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EFFECTS OF SIMULATED LEAF HERBIVORY ON GROWTH, FLOWER QUALITY AND BULB YIELD OF THE COMMON HYACINTH AND THE LILY

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ABSTRACT

Ornamental geophytes such as flower bulbs are essentially grown for flower production or as landscaping plants for aesthetic purposes. The specific effects of leaf herbivory in these plants are poorly documented. Studies were therefore conducted at the University of Sussex, UK to determine the effects of leaf herbivory on the growth and development of these plants using the common hyacinth and the lily as test plants. Results revealed that the growth of defoliated hyacinth plants was always reduced whilst flowering was least affected. Both complete and partial defoliation treatments were detrimental to the growth and development of this flower bulb. However, plants subjected to complete defoliation suffered more reductions in growth and yield parameters than those that were partially defoliated. The lily, however, responded positively to complete leaf herbivory especially if the damage was exerted at the beginning of their growth. The completely defoliated lily plants did not only exhibit compensatory regrowth of leaves, but they also had higher values of chlorophyll content, photosynthetic rate and stomatal conductance than the undefoliated control.

Keywords: Herbivory, common hyacinth, the lily, growth and development, defoliation.

1. INTRODUCTION

Herbivory maintains species diversity in plant communities by removing species that compete intensively for resources, and this may result in coexistence of other competitively inferior species (Burkepile and Duffy, 2009). In general, the growth and developmental processes of plants interact with the environmental factors such as pest and disease infestation, drought stress, nutrient deficiencies, light intensity and relative humidity to influence the level of productivity or quality of that plant. In situations where species are exposed to herbivory, the growth of the plants may be limited by factors such as the intensity by which the herbivore consumes the plant species and the availability of growth resources present in that area. Rockwood and Lobstein (1994) reported that in plants, herbivory may decrease growth, increase probability of mortality or reduce the leaf area available for photosynthesis. Marquis *et al*. (1997) also observed that when a plant loses its tissues or organs as a result of a stress, they generally use their stored compounds to replace the photosynthetic tissues lost by browsing, and for future support of biosynthesis for growth or other functions. Factors such as timing, type and extent of herbivory as well as the availability of resources in the environment to support growth (Rosenthal and Kotanen, 1994) may also influence plants' response to herbivory.

One important aspect of herbivory is defoliation that is leaf removal. During plant production, defoliation may be caused by herbivores, pests or diseases. In most cases, however, defoliation is caused by bad weather conditions. In general, physiological disorders resulting from unfavourable environmental conditions such as hail or frost may cause either a complete failure of flowering, or contribute in one way or the other to reduce growth in plants. Plants may respond to herbivory by tolerance, induced defense or by compensation. Gadd *et al.* (2001) defined tolerance as the ability of a plant to withstand and survive damage whilst induced defense involves plant's ability to reduce the rates of herbivory. Similarly, according to these authors, compensation involves the increase in growth of the plants after loss of tissues to herbivores. Wien *et al.* (2004) subjected onion to 50% leaf herbivory and reported that the additional growth of leaves coupled with their increased photosynthetic rate suggested that leaf loss due to hail

storms or diseases may have less impact on yield as long as the damage occurs early enough in the plant's life so that compensatory growth can occur and the disease-causing organism is controlled. Endan *et al*. (2006) also stated that defoliation resulted in some reserved food material in the stems being redirected to the shoot region for new growth. Similarly, studies conducted by Marquis (1984) revealed that heavy defoliation caused a reduction in yield whilst Paige and Whitham (1978) maintained that under certain conditions, herbivory could enhance yield. It is, however, generally known that, after defoliation, plants may use the reserves stored in their tissues for regrowth of vegetation (Rockwood and Lobstein, 1994), and this normally depletes the stored reserves and negatively affects reproduction.

