Research Article

Growth, Development, and Mineral Nutrient Accumulation and Distribution in Tulip from Planting through Postanthesis Shoot Senescence

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Tulips were grown under field conditions from mid-November through early-June. Plants were harvested and dissected into eight organs on twenty-one dates. These parts were dried, weighed, and analyzed for N, P, K, Ca, and Mg. A transition (as determined by curve join points) from a linear to a steep negative cubic response occurred prior to shoot emergence for N (82 days after planting (DAP)), at shoot emergence for K (93 DAP) and Ca (94 DAP), and after shoot emergence for Mg (102 DAP) and dry matter (118 DAP). A transition from a linear to a steeper linear response occurred at shoot emergence for P (93 DAP). Growth, organ development, and nutrient accumulation occurred continuously from planting to maturity (188 DAP), except for K which did not accumulate during the initial linear phase. Since the increase in accumulation of all five nutrients preceded the dry matter accumulation, these nutrients could be used as predictors in growth models. Practical implications from this study include the importance of maintaining soil Ca levels through liming and applying the N, P, and Mg as split applications with smaller rates at planting and larger rates at emergence. The entire K application may be applied at emergence.

1. Introduction

Garden tulips (*Tulipa gesneriana* L.) are geophytes that produce bulbs with an annual renewal and are composed of two to six concentric fleshy scales attached to a basal plate and enclosed in a tunic [1, 2]. Roots are produced on the surface of the basal plate. The tunic is a very thin, papery external scale. Buds located at the inner bases of the fleshy scales give rise to the organs of the mother plant. The apical bud gives rise to the aerial organs (leaves, scape, and flower) and the lateral buds give rise to daughter-bulbs. The innermost daughter-bulb (A-bulb) is the oldest and largest [3]. From the A-bulb outward, daughter-bulbs become progressively smaller and are designated alphabetically (A, B, C, etc.), with the exception of the outermost bulb which is designated as the H-bulb (H for Dutch *huid* meaning "skin" or "tunic"). Late in development, the H-bulb grows larger than some of the daughter-bulbs when food reserves from the outermost

scale are transferred to this outermost bulb as the scale dries to become the tunic. A schematic of the replacement cycle is presented by De Hertogh et al. [4].

In flowering tulip bulbs, three to five leaves are produced on a scape bearing a terminal flower [1]. Although some cultivars and species can produce more than one flower per scape, most produce only one flower per scape. The annual replacement cycle of the tulip bulb can be divided into three phases. (1) Root growth occurs rapidly following planting in the autumn. The apical bud, which has already differentiated into aerial organs, slowly elongates throughout the winter. (2) In the spring, as temperatures rise, plant growth accelerates. The scape and flower bud rapidly elongate culminating in flowering. The transformation of the vegetative buds (daughter-bulbs) into the next generation of mother-bulbs is initiated and increases after flowering. At the same time, the original mother-bulb scales desiccate. (3) Near the end of spring, the aerial organs and roots senesce and daughter-bulb

growth ceases. However, in the summer, bud differentiation (vegetative and floral) occurs within former daughter-, now mother-bulbs. Bulbs must reach a critical size (weight) before a flower bud can be initiated. Although the critical size varies by genotype, the minimum size is usually six to eight grams. This range corresponds to approximately six to nine centimeters in circumference [2, 5, 6].

If tulip bulb growers and gardeners are concerned with annual growth cycles, it has to be noticed that the botanical life cycle of a tulip bulb can span 29 to 41 months [7, 8]. Normally, the life cycle begins in February in the northern hemisphere with the initiation of a granddaughter-bulb between scales within a daughter-bulb [2]. The daughter-bulb is, in turn, enclosed between the scales within a mother-bulb. During the next 4 months, after the mother-bulb has flowered and senesced, the daughter-bulbs which have now matured to second generation mother-bulbs are lifted. The original granddaughter-bulbs have matured to second generation daughter-bulbs and are contained within the newly formed second generation mother-bulbs. In the succeeding autumn, the new mother-bulbs are planted. If they are of sufficient size by the following spring, they will flower and senesce, and the second generation daughter-bulbs within them will mature to third generation mother-bulbs. Approximately 29 months were required from initiation of the granddaughter-bulbs to maturation into mother-bulbs. If, conversely, daughter-bulbs dug at the end of the second summer are too small to flower that next year, they will require an additional year of growth before they reach flowering size for a complete life cycle of about 41 months. The duration of that period is affected by internal factors (bud position inside the bulb) and environmental factors, with fertilization being an important one.

Nitrogen (N) fertilization of tulips is usually divided between autumn and spring applications [9–11]. Small but measurable N uptake occurs from planting through winter [11–13]. Nitrogen is translocated from the mother-bulb to the shoot [13] and the roots (Benschop, unpublished data). Only trace levels of NO_3^--N are detectable in the roots. However, Ohyama et al. [14, 15] observed that tulips grown hydroponically in a complete nutrient solution in a glasshouse under natural conditions accumulated large quantities of N during the winter. It was used later during sprout growth. Following shoot emergence in the spring, an acute increase in N uptake occurs and continues until the shoot (scape) reaches its maximum height [13, 16, 17]. Nitrogen is usually applied as NO_3^- shortly after emergence to take advantage of the increased uptake [12, 16, 18]. van der Boon [19] correlated the increased uptake with increases in air temperature and transpiration. Ohyama et al. [14] suggested that N absorbed by the roots is converted to λ-methylene-glutamine for transport to other organs during flowering. It was also suggested that N accumulation in the roots in the winter supplements the N originally stored in the mother-bulb [15]. Tsutsui [20] stated that additional N can be applied following flowering to promote the growth of daughter-bulbs. However, this is generally not recommended because the presence of N under warm soil conditions tends

to stimulate the development of *Fusarium* spp. and this fungal disease is a major cause of bulb loss [1].

Phosphorous (P) and potassium (K) fertilization have been studied less than N fertilization of the tulip [1]. Smaller leaves [21] and daughter-bulbs that weigh less [22, 23] have been reported as symptoms of P deficiency. Although flower size appears to be unaffected by different sources of P [24], flowering could be delayed [25]. van der Boon [19] reported that the tulip bulb shows little or no response to K fertilizers. Potassium fertilizer applications are decreased in some regions of the Netherlands to reduce the chance of causing magnesium (Mg) deficiency [19]. Interactions between N and K have been observed [24, 26]. Tissot [24] reported a synergistic effect on the uptake of both elements when applied at high levels.

