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Effects of N–P–K deficiency and temperature regime on the growth and development of *Lilium longiflorum* 'Nellie White' during bulb production under phytotron conditions☆

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ABSTRACT

One-year-old scale bulblets of *Lilium longiflorum* Thunb. 'Nellie White' (Easter lily) were grown under a combination of six constant day/night temperature regimes and five N–P–K nutrient treatments under short days for 107 d (growing period 1 or GP-1) to compare the effects on growth and development and bulb production. Results during GP-1 were as follows: failure of bulblets to produce a shoot ("no-shows") was found at high temperatures (30/26 and 26/22 °C) and not influenced by the nutrient treatments. Flower bud abortion was observed in the minus-N, minus-P, and minus-N–P–K treatments at high temperatures (30/26 or 26/22 °C), but not observed at any temperatures in the complete and minus-K treatments. The loss of bulb fresh weight in minus-N treated bulblets was less than in the other treatments resulting in less root and shoot growth in the minus-N treatment. At the intermediate temperatures where growth was highest, omission of N, P, K, or all three resulted in losses in stem bulb fresh weight, stem plus leaf fresh weight, number of flowers, and stem root fresh weight. Omission of N, P, or all three nutrients resulted in lowest basal root fresh weight. Bulb N and K concentrations were lowest in plants grown with complete nutrient solution at the two coldest temperature regimes (14/10 and 10/6 °C). Bulb P concentration was lowest at the three coldest (18/14, 14/10 and 10/6 °C) and the warmest (30/26 °C) temperature regimes. Stem length was shorter when P was omitted. Omission of any of the three nutrients resulted in lower concentrations of the other nutrients. The one exception was where low K did not affect N concentration. In the second phase of the experiment, plants grown at 18/14 °C and irrigated with the complete nutrient solution for 107 d (GP-1) were continued at this day/night temperature regime and five N–P–K nutrient treatments for another 89 d under long days (growing period 2 or GP-2). Results during GP-2 were as follows. Basal bulb yield was not impacted by omission of N, P, or K, or all three. Of all growth measurements, only stem plus leaf fresh weight was lower and only when all three nutrients (minus-N–P–K) were omitted. At the end of GP-2, basal bulb concentrations of N and P did not differ from the concentrations in bulbs at the beginning of GP-1; however, K concentration was lower at the end of GP-2. Omission of N or P further resulted in lower bulb K concentration, suggesting that a moderate supply of N, P, and K be applied during GP-2 since an additional year of bulb production is needed to produce forcing-sized bulbs.

1. Introduction

Flower bulb yield must be high in order to maximize profitability (De Vroomen, 1993) and proper fertilization is a major requirement (De Hertogh and Le Nard, 1993). Limited research has been published on the essential nutrition requirements for bulb production of commercial lily species, especially the Easter lily (*L. longiflorum*). Most field fertilization recommendations evolved from commercial practices and experimental trials that were often in grower fields. Roberts and Blaney (1957) reported that 140 kg ha^{-1} N, 122 kg ha^{-1} P, and 166 kg ha^{-1} K per year were desirable fertilizer rates for Easter lily bulb production in northern California and Oregon. They indicated that a portion of the fertilizer should be applied at planting time in the fall and the remainder in split applications in the spring and early summer. This same

☆ The use of trade names in this publication does not imply endorsement by the North Carolina Agricultural Research Service of the products named, nor criticism of similar ones not mentioned.

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recommendation was reiterated by Blaney and Roberts (1967) and Miller (1993).

In general, most of the research in the past 50 years has focused on the timing of fertilizer applications and not on the actual rates. Under California and Oregon conditions, Roberts and Blaney (1957) stated that very little uptake of N, P, and K occurred during the fall and winter. Most nutrient uptake occurred when the soil warms up in April and continued until flower development was complete. They recommended annual P incorporation in the fall due to ease of application and because P is not subject to leaching. To avoid leaching, they recommended N and K applications in the spring when rapid stem elongation occurs. Most producers in Georgia applied N and K at 45–90 kg ha^{-1} in March and again in May (Kiplinger and Langhans, 1967). However, Baba (1971) and Ohyama et al. (1988) observed active uptake of N in tulip roots during the winter and subsequent translocation to shoots when they sprouted.

