2 NS
S1-FC2			
Initial bulb circumference	19.4**	3.5 NS	2.1 NS
Initial bulb wt	$1.5 \times 10^{4**}$	$8.8 \times 10^{3**}$	1.1×10^3 NS

^zThe factor of block on ROD is not applicable because all three plants/bulb lot were sampled from a single block.

^yData were transformed with squaring.

NS,*,**Nonsignificant and significant at $P < 0.05$ and 0.01 respectively. AN, anthesis; LSV, lily symptomless virus; ROD, relative optical density; S1-FC1, shipment 1, forcing cycle 1; S1-FC2, shipment 1, forcing cycle 2; SEM, stem emergence.

VFB ($r = 0.68$) and AN-VFB ($r = 0.77$), and the other two traits were leaf traits: leaf length ($r = 0.77$) and leaf length-to-width ratio ($r = 0.65$; Table 7). Although the correlations for only four traits were significant ($P \leq 0.05$), overall most (13 of 16) Pearson correlation values were positive, and only AN-SEM, plant height, and ROD values were negative (Table 7).

Significant differences for the mean number of ovules/stem were found between bulb lots, and initial bulb weight and stem number were significant covariates in ANCOVA (Table 4). The range for mean number of ovules/stem ranged from 357.7 mean number of ovules/stem (bulb lot number 5) to 442.4 mean number of ovules/stem (bulb lot number 14), with bulb lot nos. 14 (442.4 mean number of ovules/stem), 11 (415.4 mean number of ovules/stem), and 1 (411.3 mean number of ovules/stem) having the most (Table 11). Larger stems tended to have more ovules/stem, as shown by significant positive correlations between ovule number and plant height ($r = 0.28$), inflorescence height ($r = 0.23$), leaf length ($r = 0.19$), and width ($r = 0.19$), and number of leaves ($r = 0.28$) and flowers ($r = 0.26$; Table 3). Significant differences were also found for percentage of ovules developing into viable seeds/stem between bulb lots, and initial bulb weight was a significant covariate in the ANOVA (Table 4). The percentage of ovules developing into viable seeds/stem ranged from 9.1 viable seeds/stem (bulb lot

number 6) to 18.9 viable seeds/stem (bulb lot number 9), with bulb lot nos. 9 (18.9%), no. 1 (16.8%), and no. 3 (15.7%) having the highest percentages (Table 11). Percentage of ovules forming viable seeds was significantly and positively correlated with time to the developmental milestones SEM ($r = 0.25$), VFB ($r = 0.25$), and AN ($r = 0.16$), and plant height ($r = 0.14$; Table 3).

Discussion

Lilium longiflorum 'Nellie White' grower source significantly impacted most forcing traits (Tables 3 and 4). Variability found among growers/bulb lots confirms the assertion of greenhouse forcers that there is variable and unpredictable forcing performance that can be attributed to bulb grower source (Zlesak and Anderson, 2003). Growers frequently purchase bulbs from more than one grower annually to minimize the risk of receiving a poor-performing bulb lot (Zlesak and Anderson, 2003).

Significant variability in initial bulb weight and circumference in S2 was observed among bulb lots (Table 1). Uniform bulb size within the designated 20.3 to 22.9-cm commercial class should not have been assumed for S1 at arrival. Initial bulb weight was a significant covariate for many morphological traits, including flower and leaf number and leaf length in S2-FC1 (Table 2), and flower number, inflorescence height, and leaf width in S2-FC2 (Table 4). Initial bulb weight and circumference were also among the top three traits in S2-FC1, which had the greatest standardized canonical coefficients for the first canonical variable. Initial bulb weight was positively correlated with plant height, inflorescence height, flower number, and leaf number in S2-FC1, but not in FC2, which is likely the result of competition among multiple stems in S2-FC2, because the correlations are reported on a per-stem basis (Table 3). Larger bulbs tended to produce taller plants with greater leaf and flower numbers and is in agreement with previous reports (De Hertogh et al., 1969, 1976; Lange and Heins, 1990). Lange and Heins (1990) report decreased days to flowering with larger bulbs, but that was not found in this study (Table 3). Leaf and flower number were also positively correlated in S2-FC1, S2-FC2, and S1-FC1 (Tables 3 and 6). Larger bulbs generally produced taller plants with larger leaves, and larger plants tended to have greater leaf and flower numbers.