Forcing tulip bulbs without a calcium (Ca) fertilizer can result in deficiency symptoms including stem topple, light green foliage, stunting of leaves and scape, and flower bud abortion [27–32]. Fertilization with Ca during forcing has been shown to completely or partially prevent these deficiency symptoms [1, 33–35]. Fertilizing with Mg salts can increase the yield of tulips [26]. However, when Mg was applied on a sandy soil with cow manure, it had minimal effects on yield [19]. One or two applications of $MgCl_2$ may be applied after flowering [36]. Mügge and Richter [37] reported that yield was increased with $MgSO_4$ applied either as a spray just after deflowering or as a preplant bulb dip when the soil Mg concentration was below 30 ppm. However, the effects on foliage color and bulb yield are minimal.

Bakker [38] estimated the total kilograms per hectare of N, P, K, and Ca used for bulb production as 140 to 150, 40 to 50, 140 to 150, and 110 to 120, respectively. Khan et al. [39] found a combined application of N, P, K, and Zn at 75, 50, 50, and 5 kg·ha^{-1}, respectively, had the best growth, flower quality, and bulb production in tulips under polyhouse conditions.

Several studies followed the accumulation and distribution of biomass and nutrient resources to plant parts in various geophytes throughout the growing season including three cormous perennials (*Ixia flexuosa* [40], *Gladiolus caryophyllaceus* [41], and *Sparaxis grandiflora* subspecies *fimbriata* [42]), the tuberous Jerusalem artichoke (*Helianthus tuberosus*) [43], and the bulbous red squill (*Urginea maritima*) [44]. Subramanian et al. [45] studied the dry matter and nutrient distribution within potato (*Solanum tuberosum*) tubers at harvest. However, the measurements on potato were taken on only one date and did not include analysis of roots or shoots since harvest for food usually occurs following the senescence of these plant parts.

Fundamental knowledge of when biomass and nutrients are accumulated by a tulip and how resources are allocated within the plant is useful for understanding how these processes impact growth and development. Additionally, this information could be used to develop more efficient and ecofriendly fertilizer management plans for commercial bulb production and landscape-use. The objective of the current study was to determine the relationships among growth, development, and nutrient accumulation and distribution from planting through postanthesis senescence in tulips.

2. Materials and Methods

2.1. Field Preparation. This experiment was conducted at the North Carolina State University (NCSU) Horticulture Field Laboratory in Raleigh, NC ($35°\,47'$N latitude and $78°\,42'$W longitude at an elevation of approximately 121.9 m above sea level), in a fine, kaolinitic, and thermic Typic Kanhapludult (Cecil series) soil. A sod field was sprayed with the herbicide glyphosate at $0.17\,g\cdot m^{-2}$ acid equivalent in early-October 1981. Two weeks later, the field was rototilled using a tractor-mounted rototiller and methyl bromide was applied at $98\,g\cdot m^{-2}$. On 17 Nov., a 13 cm deep layer of composted pine bark (≤ 1.3 cm in diameter) was spread over the site along with hydrated lime and agricultural dolomitic limestone at 2.9 and $1\,kg\cdot m^{-2}$, respectively. These amendments were incorporated with the tractor-mounted rototiller to a depth of 28 cm. The final soil pH was 6.3. A tractor-mounted bed-former was then used to form a bed that was 20 cm high and 66 cm wide at the top.

Fritted trace elements (Frit-F-555HF, Pro-Sol Division, Frit Industries, Inc., Ozark, AL 36361), superphosphate (8.8% P), ammonium nitrate (34% N), and dibasic potassium sulfate (45% K) at 9.15, 250, 82.5, and $34\,g\cdot m^{-2}$, respectively, were broadcast on the tops of the beds and incorporated using a walk-behind rototiller to 15 cm deep.

2.2. Planting and Postplant Fertilization. On 17 Nov., bulbs 12 cm and larger in circumference of *Tulipa gesneriana* "Paul Richter" were planted 15 cm deep to the base of the bulb. Five bulbs were spaced 10 cm apart across the bed with 30 cm between cross-bed rows. Following planting, beds were covered with a 5 cm deep layer of pine needles. Prior to planting, five randomly selected bulbs were analyzed separately as whole bulbs for mineral nutrients. The mean macronutrient concentrations in $mg\cdot g^{-1}$ dry matter were 14.20 N, 1.52 P, 8.84 K, 0.35 Ca, and 0.66 Mg. The mean micronutrient concentrations in $\mu g\cdot g^{-1}$ dry matter were 12.4 Fe, 4.3 Mn, 14.2 Zn, and 3.4 Cu. Following shoot emergence, beds were top-dressed with ammonium nitrate and potassium sulfate at 82.5 and $34\,g\cdot m^{-2}$, respectively, on 22 Feb. (97 days after planting (DAP)).

Natural rainfall was the only source of irrigation throughout the experiment. The planting area for this experiment was surrounded on all four sides by other tulip research plots which served as border rows.

2.3. Harvest. On the day of planting (17 Nov.), three groups of five bulbs each were selected for dissection, weight, and analysis. On twenty harvest dates starting on 25 Nov. and ending on 3 Jun., five plants were dug up from each of the three blocks. Each plant was dissected into eight component parts: roots, scales, basal plate, daughter-bulb, H-bulb, leaves, scape, and flower. The parts were dried at $70°$C to constant weight, weighed, and analyzed for nutrient content. The root-to-shoot dry matter ratio was calculated by dividing the dry root weight by the sum of leaf, scape, and flower weights. In this study, the shoot was defined as all the aerial structures (those organs which have most of their mass above ground at maturity).

2.4. Tissue Analysis. Tissue was washed in 0.2 M hydrochloric acid (HCl) for 30 seconds, rinsed in deionized water, dried for 24 hours at $70°$C, and then ground to 1 mm particle size in a stainless steel Wiley Laboratory Mill Model 4 (Thomas Scientific, Philadelphia). A 100 mg subsample was analyzed for total N using a Kjeldahl procedure [46]. A 500 mg subsample of tissue was analyzed for the remaining nutrients by dry-ashing at $500°$C. After addition of 6 M HCl, the ash was heated to dryness at $100°$C to dehydrate it and then dissolved in 0.5 M HCl. Phosphate-P was determined by colorimetric analyses [47] using a Model Lambda 3 UV/VIS spectrophotometer (Perkin-Elmer, Norwalk, CT, USA). Potassium, Ca, and Mg were analyzed using an atomic absorption spectrometer AAnalyst 100 (Perkin-Elmer).