Chaplin and Roberts (1981) observed that N, P, and K concentrations measured at monthly intervals in leaves decreased from March through October in 'Ace' and 'Nellie White' Easter lilies growing at five locations in southern Oregon and northern California coastal bulb production fields. Roberts et al. (1985) presented graphs of monthly N, P, and K content of individual tissues of 'Ace' lily plants from March to October. All three nutrients increased in all tissues until anthesis. In the stem and leaves, P and K declined immediately and N about a month after anthesis. At the same time, there was an increase in the bulblets and new scales, indicating translocation to storage organs. The quantitative gain in these nutrients in the new scales and bulblets was about equal to the loss in the stem and leaves. They suggested that little uptake of N and K occurred after flowering, but that some P may have been taken up.

van der Boon and Niers (1986) investigated the timing of N fertilization for Asiatic Hybrid lily 'Enchantment'. In a sandy soil, the greatest growth came from 75 kg ha^{-1} at planting and 75 kg ha^{-1} in three split applications in mid-to-late May. In a sandy–clay soil, lower rates were required for maximum yield. Rainfall greatly impacted the optimum rates and the timing. They found it was best to eliminate the application of N during the fall planting following a dry spring. Under these dry spring conditions, excessive levels of N were present in the spring, indicating limited uptake during the previous fall and winter.

The high organic matter content (up to 7%) in Easter lily bulb production soils in California and Oregon retain and supply nutrients effectively (L.J. Riddle, personal communication). Originally, the Lily Research Station in Brookings, Ore. applied 55–85 kg ha^{-1} N from a fertilizer which also supplied P and K at approximately 130% and 250% (respectively) of the N level at planting each fall and three or four applications of 45 kg ha^{-1} N each from calcium nitrate during the following spring. However, over time it was found that the spring applications were not necessary due to soil nutrient retention.

Thus, a universal lily fertilization program cannot be developed for all production situations due to the impacts of soil nutrient buffering as well as annual temperature and rainfall patterns. An understanding of the relationship between nutritional requirements and stages of growth would allow growers to adjust their fertilization program to seasonal climatic patterns and soil types. This research can be conducted in growth chambers.

No studies correlating the combined effects of controlled temperature conditions and nutrient availability on growth and development of Easter lily bulblets have been reported (Miller, 1992, 1993). In addition, most of the nutrient research has been conducted on two Easter lily cultivars that are no longer grown ('Ace' and 'Croft') and relates primarily to toxicity. In this study, we describe the symptoms of N, P, and K nutrient deficiencies in 'Nellie White'. The objective of this study was to determine the effects of temperature regime and N–P–K fertilization on the second year growth of one-year-old Easter lily bulblets.

2. Materials and methods

2.1. Plant materials and planting conditions

One-year-old *L. longiflorum* 'Nellie White' scale bulblets propagated and grown in Smith River, Calif. (42° north latitude) were harvested, graded, packed in moist peat and shipped by air to Raleigh, N.C. in early October 1997. Scale bulblets were selected for this study, because plants grown from scale bulblets are superior to those from stem bulblets for bulb production (Kim et al., 2007a). Upon arrival, the peat had a moisture content of 77% by weight. The bulblets had been propagated one-year earlier from scales. From the date of receipt until planting, bulblets were stored at 5 °C. Bulblets were 7–9 cm (7/9) in circumference. At planting, approximately 25% of the bulblets had sprouted.

Bulblets were dipped for 5 min in a solution containing 180 mg L^{-1} etridiole and 300 mg L^{-1} thiophanate-methyl. Subsequently, individual bulblets were planted in 470 cm^3 polystyrene cups with an 8.7 cm diameter at the top and 13.0 cm depth. Four 3.5 mm diameter holes were bored in the bottom of each container. The root substrate consisted of equal parts of KRUM horticultural perilite (coarse ore from Milos, Greece) and Carolina Perlite (fine ore from No Agua, N.M.) by volume. The perlite was moistened with tap water prior to planting and leached with tap water immediately after planting. Thereafter, all treatments were given either deionized water or a nutrient solution (Table 1) prepared with deionized water. Each temperature treatment was watered independently, as required.