Initial bulb weight was not a significant covariate for SEM, VFB, and AN (Tables 2 and 4), and bulb weight was not significantly correlated with SEM, VFB, AN, or any of the differences between these flowering milestones (Table 3). Therefore, initial bulb weight was not an inherent source of variability for AN, which is fortunate for greenhouse finishers, because uniformity in date of AN is essential to meet the 2-week pre-Easter marketing window (Zlesak and Anderson, 2003). In S2-FC2, initial bulb circumference was significantly correlated with time to flowering milestones, flower number, and leaf length and width, whereas initial bulb weight was not (Table 3). Bulb circumference may be correlated with more traits than initial bulb weight in S2-FC2 because of it being more highly associated with stem number ($r = 0.44$) than initial bulb weight ($r = 0.34$; Table 3). Stems arise from daughter bulbs and the greater the daughter bulb number, the greater the tendency for increased overall bulb width relative to height (pers. obs.), resulting in greater circumference.

Table 6. Pearson correlation values on a per-stem basis and significance for morphological traits in *L. longiflorum* ‘Nellie White’ for shipment 1, forcing cycle 1 (S1-FC1) bulbs.

	A ^z	B	C	D	E	F	G ^y	H ^y	I	J	K ^y	L	M	N
A	—													
B	0.89**	—												
C	0.90**	0.94**	—											
D	-0.14 NS	0.33**	0.17*	—										
E	-0.18*	0.10 NS	0.18*	0.72**	—									
F	-0.20*	-0.39**	-0.14 NS	-0.45**	0.21**	—								
G	0.20*	0.19*	0.24**	0.01 NS	0.15 NS	0.07 NS	—							
H	0.07 NS	0.09 NS	0.16*	0.04 NS	0.23**	0.21**	0.65**	—						
I	0.02 NS	-0.02 NS	0.03 NS	-0.05 NS	0.07 NS	0.03 NS	0.47**	0.21**	—					
J	-0.52**	-0.53**	-0.51**	-0.03 NS	0.11 NS	0.17*	0.30**	0.33**	0.36**	—				
K	0.21**	0.08 NS	0.13 NS	-0.24**	-0.14 NS	0.06 NS	0.39**	0.26**	0.17*	0.22**	—			
L	-0.25**	-0.29**	-0.29**	-0.10 NS	-0.01 NS	0.09 NS	0.17*	0.30**	-0.17*	0.36**	0.31**	—		
M	0.40**	0.33**	0.36**	-0.13 NS	-0.12 NS	-0.03 NS	0.23**	0.01 NS	0.28**	-0.08 NS	0.66**	-0.49**	—	
N	-0.04 NS	-0.11 NS	-0.12 NS	-0.17 NS	-0.19 NS	0.01 NS	-0.01 NS	0.33 NS	-0.02 NS	0.28 NS	0.26 NS	0.16 NS	0.08 NS	—

^zA, days to stem emergence; B, days to visible flower bud; C, days to anthesis; D, difference in days between visible flower bud and stem emergence; E, difference in days between anthesis and stem emergence; F, difference in days between anthesis and visible flower bud; G, plant height; H, inflorescence height; I, leaf number; J, flower number; K, leaf length; L, leaf width; M, leaf length-to-width ratio; N, relative optical density for lily symptomless virus tested during forcing cycle 1 (FC1) using enzyme-linked immunosorbent assay for three plants/bulb lot.

^yData were transformed with squaring.

NS,*,**Nonsignificant and significant at $P \leq 0.05$ and 0.01 respectively.

Bulb growers often supply bulbs that are larger than the designated size class (Table 1) and consider this practice to favor the greenhouse finisher (O. Hoffman, 2005, pers. comm.). Variable bulb sizes within and across bulb lots, however, contribute to variability, as discussed, for the finished product, especially in traits related to plant size and organ number. Bulb

growers can minimize such variability for greenhouse finishers by more stringent grading practices. Pricing of potted Easter lilies at the wholesale and retail levels is usually done by flower bud number, although other plant factors are considered (Wilkins and Roh, 1976), and greater uniformity in bulb size should facilitate more uniform production, grading, and shipping of finished lilies.