2.5. Experimental Design and Statistical Analysis. The experimental design was a randomized complete block with plants from twenty-one harvest dates randomized in three replicated blocks (63 experimental units). The experimental plot consisted of a single bed divided into three blocks with 120 bulbs planted in each block. The bulbs were arranged within each block in a pattern of 24 cross bed rows of five bulbs each. The experimental unit consisted of one row of five plants. The 21 harvest dates occurred during a 198-day period. Five unplanted bulbs were randomly harvested for the first harvest date on 17 Nov. The four additional rows planted in each plot were used if there was plant mortality in a specific row during the experiment. Means and standard errors were calculated using SAS 9.3 (SAS Inst., Cary, NC) with PROC MEANS. PROC NLIN in SAS used the Gauss-Newton algorithm to fit a nonlinear response curve for total plant response over time for various dependent variables. Join points were estimated as described by Gallant and Fuller [48].

3. Results

3.1. Environmental Conditions. The maximum and minimum daily air temperatures and total daily precipitation measured at 2 m above ground level from planting through final harvest for Raleigh, NC, were provided by the State Climate Office of North Carolina, NCSU, Raleigh, NC (Figure 1). The weather station was located on the campus of NCSU at $35°48'$N latitude, $78°42'$W longitude, and an elevation of 121.9 m above sea level. The lowest temperature was $-16.1°$C recorded on 11 Jan. (55 DAP). The highest temperature was $33.3°$C recorded on both 14 and 15 May (178 and 179 DAP, resp.). The total precipitation for the dates included in this experiment was 68.2 cm for a mean daily precipitation rate of 0.34 cm per day.

3.2. Growth. Important events in the growth period of 198 days included (1) planting of mother-bulbs on 17 Nov. (0 DAP), (2) shoot emergence on 19 Feb. (94 DAP), (3) minimum plant dry matter measured on 12 Mar. (115 DAP), (4) the first anthesis on 26 Mar. (129 DAP), (5) fifty percent of the plants in bloom on 31 Mar. (134 DAP), (6) peak shoot dry matter on 13 Apr. (147 DAP), (7) maturity beginning of shoot necrosis was on 24 May (188 DAP), and

(a)

(b)
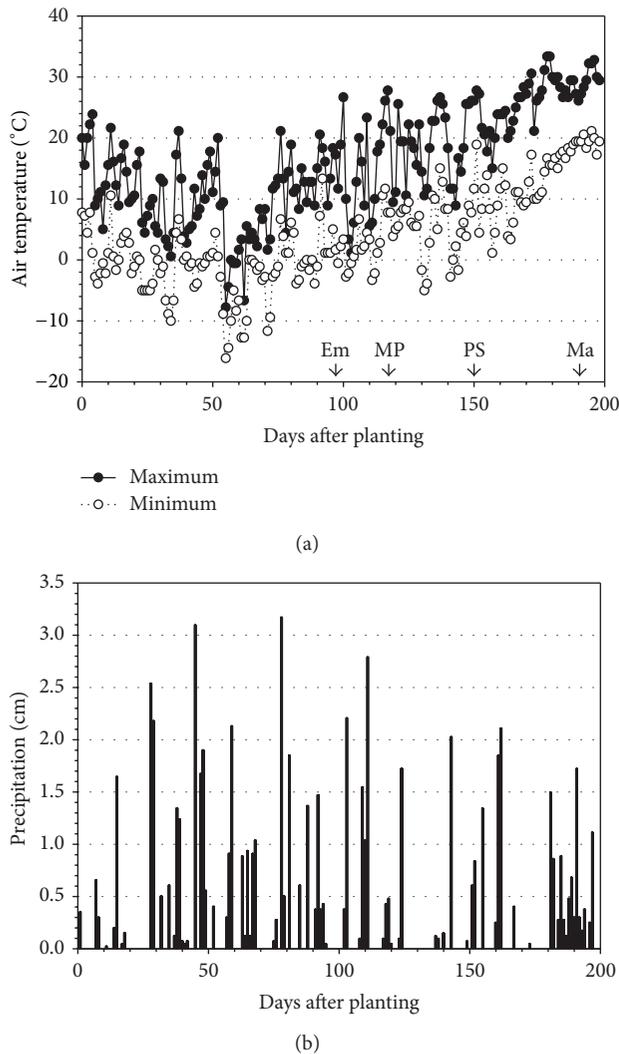
Figure 1: Maximum and minimum daily air temperatures and total daily precipitation measured at 2 m elevation from planting to the final harvest for Raleigh, NC. The arrows indicate the dates of shoot emergence (Em), minimum plant (MP) dry matter, peak shoot (PS) dry matter, and bulb maturity (Ma).

(8) plants completely straw-colored on 3 Jun. (198 DAP) (Figure 2(a)). At all times from planting to maturity, growth, and development of one or more organs occurred. (The dry matter and nutrient content data presented in Figure 2 are also presented for more accurate quantification in Tables S.1–S.6 of the Supplementary Material available online at http://dx.doi.org/10.1155/2015/341287.)

From planting to minimum plant dry matter, the whole plant dry matter diminished (Figure 2(a)). The major loss was due to declining scale dry matter. This was anticipated due to respiration. Between minimum plant dry matter and peak shoot dry matter (leaves, scape, and flower), plant matter increased at a continually increasing rate. During this period, dry matter of shoots, the H-bulb, and daughter-bulbs increased while scales continued to decrease as their content was reallocated to the cited organs. Between peak

shoot dry matter and maturity (188 DAP) plant dry matter continued to increase, but at a declining rate. Loss in scale and shoot dry matter during this period was more than offset by the gain in H-bulb and daughter-bulb dry matter. After maturity, total plant dry matter declined due to losses in all organs.

Roots appeared by 17 DAP, grew to a maximum dry matter of 0.573 g per plant by 167 DAP, and then decreased to 0.29 g at 198 DAP (Figure 2(a)). Shoot dry matter increased from planting to 147 DAP. During the first 43 days, root growth outpaced shoot growth resulting in an increase in root-to-shoot ratio from 0 at planting to 0.69 at 43 DAP (Figure 3). Beyond 43 DAP, root growth slowed as it approached maximum size while shoot growth continued to increase, particularly after emergence. During this period, the root-to-shoot ratio declined to 0.05. Then, the root-to-shoot ratio increased to 0.13 in the post-shoot-peak period as shoot dry matter declined faster than root dry matter.