2.2. Growing conditions

This study was conducted in growth chambers at the Southeastern Plant Environment Laboratories (Thomas et al., 2004) from 29 October 1997 to 13 May 1998 (196 d).

During the first growing period (GP-1), six growth chambers were maintained at continuous day/night temperature regimes of 30/26, 26/22, 22/18, 18/14, 14/10, and 10/6 °C under a 9-h photoperiod (short days) from 29 October to 13 February Five blocks were established within each temperature chamber; five

Table 1
Nutrient treatments applied to *L. longiflorum* 'Nellie White'

Treatments[a]	NH_4^+ (mM)	NO_3^- (mM)	$H_2PO_4^-$ (mM)	K^+ (mM)	Ca^{2+} (mM)	SO_4^{2-} (mM)	Mg^{2+} (mM)
Complete	4.5	25.5	3	8.5	8.5	2.75	2
Minus-N	0	0	3	8.5	5	9.75	2
Minus-P	4.5	25.5	0	8.5	8.5	4.25	2
Minus-K	4.5	25.5	3	0	12.75	2.75	2
Minus-N–P–K	0	0	0	0	5	7	2

[a] Each treatment also contained 17 μM BO_3^{3-}, 19 μM Fe^{3+}, 20 μM Mn^{2+}, 5 μM Cu^{2+}, 10 μM Zn^{2+}, 0.06 μM MoO_4^-.

nutrient treatments (Table 1) were randomized within each block. Throughout the entire study, light was provided in the growth chambers from a combination of VHO cool-white fluorescent and incandescent lamps at an input wattage ratio of 10:3 for 9 h from 0800 to 1700 h at a PPF of 600 μmol m^{-2} s^{-1}. Two plants from each experimental unit were destructively harvested at the end of GP-1 on 13 February (107 d).

Due to limited plant materials, labor and other resources, only plants from the 18/14 °C temperature regimes were grown into the second growing period (GP-2). Also, a very high percentage of shoots failed to emerge from the substrate ("no-shows") in some of the growth chamber treatments during GP-1 and this contributed to this decision.

On 13 February, plants from the 18/14 °C temperature treatment which had been irrigated with the complete nutrient solution were arranged and segregated by shoot size (largest to smallest) into blocks (1–5) within their respective temperature groups. Irrigation with the five nutrient treatments (Table 1) was initiated. After 107 d (13 February), a long day photoperiod was provided during GP-2 in the growth chambers by a 3-h incandescent light interruption from 2300 to 0200 at a PPF of 37 μmol m^{-2} s^{-1}. The photoperiod sequence was utilized to simulate the seasonal photoperiod in the bulb growing fields in which the short days of fall and winter are followed by the long days of spring and summer. All plants were destructively harvested on 13 May (196 d).

During each destructive harvest, plant organs were separated into main and stem bulbs; stem, leaves, and flower buds; and basal and stem roots. Fresh weights of all organs were measured to 0.01 g. Stem length (cm) was measured from the basal plate to the apical meristem. The number of leaves, flower buds, and stem bulbs were counted along the entire stem.

2.3. Tissue analysis

Main bulbs were used for nutrient analysis. Tissue was washed in tap water, followed by 0.2 N HCl for 1 min, rinsed in distilled water, dried at 70 °C, and ground in a Waring blender. A subsample was then taken from the ground tissue for nutrient analysis. A 1.25 g sample was combusted at 490 °C for 6 h. The resulting ash was dissolved in 10 ml 6 N HCl and diluted to 50 ml with deionized water. Phosphorus and K concentrations were determined by inductively coupled plasma emission spectroscopy. Nitrogen was determined with a PerkinElmer 2400 CHN elemental analyzer on 10 mg samples. All bulb analyses were conducted at the Analytical Services Laboratory, Dept. of Soil Science, N.C. State Univ.

2.4. Experimental design and statistical analysis

In GP-1, each of the six continuous chambers was divided into five blocks, and five fertilizer treatments were randomized within each block for a total of 30 treatment combinations (150 experimental units). Each experimental unit consisted of two cups containing one bulb each. The experimental design was a split plot with six temperature treatments as the main plots (with five blocks within) and five fertilizer treatments as subplots.