Forcing the same shipment of bulbs over two FCs allows for bulbs being grown in FC2 to have been in a common environment during the previous clonal generation (FC1). Environmental conditions during field bulb production, harvest, and shipping affect bulb maturity and dormancy, thus influencing subsequent growth during greenhouse forcing (Erwin and Engelen-Eigles, 1998). Greater uniformity for SEM was observed among bulb lots in S2-FC2 (7.7-d range) than S2-FC1 (15.7-d range; Table 1). The reduction of the range of SEM by about half in FC2 relative to FC1 suggests that much of the variability in SEM in FC1 may be attributed to variation in dormancy levels instilled by the environmental conditions bulbs were exposed to in the clonal cycles before shipment. Although the range in SEM among bulb lots in S2-FC2 was considerably reduced relative to S2-FC1, partitioning the phenotypic variability for SEM or any trait into its genetic, environmental, and genetic $\times$ environmental components poses challenges. Bulbs are 2 or 3 years old when they are sold to greenhouse finishers (Dole and Wilkins, 1999), and although all S2 bulbs shared a common forcing environment (FC1) before FC2, the lasting effect of factors such as variable bulb age and growth in different field environments during previous years is unknown. For instance, a significant positive correlation ($r = 0.30$) was found for SEM for S2-FC1 and S2-FC2, and it is unclear whether the association may be the result of lasting physiological factors across FCs, underlying genetic factors, or both. Additionally, variable stem number in S2-FC2 complicates direct comparisons across FCs for traits other than SEM, which alters plant architecture and complicates the ability to detect whether other traits also have less variability in FC2 as a

Table 7. Pearson correlation values and significance of bulb lot means of *L. longiflorum* ‘Nellie White’ morphological traits measured in bulb shipment 1, forcing cycle 1 (S1-FC1) and shipment 2, forcing cycle 1 (S2-FC1) and relative optical density (ROD) for lily symptomless virus (LSV) using enzyme-linked immunosorbent assay in S1-FC1 and S2-FC2.

Trait	Pearson’s correlation (r)
SEM (d)	0.48 NS
VFB (d)	0.68*
VFB-SEM	0.27 NS
AN (d)	0.58 NS
AN-SEM	-0.21 NS
AN-VFB	0.77**
Flower no.	0.55 NS
Plant ht	-0.16 NS
Inflorescence ht	0.07 NS
Leaf no.	0.32 NS
Leaf length	0.77**
Leaf width	0.23 NS
Leaf length-to-width ratio	0.65*
Initial bulb wt before FC2	0.36 NS
Initial bulb circumference before FC2	0.42 NS
ROD for LSV ^z	-0.61 NS

^zAfter removal of an outlier (bulb lot number 12), the correlation became nonsignificant.

NS,*,**Nonsignificant and significant at $P < 0.05$ and 0.01 respectively.

AN, anthesis; FC2, forcing cycle 2; LSV, lily symptomless virus; ROD, relative optical density; SEM, stem emergence; VFB, visible flower bud.

Table 8. Mean bulb lot values for morphological traits of *L. longiflorum* ‘Nellie White’ shipment 1, forcing cycle 1 (S1-FC1) bulbs with a single stem/plant, relative optical density (ROD) for lily symptomless virus (LSV), and initial bulb circumference and weight before forcing cycle 2 (FC2).