The shoot grew continually from planting and reached maximum dry matter at 147 DAP (Figure 2(a)). The shoot was 41.4% of the plant dry matter at this stage. However, the daughter-bulbs and H-bulb combined had already grown to 47.0% of the plant dry matter. As the plant matured, the shoot lost dry matter and the scales continued to lose dry matter as resources were allocated to the daughter-bulbs and H-bulb. At maturity, the senescing shoot was only 9.8% of the total dry matter; the daughter-bulbs and H-bulb combined had grown to 86.5% of the total dry matter; the scales had shrunk to 1.6% of the total dry matter. (The relative distribution of dry matter and nutrients among the eight organs for five stages of growth shown in Figure 2 is also presented for more accurate quantification in Table S.7 of the Supplementary Materials.)

3.3. Nutrients. Curves for whole plant dry weight and nutrient content are presented in Figures 4(a)–4(f). Each curve was best defined by two connected functions. For all six dependent variables, the best fit for the data was a linear function for the first phase. This was followed by a cubic function ending at senescence for dry matter and total N, K, Ca, and Mg content. The initial linear function for total P content was followed by a second linear function with a steeper positive slope. The join point, as determined by the NLIN program, defines the boundary between the two functions. Although shoot emergence occurred at 94 DAP, the join point for dry weight occurred at 118 DAP. Weight loss from respiration continued to exceed photosynthetic weight gain for the period from shoot emergence to 118 DAP, after which, photosynthetic weight gain prevailed.

The linear phase of whole plant nutrient content for N, P, K, Ca, and Mg occurred between planting and 84, 95, 93, 94, and 102 DAP (Figures 4(b)–4(f)). This places the initial point of rapid uptake of N, P, K, Ca, and Mg at 34, 23, 25, 24, and 16 days prior to initial weight increase, respectively. Nutrient concentration changes during the initial linear phase were calculated using regression equations from Figure 4. The N, P, and Mg contents increased by 7%, 14%, and 31%, respectively. In contrast, calcium content increased by 112%. However, dry matter and K content declined by 24% and 7% during this period, respectively.
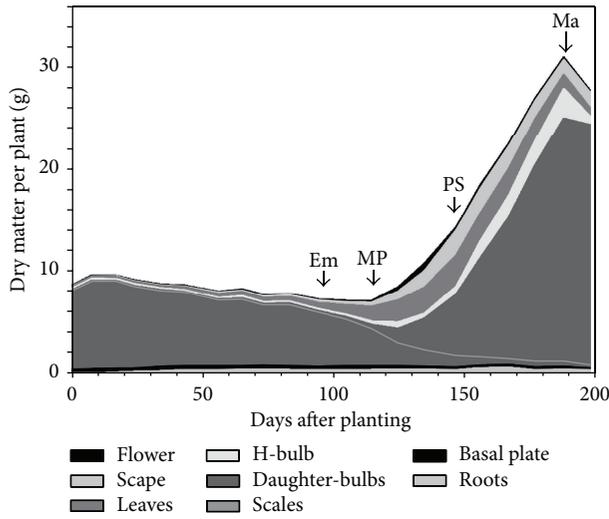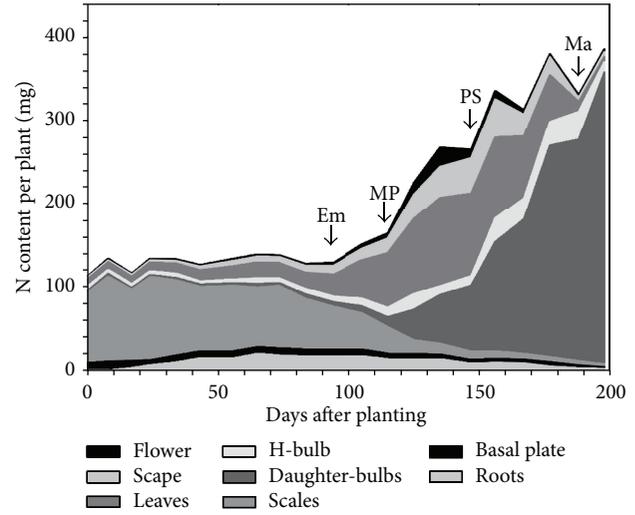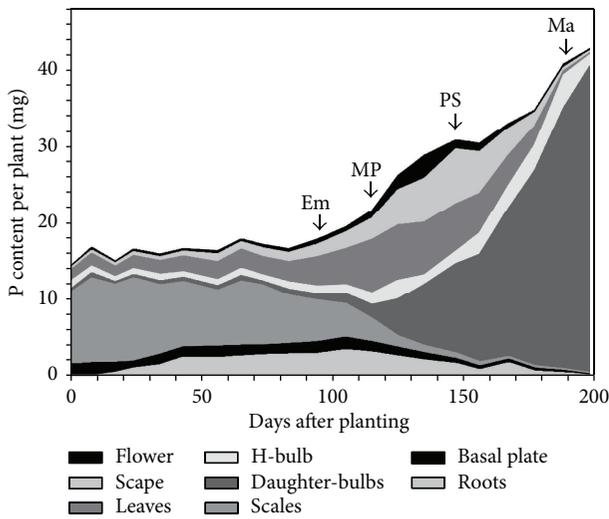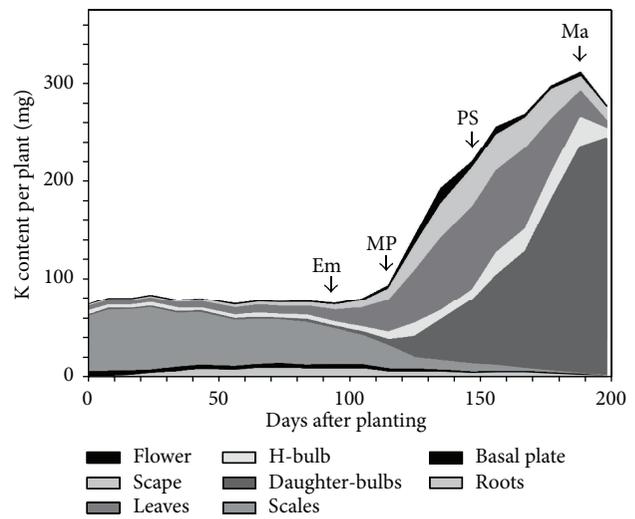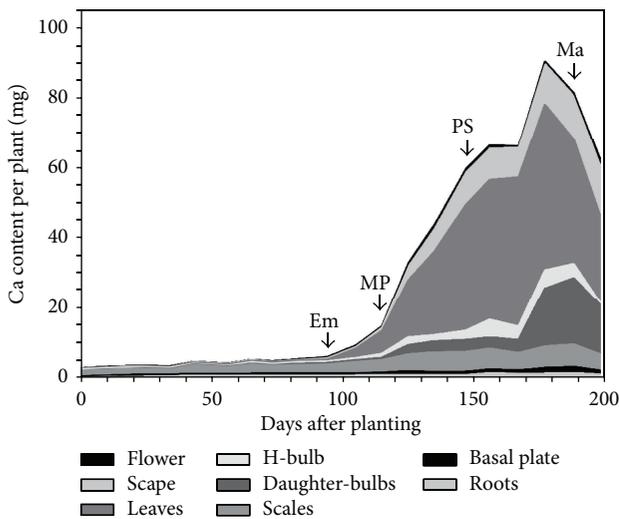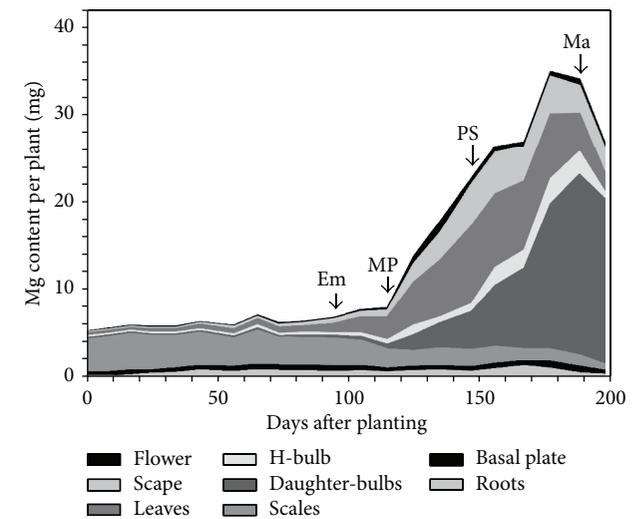
FIGURE 2: Profile showing the allocation of dry matter (a), N (b), P (c), K (d), Ca (e), and Mg (f) to organs of *T. gesneriana* "Paul Richter" during the growing season. Organs appear within each graph in the same order (top to bottom) as listed in the key. Data are plotted additively with vertical distances between lines indicating the quantity of a particular nutrient in each organ. The arrows indicate the dates of shoot emergence (Em), minimum plant (MP) dry matter, peak shoot (PS) dry matter, and bulb maturity (Ma).
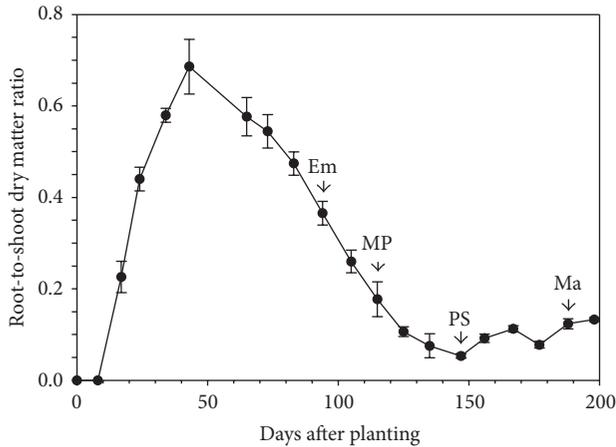
FIGURE 3: Changes in root-to-shoot dry matter ratio from planting to final harvest in *T. gesneriana* "Paul Richter." The arrows indicate the dates of shoot emergence (Em), minimum plant (MP) dry matter, peak shoot (PS) dry matter, and bulb maturity (Ma).