In GP-2, the experimental design was a randomized complete block. The 18/14 °C chamber was divided into five blocks and five fertilizer treatments were randomized within each block (25 experimental units). Each experimental unit consisted of two cups containing one bulb each.

Each GP was analyzed separately. Data were subjected to analysis of variance using SAS 8.2 (Statistical Analysis System, SAS Institute, Cary, N.C.). Means were separated using a protected LSD.

3. Results and discussion

3.1. General observations

For purposes of comparison, all statements will relate to plants grown with a complete nutrient solution as a positive control, unless otherwise noted. Wherever there was no temperature × fertilizer interaction, temperature data was not reported. These temperature effects were reported in Kim et al. (2007a). The mean N, P, and K dry weight concentrations in the bulblets at the beginning of the experiment were 1.06, 0.08, and 1.64%, respectively.

3.2. Growth

3.2.1. GP-1

Sixteen percent of bulblets at 30/26 °C and 12% at 26/22 °C failed to produce a shoot ("No shows"). This adverse high temperature response was not influenced by nutrient treatments. Kim et al. (2007b) suggested that bulblets should be grown initially at 14/10 °C and then shifted to a higher temperature following emergence to minimize the number of "no-shows".

Late in GP-1, flower buds aborted in some treatment combinations; however, vegetative growth was not affected. Flower bud abortion did not occur in the complete nutrient treatment (Fig. 1A). When P was omitted, flower bud abortion occurred only at 26/22 °C and when either N or all three nutrients were omitted, flower bud abortion occurred only at 30/26 °C.

There was no interaction between temperature and fertilizer on main bulb fresh weight during GP-1. The only effect of nutrient treatment on bulb weight was that the minus-N bulb weight was higher (Table 2). Since the initial weight of bulbs planted was 5.9 g, bulbs in the minus-N treatment lost less weight than bulbs in the other fertilizer treatments during GP-1. This indicates that during the initial period of growth, minus-N bulbs mobilized fewer stored reserves for root and shoot development. This process was described by Blaney and Roberts (1966) and these results confirm their findings.

There was a temperature × fertilizer interaction for stem bulb fresh weight and stem plus leaf fresh weight. Stem bulb fresh weight was lower at the end of GP-1 in the minus-N, minus-P, minus-K, and minus-N–P–K treatments, but only at 18/14 °C. At 26/22 °C, minus-K resulted in higher stem bulb weight (Fig. 1B).

Stem plus leaf fresh weight was lower in the minus-N, minus-P, and minus-N–P–K treatments at 26/22, 22/18, and 18/14 °C and in the minus-K treatment at 18/14 °C. At 26/22 °C, minus-K resulted in higher stem plus leaf weight (Fig. 1C). It was previously reported

Table 2
Effect of fertilizer treatments averaged over six continuous temperature regimes on mean bulb fresh weight and stem length of *L. longiflorum* 'Nellie White' grown under short days for 107 d[a]

Fertilizer treatment	Bulb wt.[b] (g)	Stem length (cm)
Complete	4.23	8.6
Minus-N	4.67	8.1
Minus-P	4.00	7.3
Minus-K	4.14	9.1
Minus-N–P–K	4.28	7.2
$LSD_{0.05}$	0.42	0.8

[a] Since there were no interactive effects between the six phytotron temperature regimes and the five fertilizer treatments for these dependent variables, temperature treatment effects were averaged over the five fertilizer treatments.
[b] The mean bulb fresh weight at the start of the experiment was 5.9 g.