Trait	Bulb lot no.											MSE ^z
	1	2	3	4	5	6	7	11	12	13	14	
S1-FC1												
VFB (d)	53.7 ab ^y	59.9 cd	51.1 a	51.3 a	50.4 a	52.7 ab	61.5 a	59.6 cd	69.8 e	57.93 bc	63.5 d	20.9
VFB-SEM	43.3 ab	44.1 abc	45.8 abc	43.8 abc	44.7 abc	42.9 a	44.9 abc	47.2 c	46.9 bc	44.3 abc	44.9 abc	11.9
AN (d)	87.1 ab	92.2 cd	84.5 a	84.8 a	84.3 a	86.1 ab	96.1 de	92.6 cd	100.5 e	90.1 bc	96.4 de	22.7
AN-SEM	76.7 ab	76.3 a	79.2 abc	77.3 abc	78.7 abc	76.3 a	80.0 bc	80.3 c	78.34 abc	76.5 ab	77.5 abc	11.7
AN-VFB ^x	33.5	32.3	33.4	33.5	33.9	33.3	33.1	33.1	31.5	32.2	32.8	3.6
Flowers no.	5.9 abcd	5.4 bcde	7.1 a	5.3 bcde	7.1 a	6.2 abc	6.3 ab	4.6 de	4.3 e	4.7 cde	4.9 bcde	1.5
Plant ht (cm) ^w	51.3 abc	54.3 cd	50.6 abc	49.3 ab	50.0 abc	49.9 abc	56.7 d	47.5 a	52.0 abcd	48.2 a	54.0 bcd	475.8
Inflorescence ht (cm) ^{x w}	18.7	19.9	19.8	19.8	19.3	18.9	21.3	19.7	18.9	18.7	19.8	99.6
Leaves (no.)	95.2 ab	99.1 bc	93.2 ab	91.0 ab	95.8 abc	91.4 ab	104.3 c	89.2 a	91.3 ab	88.7 a	98.3 bc	41.8
Leaf length (mm) ^w	112.0 bc	123.9 c	116.4 bc	105.9 a	119.0 bc	124.9 c	121.0 c	110.9 ab	118.3 bc	122.5 c	122.8 c	1832.4
Leaf width (mm)	20.4 ab	19.6 ab	20.9 a	20.7 ab	20.5 ab	20.6 ab	20.3 ab	20.0 ab	19.2 b	20.5 ab	19.3 b	1.6
Leaf length-to-width ratio	5.9 bcd	6.3 cd	5.6 ab	5.1 a	5.8 bc	6.1 bcd	6.0 bcd	5.6 ab	6.2 cd	6.0 bcd	6.4 d	0.2
ROD for LSV ^x	0.34	0.26	0.34	0.25	0.26	0.29	0.27	0.30	0.19	0.27	0.27	5.0 × 10 ⁻³
S1-FC2												
Bulb circumference (cm)	29.9 ab	30.7 a	29.0 bcd	29.4 abc	28.8 bcd	29.2 abc	30.3 ab	27.5 de	27.0 e	28.0 cde	29.5 abc	2.1
Bulb wt (g)	254.7 abc	281.2 a	221.0 cde	266.3 ab	235.6 bc	235.5 bc	272.7 ab	191.1 de	179.9 e	230.8 bcd	240.3 abc	1099.0

^zEstimate of MSE used to calculate Tukey's HSD at $P \leq 0.05$ for mean separation.

^yMeans within row followed by the same letter do not differ significantly using Tukey's HSD ($P \leq 0.05$).

^xBulb lot was not a significant factor using ANOVA.

^wData were transformed with squaring.

AN, anthesis; LSV, lily symptomless virus; ROD, relative optical density; S1-FC1, shipment 1, forcing cycle 1; S1-FC2, shipment 1, forcing cycle 2; SEM, stem emergence; VFB, visible flower bud.

Table 9. Mean bulb lot values for morphological traits of *L. longiflorum* 'Nellie White' from different growers in shipment 2, forcing cycle 1 (S2-FC1) plants with one flowering stem, relative optical density (ROD) for lily symptomless virus (LSV) and stem number during shipment 2, forcing cycle 2 (S2-FC2).

Trait	Bulb lot no.												
	1	2	3	4	5	6	7	9	11	12	13	14	MSE ^z
S2-FC1													
VFB (d)	62.5 abc ^x	65.1 bc	55.7 a	61.5 abc	56.8 ab	67.7 c	68.9 c	62.9 abc	65.1 bc	66.8 bc	62.1 abc	66.9 c	6.4 × 10 ⁻³
VFB-SEM to stem	51.5	54.6	51.4	54.4	54.7	50.2	52.6	51.7	52.2	55.7	53.9	52.9	24.8
AN (d)	94.2 abc ^x	95.9 bc	88.5 a	94 abc	90.8 ab	100.2 c	97.1 bc	94.3 abc	95.9 bc	96.4 bc	93.4 abc	99.1 c	25.2
AN-SEM	83.2 ab ^x	85.4 ab	84.1 ab	86.9 ab	88.6 b	83.8 ab	81.9 a	82.4 ab	83.9 ab	85.3 ab	85.2 ab	85.1 ab	19.0
AN-VFB ^w	31.7	30.7	32.7	32.5	33.9	30.4	31.3	31.0	31.8	29.5	31.3	32.2	7.2
Flowers (no.) ^v	7.5 cd	6.3 e	8.5 b	7.5 cd	8.8 ab	6.2 e	7.1 de	8.2 bc	6.7 de	6.5 de	9.5 a	7.3 cd	
Plant ht (cm)	78.0 cde ^x	69.5 ab	75.3 bcd	72.6 abc	70.7 abc	81.9 de	74.9 bcd	86.2 e	73.0 abc	65.7 a	72.5 abc	71.3 abc	37.0
Inflorescence ht (cm)	27.0 bcd ^x	24.8 ab	29.5 cd	27.5 bcd	27.5 bcd	24.8 ab	25.3 ab	29.9 d	26.4 abc	23.4 a	26.3 ab	25.7 ab	5.2
Leaves (no.) ^v	101.8 ab	94.7 bc	100.7 ab	92.8 c	93.2 c	103.8 a	102.0 ab	105.0 a	91.4 c	93.0 c	97.2 abc	92.8 c	
Leaf length (mm) ^v	148.8 bcd	156.5 ab	142.1 de	136.2 e	143.9 de	159.6 a	153.1 abc	156.5 a	144.1 cde	139.6 de	146.9 cd	146.8 cd	
Leaf width (mm) ^w	24.6	24.5	24.0	24.0	26.0	25.6	23.9	22.8	24.3	23.4	24.1	24.8	6.8
Leaf length-to-width ratio	5.9 bc ^x	6.6 ab	5.9 bc	5.8 bc	5.5 c	6.3 ab	6.3 abc	6.8 a	6.0 bc	6.2 abc	6.3 abc	6.2 abc	0.4
S2-FC2													
ROD for LSV ^u	0.32	0.56	0.44	0.80	0.69	0.38	0.59	0.45	0.77	0.81	0.44	0.72	3.8 × 10 ⁻²
Stems (no.) ^v	1.7 bcd	1.9 abcd	2.3 a	1.5 cd	1.9 abcd	1.8 abcd	1.4 d	1.7 bcd	1.7 bcd	2.1 ab	2.4 a	2.0	