After the start of the cubic, sigmoidal progression of nutrient accumulation for all nutrients but P, total accumulation closely paralleled the sigmoidal growth curve. The inflection point between increasing and decreasing rates of accumulation in the cubic phase of the curves occurred at approximately 147 DAP, the point of peak shoot dry matter. Postmaturity, 188 DAP, decline in dry matter was closely tracked by downward shifts in accumulation of N, K, Ca, and Mg. Accumulation of P differed. It did not decline after maturity but continued to increase up to senescence, 198 DAP.

Scales, being a source of carbon and mineral nutrients for other growing organs, declined in mass and nutrient content throughout the growing season with the exception of Ca which increased up to the time of maturity.

4. Discussion

From the perspectives of commercial production and gardening the annual replacement cycle of the tulip bulb begins with planting of the mother-bulb in the autumn and concludes after flower senescence, about an eight-month period [49]. The bulbs are dug up in early summer. During any given year of the tulip life cycle, originating at planting of the mother-bulb and ending with the harvest of the next generation of mother-bulbs, this study shows that the source-sink relationships for mobile nutrient accumulation (N, P, K, and Mg) are as follows (Figure 2). From planting to emergence, the scales of the mother-bulb and soil solution are the sources for the sinks that include the shoot (leaves, scape, and plus flowers), daughter-plus H-bulbs, and roots. After emergence, sources include mother-bulb scales, roots, basal plate, and soil solution while the sinks are the daughter- plus H-bulbs, and the shoot up to peak shoot dry matter. After peak shoot dry matter, the shoot becomes a source along with mother-bulb scales, roots, basal plate, and soil solution with the daughter- and H-bulbs being the sinks. Translocation of N from shoot and root to daughter-bulbs in this final stage was likewise reported by Zhou et al. [50].

As in other plants [51], Ca^{2+} is likewise an immobile nutrient in tulip [52]. They reported that Ca^{2+} does not translocate from tulip foliage to daughter-bulbs during senescence. The proportionally larger root uptake of Ca^{2+} prior to shoot emergence compared to other macronutrients was necessitated by the immobility of Ca^{2+}. During this period, concentration of Ca^{2+} increased in all tissues with the exception of leaves and flowers (Table 1). The source of Ca^{2+} during this period would be solely root uptake. This was unlike the accumulation of the other macronutrients where the source was a combination of translocation from the scales and root uptake. This is indicated by the decreasing scale content of the other macronutrients contrasted by increasing Ca^{2+} content in the scales (Figure 2).