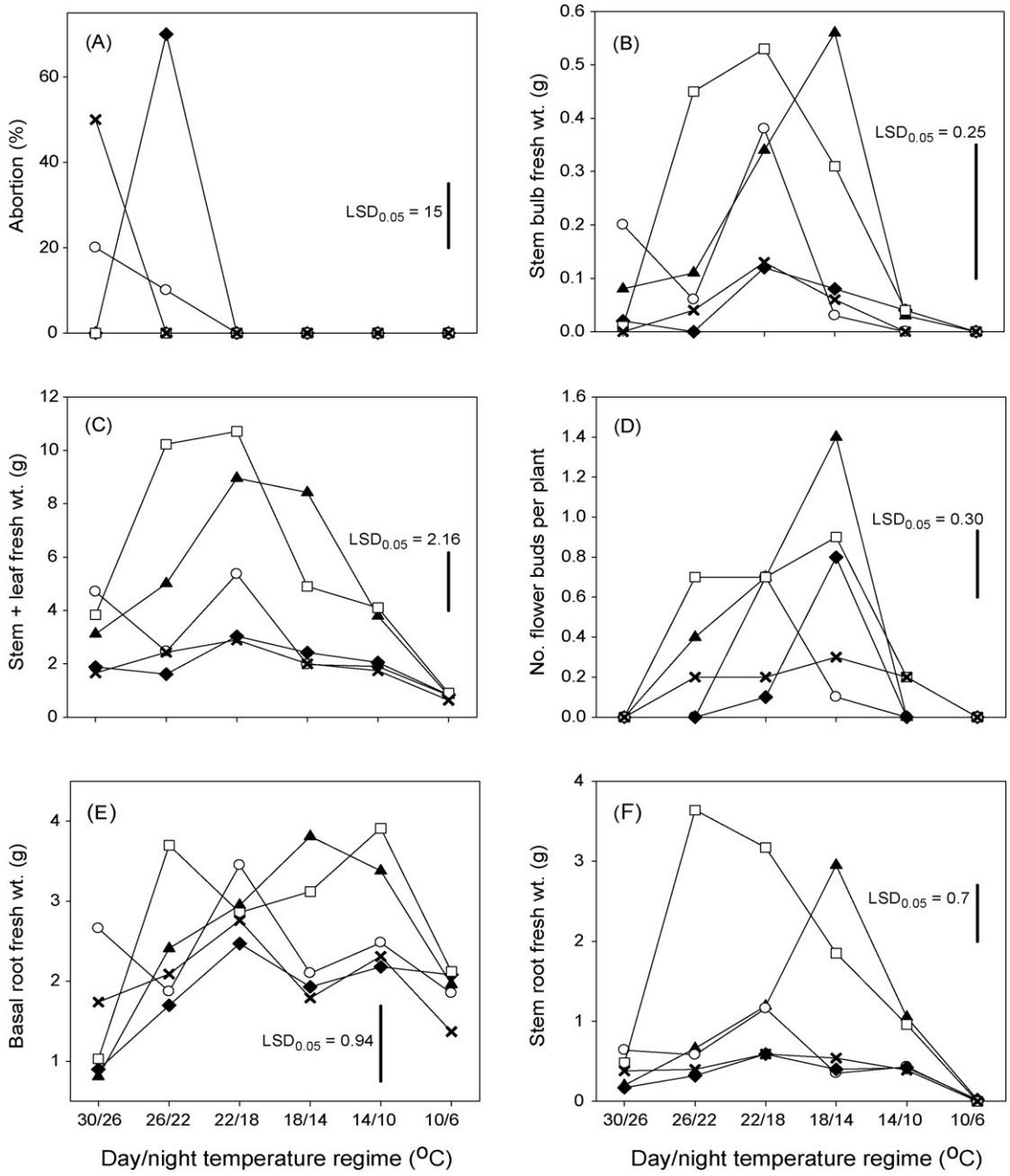

Fig. 1. Effect of temperature regime and fertilizer treatments on (A) flower bud abortion, (B) stem bulb fresh weight, (C) stem plus leaf fresh weight, (D) number of flower buds, (E) basal root fresh weight, and (F) stem root fresh weight of ***L. longiflorum*** grown under short days for 107 d. The fertilizer treatments are complete (▲), minus-N (○), minus-P (◆), minus-K (□), and minus-N–P–K (×) nutrient solutions. $LSD_{0.05}$ values and bars are for comparing fertilizer treatments within a given temperature regime or temperature regimes within a given fertilizer treatment.

that stem bulb weight and stem plus leaf fresh weight were greatest at 18/14 and 22/18 °C (Kim et al., 2007a). The higher and lower temperatures adversely reduced growth to a level where the potential for further reductions in these parameters from nutrient deficiencies were too limited to be significant.

Fewer flower buds were initiated in the minus-N, minus-P, minus-K, and minus-N–P–K treatments at 18/14 °C and in the minus-P and minus-N–P–K treatments at 22/18 °C (Fig. 1D).