^zEstimate of MSE used to calculate Tukey's HSD at $P \leq 0.05$ for mean separation.^yData were transformed with square root.^xMeans within row followed by the same letter do not differ significantly using Tukey's HSD ($P \leq 0.05$).^wBulb lot was not a significant factor using ANOVA.^vAdjusted means are presented resulting from a significant covariate. Means within a row followed by the same letter do not differ significantly using LSD ($\alpha = 0.05$).^uAlthough bulb lot was a significant factor ($P \leq 0.05$) using ANOVA, Tukey's HSD did not distinguish differences among bulb lots at $P \leq 0.05$.

AN, anthesis; LSV, lily symptomless virus; ROD, relative optical density; S2-FC1, shipment 2, forcing cycle 1; S2-FC2, shipment 2, forcing cycle 2; SEM, stem emergence; VFB, visible flower bud.

Fig. 1. Eigenvalues of the ordered canonical variables from multivariate analysis of variance of shipment two *L. longiflorum* 'Nellie White' bulbs in FC1 (A) and FC1 (B).

result of a common FC1 environment. Canonical variable analysis also points to the possibility of a reduction in physiological differences in bulb lots S2-FC2 relative to S2-FC1 because of more unique clustering in S2-FC2 (Fig. 2B) of especially bulb lot numbers 4 and 9 relative to clustering with other bulb lots in S2-FC1 (Fig. 2A).

In S2-FC2 relative to S1-FC2, a much higher percentage of bulbs with one or more emerged stem (99% vs. 78% respectively) and percent emerged bulbs with one or more flowering stem (100% vs. 52% respectively) were found. Improved forcing in S2-FC2 is most likely the result of the altered environmental conditions between S2-FC1 and S2-FC2. In the post-S2-FC1 environment, plants were exposed to a decreasing photoperiod the final 8 weeks before bulb harvest, an extended vernalization (4 °C) duration (8 weeks vs. 6 weeks), and holding bulbs at 21 °C for 9 d after vernalization. One or a combination of these factors likely led to greater uniformity in bulb dormancy and vernalization treatment, allowing for greater uniformity in S2-FC2 for stem emergence and flowering than in S1-FC2 bulbs. Many of the S1-FC2 plants produced stems that continued to grow vegetatively and did not initiate flower buds, a common response for bulbs potted after field harvest and grown at temperatures ≥ 21 °C (Lin and Wilkins, 1973). The S1-FC2 bulbs were brought directly to the greenhouse (28.8 °C mean day high temperature) from the cooler (4 °C), which may have resulted in devernization, a

Table 10. Standardized canonical coefficients (SCC) used to generate the first canonical variable for *L. longiflorum* 'Nellie White' S2-FC1 and S2-FC2 bulbs from bulb lots representing different growers with ranked trait weight.