It is interesting to examine the driving force for Ca^{2+} uptake during the preemergence period. Transpiration plays a dominant role in Ca uptake in plants in general [53, 54]. However, transpiration did not play a role during this period because the shoot had not yet emerged. Growth dilution of Ca is part of the driving force for uptake [55]. Prior to shoot emergence the shoot, daughter-bulbs, and roots are growing at the expense of stored carbohydrates in the scales, giving rise to new exchange sites in the newly forming cell walls of these organs. Since Ca required for these exchange sites is not transported from the scales, its source becomes the soil. During the preemergence period, the basal plate and scales decreased in dry matter, the H-bulb remained constant, the flower, scape, leaves, and daughter-bulbs increased in dry matter, and roots appeared and grew (Figure 2). Collectively, there was a 143% increase in dry matter of flower, scape, leaves, daughter-bulbs, and H-bulbs and a 170% increase in Ca content. These organs accounted for 1.29 mg of the 3.09 mg increase in Ca content of the total bulb. Ca content of developing roots accounted for an additional 0.53 mg of Ca. Uptake of the combined 1.82 mg of Ca can be accounted for by dilution caused by additional growth. The remaining increase of 1.27 mg Ca that occurred in the basal plate and scales is more difficult to explain. The combined dry matter of these two organs was diminished by 31% during this period. One possible explanation is consolidation of Ca^{2+} ion solutes into insoluble Ca^{2+} compounds such as phosphates, carbonates, and oxalates [55].

During the period from emergence to maturity, whole plant dry matter increased by 302%, while Ca^{2+} content increased by 1,244% as calculated using regression equations from Figure 4. This great upsurge in Ca^{2+} was not surprising since shoot mass increased to 41% of the plant by peak shoot dry matter (147 DAP). At this point, 78% of Ca^{2+} was in the shoot with the largest portion in the leaves (61%). This is probably due to the fact that leaf stomata support transpiration, a major driving force for passive Ca accumulation in plants. Nelson et al. [35] reported a relationship between Ca^{2+} uptake and transpiration in tulip. Döring [56] reported that the leaves and the perianth (modified leaves) have stomata on both the upper and lower surfaces. In addition, the scape is a green tissue with stomata (Niedziela, personal observation); however, specific Ca uptake is significantly lower in the scape. Concentrations of Ca at peak shoot formation for the leaves
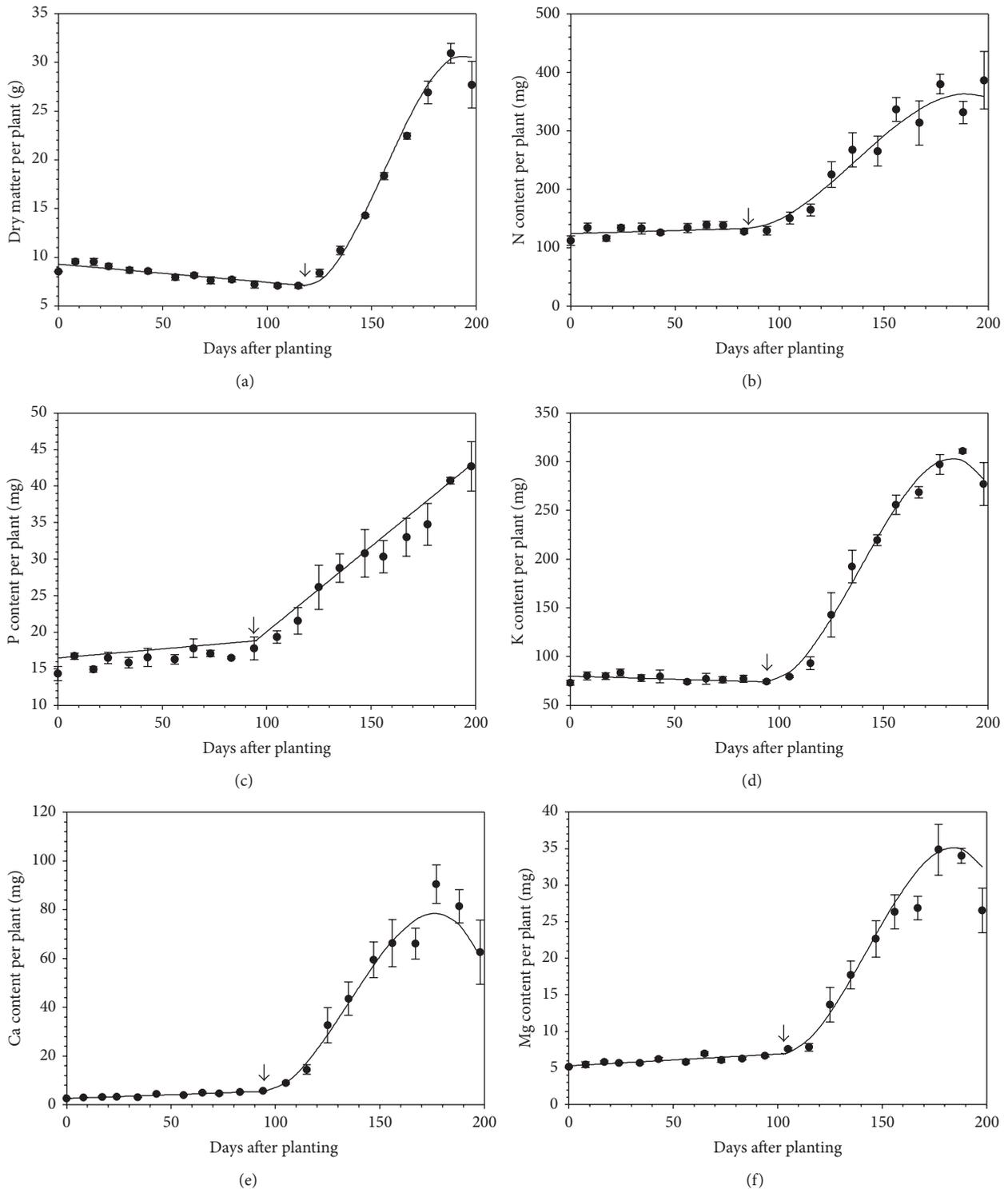
FIGURE 4: Changes in total dry matter (a) and N (b), P (c), K (d), Ca (e), and Mg (f) content from planting through final harvest in *T. gesneriana* "Paul Richter" during the growing season. For dry matter, N, K, Ca, and Mg, the arrow in each graph indicates the join points for the linear and cubic components of each curve. For P, the arrow in the graph indicates the join point for the two linear components of the curve. The equations for the above curves are as follows. (a) If $x \leq 117.7$, then $y = 9.287 - 0.0186x$ and if $x > 117.7$, then $y = 9.287 - 0.0186x + 0.0127(x - 117.7)^2 - 0.00011(x - 117.7)^3$. (b) If $x \leq 83.88$, then $y = 124.2 + 0.1040x$ and if $x > 83.88$, then $y = 124.2 + 0.1040x + 0.0598(x - 83.88)^2 - 0.00038(x - 83.88)^3$. (c) If $x \leq 94.73$, then $y = 16.48 + 0.0248x$ and if $x > 94.73$, then $y = 16.48 + 0.0248x + 0.2084(x - 94.73)$. (d) If $x \leq 93.26$, then $y = 79.89 - 0.0631x$ and if $x > 93.26$, then $y = 79.89 - 0.0631x + 0.0866(x - 93.26)^2 - 0.00064(x - 93.26)^3$. (e) If $x \leq 94.45$, then $y = 2.600 + 0.0308x$ and if $x > 94.45$, then $y = 2.600 + 0.0308x + 0.0318(x - 94.45)^2 - 0.00026(x - 94.45)^3$. (f) If $x \leq 102.1$, then $y = 5.291 + 0.0161x$ and if $x > 102.1$, then $y = 5.291 + 0.0161x + 0.0122(x - 102.1)^2 - 0.00010(x - 102.1)^3$.