Basal root fresh weight was lower at 14/10 and 18/14 °C in the minus-P and minus-N–P–K treatments; and at 18/14 °C in the minus-N treatment. Conversely, root weight was higher at 30/26 °C in the minus-N and at 26/22 °C in the minus-K treatments (Fig. 1E). Stem root fresh weight was lower in all of the minus treatments at 18/14 °C and higher in the minus-K at 26/22 and 22/18 °C (Fig. 1F).

There was no interaction between temperature and fertilizer on stem length during GP-1. Stem length was shorter in the minus-P and minus-N–P–K treatments regardless of temperature regime (Table 2). P deficiency has been reported to yield smaller, more compact plants in other crops (Epstein and Bloom, 2004; Mengel and Kirkby, 2001).

3.2.2. GP-2

Plants in the fertilizer treatments during GP-2 were supplied with complete nutrients during GP-1. When compared to the complete fertilizer treatment at the end of GP-2, the other treatments had no

Table 3
Effect of fertilizer treatments on stem plus leaf fresh weight and percent N, P, and K in the dry bulb of *L. longiflorum* 'Nellie White' at the end of growing period 2 (GP-2) after being grown at 18/14 °C under short days for 107 d followed by long days for 89 d[a]

Fertilizer treatment	Stem + leaf wt. (g)	N (%)	P (%)	K (%)
Complete	20.09	1.56	0.26	1.70
Minus-N	17.94	1.06	0.26	1.32
Minus-P	18.04	1.41	0.10	1.50
Minus-K	17.42	1.98	0.28	1.04
Minus-N–P–K	13.76	0.87	0.09	0.79
$LSD_{0.05}$	3.88	0.23	0.04	0.14

[a] Plants were fertilized with complete fertilizer solution for the 107 d under short days during growing period 1 (GP-1) and subjected to fertilizer treatments for 89 d during GP-2. The mean N, P, and K concentrations at the start of GP-1 were 1.06, 0.08, and 1.64%, respectively, and at the end of short days (end of GP-1) were 1.58, 0.16, and 1.78%, respectively.

effects on any growth measurements with the exception of stem plus leaf fresh weight. Stem plus leaf weight was lower when the combination of all three nutrients was omitted (Table 3).

3.3. Deficiency symptoms

The visual deficiency symptoms at the end of GP-1 for all five fertilizer treatments are shown in Fig. 2A and described below. No visual deficiency symptoms were observed during GP-2.

The first symptom of N deficiency was observed as lighter green than the normal green color over the entire plant (Fig. 2B). The oldest leaves became lighter green earlier than the newer leaves. Chlorosis in older leaves intensified until the leaves were uniformly yellow. A tan necrosis followed chlorosis in older leaves and intensified uniformly across these leaves. The symptoms of chlorosis and necrosis progressed up the plant. Seeley (1950) observed that 'Croft' Easter lilies forced in a minus-N nutrient solution were initially a lighter green and smaller than the control. The symptoms progressed at anthesis to either yellow or completely necrotic leaves on the lowest 8 cm of the plant.

Similar symptoms have been reported in *Narcissus* 'Garden Giant' grown under hydroponic conditions by Ruamrungsri et al. (1996a,b). In addition, Cheal and Hewitt (1962) reported pale-green leaves and early senescence with a minus-N treatment in *Tulipa* 'Golden Harvest' and 'Krelage's Triumph' using sand culture.

Phosphorus deficiency (Fig. 2C) initially appeared as stunted plants with normal green leaf pigmentation. The deeper than normal green color or purple pigmentation often associated with P deficiency in many other species (Epstein and Bloom, 2004; Mengel and Kirkby, 2001) did not occur. The second set of symptoms was manifested on the lowest leaves as uniform chlorosis of the entire leaf. Following chlorosis, the lowest leaves developed a tan-brown necrosis. Chlorosis and necrosis progressed up the plant. These latter two symptoms were similar to the symptoms of N deficiency in appearance, location, sequence, and progression.