Trait	S2-FC1		S2-FC2	
	SCC	Ranked wt	SCC	Ranked wt
Initial bulb wt (g)	2807.6 ^z	2	-0.08	15
Initial bulb circumference (cm)	-1.02×10^{5y}	1	2.95	5
Stem no.	-19.84	5	0.11	13
SEM (d)	-0.09 ^x	14	3.03 ^w	4
VFB (d)	245.82 ^v	3	1.10×10^{5y}	2
AN (d)	-12.68	6	-3.14×10^{5y}	1
VFB-SEM	-2.04	10	-0.16	11
AN-VFB ^u	12.41	7	-1.66	7
Plant ht (cm)	0.21	13	0.10	14
Inflorescence ht (cm)	-0.69	11	0.81	8
Flower no.	3.48	9	-1.91	6
Leaf no.	0.03	15	0.25	10
Leaf length (mm)	-0.30	12	-0.06	16
Leaf width (mm)	3.68	8	0.41	9
Leaf length-to-width ratio	29.38	4	3.75	3
Ovule no.			3.52×10^{-3}	17
Ovules forming seeds (%)			-0.15	12

^zData for trait within forcing cycle (FC) were transformed with one over the square root.

^yData for trait within FC were transformed with one over the square.

^xData for trait within FC were transformed by squaring.

^wData for trait within FC were transformed with the inverse.

^vData for trait within FC were transformed with the square root.

^uAnthesis (AN)-stem emergence (SEM) was omitted from analysis because it is the sum of AN-visible flower bud (VFB) and VFB-stem emergence (SEM), which complicated the generation of canonical variables.

S2-FC1, shipment 2, forcing cycle 1; S2-FC2, shipment 2, forcing cycle 2; SCC, standardized canonical coefficients.

common occurrence when bulbs are exposed to temperatures more than 21 °C immediately after vernalization (Miller and Kiplinger, 1966). Devernization may explain the shoots that did not flower. Temperatures more than 21 °C may also have erased the effect of chilling on release of dormancy and lack of shoot emergence as well. If freshly dug Easter lilies are potted and never exposed to temperatures less than 21 °C, plants can emerge and produce high leaf numbers, and instead of ending in flowers, produce a bulb (Wilkins, 1980, 2005). This phenomenon was observed in several S1-FC2 plants. However, if Easter lilies are exposed to temperatures less than 21 °C, they will eventually flower (Weiler and Langhans, 1968). Extending the vernalization (4 °C) duration from 6 to 8 weeks was done with S2 bulbs between FC1 and FC2 to compensate for the lack of potential accumulation of chilling hours typically experienced in the field before harvest at temperatures less than 21 °C, which was lacking in the greenhouse. The mean SEM for S2-FC2 bulbs was 20.1 d, compared with 11.1 d during S2-FC1 (Table 1), suggesting that the additional 2 weeks at 4 °C did not fully compensate for the chilling hour accumulation during field and shipping conditions because longer chilling treatments tend to result in faster SEM (Dole and Wilkins, 1999).

Fig. 2. Scatter plots of the two highest ordered canonical variables plotted for each flowering stem of *L. longiflorum* 'Nellie White' S2 bulbs and designated by bulb lot during FC1 (A) and FC2 (B). Circles and ellipses signify bulb lots (dashed line, bulb lot four; solid line, bulb lot nine) with unique clustering relative to other bulb lots in S2-FC2 versus S2-FC1.

Significant differences among bulb lots existed for ovule number and percentage of ovules forming viable seeds, even after the variability because the covariates (initial bulb weight and stem number) were removed (Tables 4 and 11). In addition, there were significant positive correlations ($0.14 < r < 0.25$) between percentage of ovules forming viable seeds and SEM, VFB, AN, and plant height. The reason for association between a longer time to flowering milestones and higher percentage of ovules forming viable seeds is unclear. Taller plants being associated with a greater percentage of ovules forming viable

seeds may be related to a competitive advantage of taller plants for light, resulting in an advantage for photosynthate generation. Variability among bulb lots for percentage of ovules forming viable seeds may be the result of varying levels of accumulated deleterious mutations among grower bulb intraclonal strains and can be explained by Muller's ratchet (Muller, 1964). Meiosis and genetic recombination in sexual reproduction maintain genetic variation and allow for selection of individuals in a population with greater fitness (fewer deleterious alleles), circumventing the negative effects of sequential mutation accumulation known as the "ratchet." 'Nellie White' is a clone propagated for more than 60 years. Assuming a minimum of one clonal cycle/year in bulb production, the current 'Nellie White' ramets are at least 60 clonal cycles removed from the original selected genotype (ortet), as well as the last meiotic screen and meiotic recombination event. In addition, independent clonal selection by bulb growers has allowed for the possibility for different degrees and types of negative mutations to accumulate (different degrees of tightening of the "ratchet") among the various intraclonal strains, which may affect fertility to differing degrees (Anderson and Ascher, 1994).