TABLE 1: Concentrations (means ± s.e.) of N, P, K, Ca, and Mg in the eight organs of *T. gesneriana* "Paul Richter" at five stages of growth.

Plant organ	Macronutrients (mg·g^{-1} dry wt.)				
	N	P	K	Ca	Mg
(a) Planting (0 DAP, 17 Nov.)*					
Roots	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Basal plate	24.67 ± 0.84	4.13 ± 0.09	14.00 ± 0	1.00 ± 0.06	1.20 ± 0.00
Scales	11.00 ± 0.87	1.23 ± 0.09	7.33 ± 0.20	0.20 ± 0.00	0.50 ± 0.00
Daughter-bulbs	35.37 ± 1.30	6.80 ± 0.12	17.57 ± 0.90	1.73 ± 0.09	2.00 ± 0.00
H-bulb	27.37 ± 0.20	5.10 ± 0.29	22.10 ± 0.64	1.50 ± 0.12	1.30 ± 0.00
Leaves	43.80 ± 1.21	7.20 ± 0.29	24.60 ± 0.12	1.10 ± 0.00	1.73 ± 0.03
Scape	43.47 ± 2.68	7.70 ± 0.23	20.00 ± 0.64	1.03 ± 0.03	2.20 ± 0.06
Flower	43.90 ± 1.38	8.80 ± 0.06	28.70 ± 0.35	3.00 ± 0.00	2.33 ± 0.03
(b) Shoot emergence (94 DAP, 19 Feb.)					
Roots	46.97 ± 4.34	8.17 ± 1.27	22.37 ± 0.61	1.53 ± 0.09	1.50 ± 0.10
Basal plate	30.47 ± 0.26	5.57 ± 0.28	17.00 ± 0.68	2.57 ± 0.26	2.40 ± 0.15
Scales	9.73 ± 0.93	1.03 ± 0.12	6.83 ± 0.39	0.47 ± 0.03	0.60 ± 0.00
Daughter-bulbs	34.20 ± 1.41	5.47 ± 0.18	16.57 ± 0.83	2.50 ± 0.32	2.00 ± 0.25
H-bulb	33.80 ± 0.81	5.03 ± 0.27	21.97 ± 1.46	2.20 ± 0.12	1.60 ± 0.06
Leaves	44.67 ± 0.64	6.40 ± 0.47	20.37 ± 0.43	1.03 ± 0.03	1.77 ± 0.07
Scape	39.73 ± 0.81	6.00 ± 0.21	18.27 ± 0.42	1.43 ± 0.03	1.87 ± 0.07
Flower	43.80 ± 2.64	7.27 ± 0.14	22.30 ± 0.20	2.50 ± 0.12	1.80 ± 0.00
(c) Minimum plant dry matter (115 DAP, 12 Mar.)					
Roots	37.53 ± 3.03	8.53 ± 1.57	12.73 ± 1.29	1.87 ± 0.17	1.33 ± 0.14
Basal plate	22.13 ± 0.55	4.40 ± 0.35	11.17 ± 0.43	2.20 ± 0.10	1.43 ± 0.14
Scales	8.67 ± 0.73	0.83 ± 0.07	6.40 ± 0.56	0.97 ± 0.24	0.60 ± 0.06
Daughter-bulbs	29.03 ± 0.64	4.40 ± 0.10	15.20 ± 0.36	1.73 ± 0.18	1.33 ± 0.03
H-bulb	34.17 ± 2.89	4.77 ± 0.03	22.60 ± 0.98	3.37 ± 0.20	1.57 ± 0.03
Leaves	45.80 ± 2.00	4.83 ± 0.30	22.73 ± 0.28	4.43 ± 0.22	1.83 ± 0.03
Scape	44.43 ± 3.31	7.00 ± 0.21	30.50 ± 1.04	2.50 ± 0.20	1.93 ± 0.07
Flower	35.33 ± 3.72	5.43 ± 0.13	18.60 ± 0.38	2.00 ± 0.26	1.50 ± 0.00
(d) Peak shoot dry matter (147 DAP, 13 Apr.)					
Roots	25.50 ± 4.77	5.10 ± 0.96	10.37 ± 0.95	2.20 ± 0.25	1.77 ± 0.20
Basal plate	18.60 ± 0.61	2.60 ± 0.30	6.00 ± 0.35	3.80 ± 0.70	2.17 ± 0.13
Scales	8.73 ± 0.55	0.63 ± 0.09	7.23 ± 0.37	4.97 ± 0.35	1.73 ± 0.18
Daughter-bulbs	13.37 ± 1.53	1.97 ± 0.14	11.00 ± 0.61	0.57 ± 0.09	0.73 ± 0.07
H-bulb	14.70 ± 1.35	2.10 ± 0.23	13.87 ± 0.88	3.43 ± 0.09	1.17 ± 0.09
Leaves	32.60 ± 3.01	2.03 ± 0.20	27.43 ± 1.19	11.73 ± 1.28	2.90 ± 0.40
Scape	16.90 ± 0.81	2.87 ± 0.45	16.10 ± 0.93	3.67 ± 0.33	1.93 ± 0.03
Flower	32.00 ± 1.06	4.00 ± 0.47	22.20 ± 0.60	1.73 ± 0.13	1.73 ± 0.07
(e) Maturity (188 DAP, 24 May)					
Roots	7.20 ± 0.75	1.00 ± 0.15	4.53 ± 0.66	3.30 ± 0.29	1.00 ± 0.10
Basal plate	12.30 ± 0.91	1.07 ± 0.12	3.47 ± 0.12	6.53 ± 0.35	2.83 ± 0.12
Scales	10.07 ± 0.39	0.43 ± 0.03	1.43 ± 0.09	12.57 ± 0.03	2.50 ± 0.17
Daughter-bulbs	11.17 ± 0.71	1.43 ± 0.03	9.73 ± 0.20	0.80 ± 0.06	0.87 ± 0.03
H-bulb	11.73 ± 1.03	1.47 ± 0.09	10.30 ± 1.01	1.40 ± 0.38	0.90 ± 0.12
Leaves	8.60 ± 0.57	0.40 ± 0.10	19.47 ± 1.64	26.17 ± 0.09	3.27 ± 0.12
Scape	3.73 ± 0.37	0.30 ± 0.10	9.83 ± 0.75	8.50 ± 0.64	2.17 ± 0.14
Flower	15.70 ± 2.01	1.97 ± 0.09	22.00 ± 0.79	2.77 ± 0.27	2.60 ± 0.21