Symptoms of K deficiency (Fig. 2D) occurred initially on the leaves of the upper half of the plant. Dark brown pigmented streaks developed in a zone covering the mid 40–60% of the tip to base axis of the leaf. Position of the initial symptom within this zone varied from leaf to leaf appearing either on the margins of the leaf, along the mid vein, or across the entire leaf width. The pigmented tissue became necrotic and appeared to desiccate. Tissue at the terminal end of these leaves turned light green. The symptoms of dark pigmentation and necrosis spread toward both ends of the affected leaves and to leaves basipetally on the plant.

3.4. Bulb analysis

As expected, compared to the control nutrient treatment, there were decreases in the omitted nutrients in the respective deficiency treatments at the end of GP-1 (Fig. 3A), i.e., lower N concentration in minus-N treated bulbs. In the complete treatment, N and K bulb concentrations were lowest at the two cool temperatures of 14/10 and 10/6 °C. Phosphorus concentration was lowest at the warmest temperature (30/26 °C) and three coolest temperatures (18/14, 14/10 and 10/6 °C).

The minus-N treatment resulted in a lower concentration of P in the 26/22, 22/18, 18/14, and 14/10 °C regimes and lower K in the 26/22, 22/18, and 18/14 °C regimes. The minus-P treatment resulted in a lower concentration of N at all temperature regimes except 10/6 °C and lower K in the 26/22 and 22/18 °C regimes. The minus-K treatment had no effect on N concentration, but there was a lower concentration of P in the 18/14 °C regime. Overall, in the

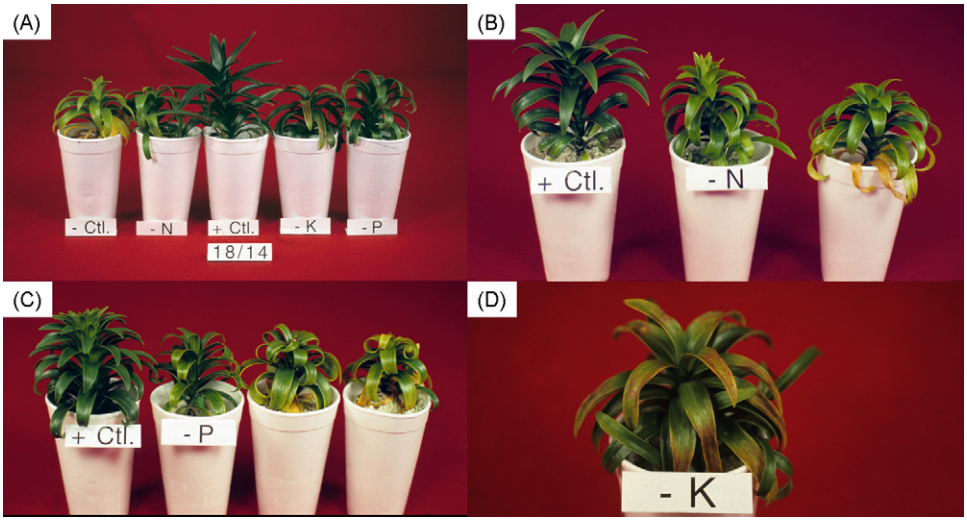

Fig. 2. ***L. longiflorum*** 'Nellie White' plants were grown from one-year-old scale bulblets under short days for 107 d referred to as growing period 1 (GP-1) and irrigated with the following nutrient treatments: minus-N–P–K (−Ctl.), minus-N (−N), complete (+Ctl.), minus-K (−K), and minus-P (−P). Individual photographs show representative plants with: (A) all five nutrient treatment groups, (B) one complete and two minus-N plants, (C) one complete and three minus-P plants, and (D) a minus-K treated plant.