Because of the lack of a central propagator for *L. longiflorum* 'Nellie White', growers maintain their own clonal propagation stock. Natural mutation allows for genetic changes to occur, and each grower can select unique genotypes for clonal propagation and commercialization. Intraclonal 'Nellie White' selection and propagation is practiced by all Easter lily bulb growers, resulting in differing commercial strains over years, both within and between growers (Zlesak and Anderson, 2003). Key traits selected by bulb growers during intraclonal selection are late SEM in the field to avoid damage from spring hail storms, and fast growth rates to compensate for late emergence (Zlesak and Anderson, 2003). Significant differences among bulb lots for SEM and AN-SEM in both S2-FC1 and S2-FC2 (Tables 3 and 4), and consistently negative correlations for these traits in S1-FC1 and S2-FC1, may reflect the varying selection success rates among growers. Intraclonal selection has been successful in *Solanum tuberosum* 'Russet Norkotah', improving quantitative traits such as yield and tuber size (Hale et al., 2005; Miller et al., 2004). Collaborative work among lily bulb growers to identify and market superior strains of 'Nellie White' can benefit the potted Easter lily market. For instance, the bulbs of bulb lot numbers 3 and 5 performed significantly better than other bulb lots in S1-FC1 and S2-FC1, as shown by repeatedly ranking among the top bulb lots for key traits such as fast SEM and AN, short plant stature, and high flower bud count (Tables 1 and 5). In addition, bulb lot numbers 3 and 5 ranked among the top four bulb lots for percentage of ovules forming

Table 11. Mean bulb lot values for number of ovules for the first flower coming to anthesis and percentage of ovules forming viable seeds of *L. longiflorum* 'Nellie White' shipment 2, forcing cycle 2 (S2-FC2) pollinated with *L. longiflorum* 'Europa'.

Trait	Bulb lot no.											
	1	2	3	4	5	6	7	9	11	12	13	14
Flowering Stems (no.)	23	21	31	21	26	28	18	29	14	20	26	19
Ovules (no.) ^z	411.3 ab	370.9 ab	379.2 ab	367.8 b	357.7 b	370.0 ab	380.2 ab	405.6 ab	415.4 ab	393.1 ab	383.4 ab	442.4 a
Ovules forming seeds (%) ^z	16.8 ab	10.6 bc	15.7 abc	11.2 abc	14.8 abc	9.1 c	9.6 bc	18.9 a	12.2 abc	12.5 abc	13.9 abc	11.4 abc

^zAdjusted means are presented because of a significant covariate. Means within a row followed by the same letter do not differ significantly using LSD ($\alpha = 0.05$).

viable seeds. This may reflect less genetic load and a lower accumulation of negative mutations than in other intraclonal strains. It would be of value to explore whether these bulb sources will continue to produce superior plants during greenhouse forcing if such selections were propagated by a central propagator and grown by multiple field bulb growers.

Efforts have been made to eliminate virus in lily cultivars because disease symptoms often include streaking and mottling on leaves, distorted/twisted growth, and reduced vigor and plant size (McRae, 1987). For instance, virus-free plants of the Asiatic cultivar Enchantment were 34% taller and had 26% more flowers than LSV-infected plants (Allen et al., 1974). In S2-FC1 there was a significant negative correlation between ROD and plant height ($r = -0.51$, Table 3). Linderman et al. (1976) reported faster in vitro callus growth of LSV-infected *L. longiflorum* 'Ace' and 'Nellie White' for callus with relatively less LSV titer. This may parallel the association of less virus titer and taller plants in S2-FC1. Because LSV is in all plants of 'Nellie White' from all bulb lots tested, LSV may be a critical factor necessary to control plant height effectively in conjunction with current height control methods like temperature manipulation and plant growth regulators (Dole and Wilkins, 1999). Lily symptomless virus, as the name implies, does not generally result in typical viral symptoms like mottling and streaking of leaves and flowers, and may have led to LSV being indirectly selected for by growers because of effects on plant height. Virus-free 'Nellie White' propagules were generated and distributed to growers in the 1970s (Allen et al., 1980); however, their performance relative to LSV-infected plants and whether they were commercialized was not reported. Eliminating 'Nellie White' of LSV may not be a practical solution to reduce variability during forcing. Unpublished research on virus-free plants of Easter lily 'Ace' in the 1970s found that plant height of virus-free plants could not be reduced to commercially acceptable levels with conventional plant growth regulator rates (P. Ascher, 2003, pers. comm.). Perhaps if virus-free 'Nellie White' were available, combining current alternatives for height control such as differential day/night temperatures (Erwin et al., 1989) and plant growth regulators (Dole and Wilkins, 1999) would allow for acceptably compact potted plants to be produced.