*DAP: days after planting.

and scape were 11.7 and 3.7 mg·g^{-1} dry matter, respectively (Table 1). Lower Ca uptake in the scape may be due to the lower specific surface area of the round scape organ as compared to the laminar shaped leaves, the possibility of a lower density of stomata on the scape as compared to leaves, or a combination of these two factors. No references were found concerning the density of stomata on the scape. The tunic and all of the scales of the tulip have stomata, with the exception of the innermost surface of the innermost scale of the tulip [49]. However, scale stomata would contribute little to Ca uptake since these are subterranean organs.

Potassium uptake follows a different pattern than the other nutrients during the initial linear phase of whole plant nutrient content. Potassium decreased by 7% between planting and join point at 93 DAP, while all other nutrients increased during this period. This clarifies the report by van der Boon [19] that there was little response to K fertilization during bulb production, at least prior to emergence in our study. However, the 238 mg uptake of K per plant after emergence observed in our study, between 93 and 188 DAP (maturity), is in contrast to van der Boon's observation of little need for K fertilization. Ramírez-Martínez et al. [57] reported there is heavy partitioning of K into newly forming bulbs. This indicates a significant postemergence requirement for K. The implication from a low K fertilization response coupled with a sizeable K bulb requirement is that the tulip plant is a very efficient accumulator of K. This suggests a low C_{min} value, the bathing solution concentration where influx of a given nutrient equals efflux. A low C_{min} value enables the plant to achieve a net K uptake at soil solution concentrations supported by mineralization of soil minerals and organic matter. Claassen and Jungk [58] reported average K soil solution C_{min} values of 2-3 μmol·L^{-1} for soil-grown plants, while Caassen and Barber [59] reported K C_{min} values of 1-2 μmol·L^{-1} for young corn plants. The low requirement for K fertilization is further supported by the low sufficiency concentration value of 0.1 to 0.5% K in bulbs at harvest reported by Hansen [16] and Tissot [24]. There are strong implications from these results relative to fertilization practices for the tulip. The main one is that K fertilization is not needed at planting and only a moderate application is beneficial at emergence.

It is noteworthy that the join points in the graphs for accumulation of all five nutrients preceded the join point for biomass accumulation by 16 to 34 days (Figure 4). This indicates that nutrient accumulation could be an effective parameter for modeling growth in tulip. This would be particularly true for N since the join point for N accumulation preceded net dry matter accumulation by 34 days, the longest period for any nutrient (Figure 4).

5. Conclusions

Moderate uptake of N, P, Ca, and Mg by tulips occurred from root appearance until near shoot emergence from the soil, while K content decreased slightly. During this period, relative uptake of Ca was considerably higher than that of the other nutrients. A substantial increase in uptake began prior to shoot emergence for N; at about the same time as shoot emergence for P, K, and Ca; and following shoot emergence for Mg. All of these upsurges preceded a similar rise in dry matter. Since the transition (join point) from the initial to the accelerated uptake phases of N, P, K, Ca, and Mg occurred prior to initial dry matter increase, the accumulation of these nutrients (N in particular) could be used to predict changes in tulip plant growth.

Major sources for dry matter and nutrients throughout the entire annual bulb replacement cycle included scales (dry matter and nutrients), soil solution (nutrients), and photosynthesis in shoots (dry matter). Shoots as well as roots (dry matter and nutrients) became sources after their senescence. Major sinks for dry matter and nutrients consisted of daughter- plus H-bulbs throughout the cycle, shoots up to peak shoot dry matter (147 DAP), and roots up to bulb maturity (167 DAP).

There are also practical fertilization applications from this study. Although some N, P, and Mg were taken up prior to emergence, the bulk of the uptake occurred after emergence. These data suggest applying these nutrients as a split application with a smaller application at planting and a larger application at or shortly after emergence. Since there was a decline in K content up to emergence with net uptake restricted to postemergence, a K fertilizer could be applied only at or shortly after emergence. Calcium was taken up throughout the experiment emphasizing the need to maintain optimum soil levels through application of lime for pH maintenance.

Disclaimer

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.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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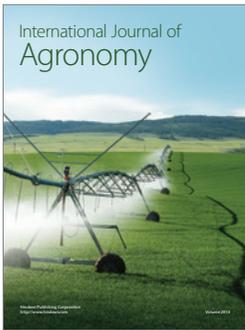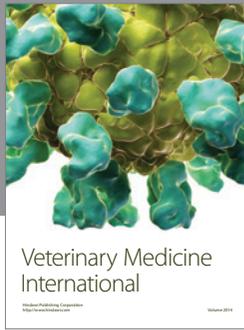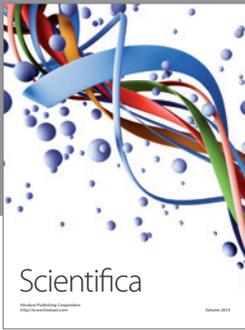
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