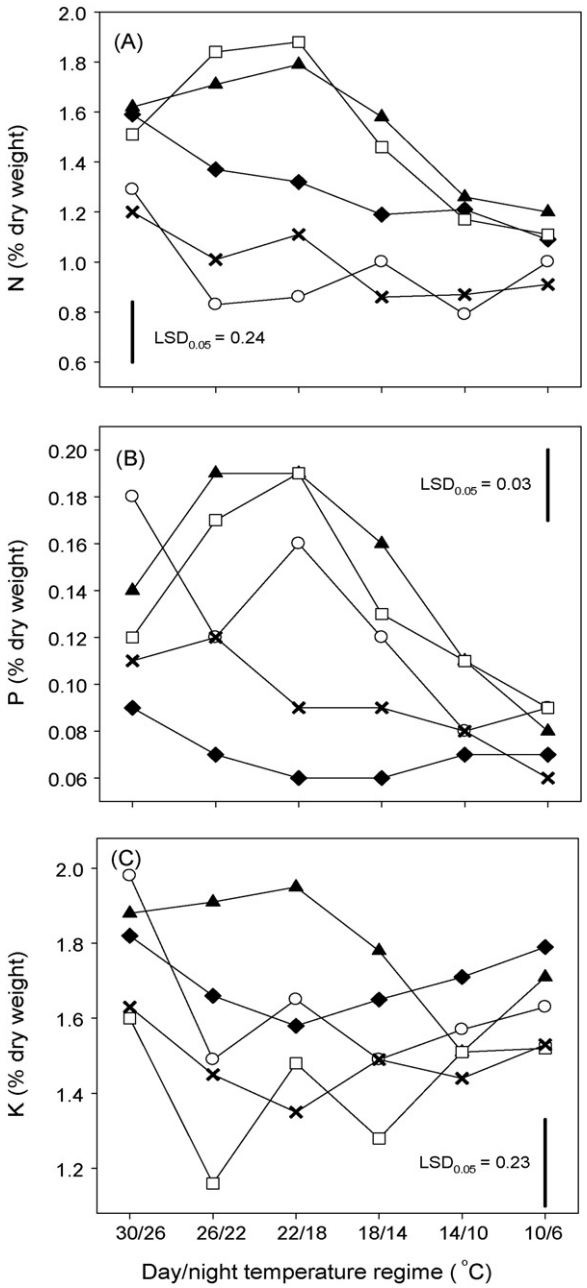

Fig. 3. Effect of temperature regime and fertilizer treatments during growth period 1 (GP-1) on (A) N, (B) P, and (C) K concentration in dry bulbs of ***L. longiflorum*** 'Nellie White' grown under short days for 107 d. The mean N, P, and K concentrations at the start of GP-1 were 1.06, 0.08, and 1.64%, respectively. The fertilizer treatments are complete (▲), minus-N (○), minus-P (◆), minus-K (□), and minus-N–P–K (×) nutrient solutions. $LSD_{0.05}$ values and bars are for comparing fertilizer treatments within a given temperature regime or temperature regimes within a given fertilizer treatment.

mid temperature ranges where growth was maximized, a shortage of any one of the three nutrients N, P, or K resulted in decreased concentrations of the other two nutrients with the one exception, where low K did not affect N concentration.

At the end of GP-2, bulb concentration of K was lowered by omission of any of the nutrients N, P, or K in the nutritional program (Table 3). Potassium levels were lowest when all three nutrients were omitted. In contrast, bulb concentration of N and P were only lowered by omission of the respective nutrient. This explains why the bulb concentration of K in the minus-N–P–K treatment was lower than in any other treatment where a single nutrient was omitted. The bulb concentration of N or P in the minus-N–P–K treatments was not different from the level in the minus-N or minus-P treatments. In contrast to these direct relationships, omission of K resulted in an inverse relationship with N, where N was higher in the bulb. This was likely due to relief of the antagonistic interaction where ammonium depresses K uptake (Robson and Pittman, 1983).

4. Summary

Although N, P, and K were required for maximum plant growth and development during GP-1, the absence of N and P fertilization had a greater negative impact on growth than the absence of K. Plants grown at 18/14 °C, and supplied N, P, and K during GP-1 but no nutrients during GP-2, produced the same yield of basal bulbs as those supplied N, P, and K during GP-2. While bulb concentrations of N and P at the end of GP-2, in plants that did not receive these nutrients, were similar to concentrations at the start of GP-1, the K concentration was lower. This suggests that K should be supplied during GP-2. Omitting all three nutrients further depletes bulb K concentration and decreases the stem plus leaf weight, which may impact future bulb development. This indicates that all three nutrients may have some benefit during GP-2. However, the demand for nutrients during GP-2 was much lower than GP-1, indicating strong reliance on translocated nutrients during these later stages of development.

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