In S1-FC1 and S2-FC2, the correlations between ROD and plant height were not significant (Table 3). In addition, concentration and distribution of LSV can be variable even within a lily plant (Cohen et al., 1985; Van Schadowijk, 1986), making virus titer measurements challenging. Moreover, there was a non-significant negative correlation ($r = -0.61$) between S1 and S2 for ROD (Table 7). Virus titer within bulbs, within bulb lots, and across grower sources may vary considerably from year to year and may be an unpredictable source of variability during greenhouse forcing. In S2, ELISA analysis was performed in FC2. Significant positive correlations between ROD and S2-FC1 initial bulb weight ($r = 0.42$) and circumference ($r = 0.42$) were found. However, there were significant negative correlations between S2-FC2 initial bulb weight ($r = -0.40$) and circumference ($r = -0.40$; Table 3). This suggests that larger initial bulbs in S2-FC1 had a tendency to accumulate more virus and become relatively smaller bulbs by S2-FC2. In addition, in S2-FC2 there were significant positive correlations between ROD and SEM ($r = 0.45$), VFB ($r = 0.41$), and AN ($r = 0.39$), suggesting the greater the virus titer the longer it takes for plants to reach flowering milestones. Further research is warranted to document LSV titer in 'Nellie White' and its effects on greenhouse forcing.

"Somaclonal variation" is a term coined to describe the variability that can arise in ramets of a clone through in vitro culture (Larkin and Scowcroft, 1981; Veilleux and Johnson, 1998). Greater variability among in vitro-propagated ramets is often associated with adventitious shoot regeneration rather than regeneration from established apical and axillary meristems (Veilleux and Johnson, 1998). Greater variability among ex vitro propagated ramets via adventitious versus apical or axillary meristems has been documented in clonally propagated sweet potato (Villordon and LaBonte, 1996). Perhaps the phenotypic variability found among bulb lots of 'Nellie White' has been compounded by scale propagation (adventitious meristems) rather than the use of stem bulbils (axillary meristems) (Dole and Wilkins, 1999). Future studies can explore the influence of meristem source on ramet variability by comparing ramets propagated from intraclonal selections using stem bulbils versus scale propagation.

Significant clonal variability within *L. longiflorum* 'Nellie White' grower bulb lots was found for every trait examined except AN-VFB (Tables 2, 4, and 5) and led to variable forcing characteristics, depending on from which grower source the bulbs were obtained. Likewise, results from the same grower can be variable across shipment years. Variable performance across grower bulb lots in this study can be attributed to variation in initial bulb size, LSV titer (ROD), previous FC environment, and underlying genetic or epigenetic differences among grower lots. More work is warranted to better characterize the genetic or epigenetic differences among grower intraclonal strains. One possible method to detect genetic differences among intraclonal strains of 'Nellie White' is DNA fingerprinting. Amplified fragment length polymorphisms is an especially amenable marker system because it is random and genome wide, has high band numbers (which increases the probability of finding potentially rare polymorphisms), has high reproducibility, and no previous knowledge of the genome is necessary (Weising et al., 2005). However, the large genome size of Easter lily [77.1 pg DNA per somatic nucleus (2C) (Lim et al., 2001)] may complicate amplified fragment length polymorphism analysis (Fay et al., 2005) or other random, genomewide markers. An additional approach is to generate virus-free plants of intraclonal strains and compare their morphology when grown in common propagation, bulb production, and forcing environments. Virus-free plants grown in a common environment from propagation through forcing should minimize the effects of environmental factors, which may confound the detection of genetic/epigenetic differences. To reduce the variability among grower bulb lots found by greenhouse finishers, barring the institution of a central producer company, bulb growers and the Easter Lily Research Foundation must work closely together to produce a more uniform product. They can develop more stringent grading practices; monitor and understand better the effect of LSV titer; minimize environmental differences among growers during production, grading, and shipping; and collaborate to identify, produce, and sell superior intraclonal strains of 'Nellie White'.

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