The common hyacinth, *Hyacinthus orientalis* and the lily (*Lilium longiflorum*) are horticulturally important plants cultivated mainly for the production of cut flowers, as potted plants or as landscaping plants. These species occupy a significant position within the world-wide production and trade in cut flowers. Available literature shows that information on herbivory on plant species such as grasses, timber trees and some temperate crops (Mendoza *et al.*, 1987) are known, but the specific effects of herbivory or defoliation in ornamental geophytes such as hyacinth and the lily are poorly documented. In general, plant growth and productivity are dependent not only on photosynthesis, but also on the integrated processes of allocation, accumulation and utilisation of photoassimilated carbon, which collectively control the carbon budget of the plant. The relationships between assimilate supply and demand can be studied by removing leaves and hence the source of photoassimilates for the plant. Bulbs of the common hyacinth and the lily were therefore subjected to various levels of simulated leaf herbivory, with a view to investigating into the effects of these treatments on the growth, development and yield of these plants. Understanding the physiological mechanisms of these bulbs to cope with herbivory in relation to their growth as well as flower and bulb production would not only allow growers to produce good quality bulbs but will also allow breeders to develop efficient strategies to screen available germplasm or lines of these bulbs to identify genotypes that could be resistant to, or escape damages caused by herbivores, diseases or drought.

2. MATERIAL AND METHODS

2.1 EXPERIMENTAL DESIGN AND PLANTING

Bulbs of 55 g (hyacinth) or 40 g (lily) average mass weight were planted in plastic pots. The pot used for planting had a capacity of 0.01 m^3. Four bulbs per pot were planted, using compost and perlite mixture in a ratio of 2:1 by volume as the planting medium. The units were arranged randomly on greenhouse benches in a randomized complete block design. At 14 weeks after planting (in the case of hyacinth) either all leaves (1^{st} 100% defoliation) or half of each leaf on each plant (1^{st} 50% defoliation) were manually removed. Similar leaf removal activities were carried out at 18 weeks after planting (2^{nd} 100 and 50% defoliation). In the case of the lily, defoliation was done by shoots removal at 3 and 5 weeks after planting for first and second shoot removal treatments, respectively. In this case, either the whole shoot or half the shoot system of each plant was artificially removed (100 and 50% shoot removal, respectively).

2.2 METHODS OF DATA COLLECTION

Leaf length was measured as length of the leaf from the base to the leaf tip. Leaf width was also recorded as the growth in girth at the middle section of the leaf where it was broadest. Total leaf length and width were recorded as the sum of all the individual leaf lengths and widths for one particular plant. Total leaf area was calculated from leaf length and width values as described below.

2.2.1 DETERMINATION OF LEAF AREA

The method used here was modified from the procedure employed by Darkwa (2008). Leaves of 40 plants from both species grown in the greenhouse were obtained through destructive sampling. The product of the length and broadest part of the leaf (width) was recorded as measured leaf area (MLA) for all these leaves. Then, outlines or shapes of these leaves were sketched on A-4 papers, and cut out with a pair of scissors. These pieces of papers were weighed separately using an electronic weighing balance and the weight of each piece of paper was recorded as leaf paper weight (LPW). The lengths and widths of three of such A-4 papers were multiplied in order to get areas of these A-4 papers, and the average area of the three A-4 papers was divided by the average weight to get a constant value. This constant value was multiplied by the weight of each piece of paper (LPW) obtained by cutting out the leaf outlines and the value recorded as the leaf true area (LTA). A graph of LTA was plotted against MLA and a line of best fit was made to pass through the points. The gradient of this line was taken as the leaf area constant value for each species as shown in Figure 1. Thus for instance, the leaf area constant value for hyacinth was 0.9543 whilst that of lily was 0.8921. Therefore in the case of hyacinth, the leaf area (LA) for one particular leaf was

calculated as MLA x 0.9543, and the total leaf area for the whole plant is the sum of (MLA x 0.9543) of all leaves on one particular plant. In the lily, four leaves from different positions of each plant that is lower part of the shoot, middle section, towards the top of the plant and at the shoot tip were considered in the computation of (MLA x 0.8921), and the average value was obtained. Thus the total leaf area for the lily was calculated as the average of (MLA x 0.8921) x total number of leaves on the plant at that particular time.

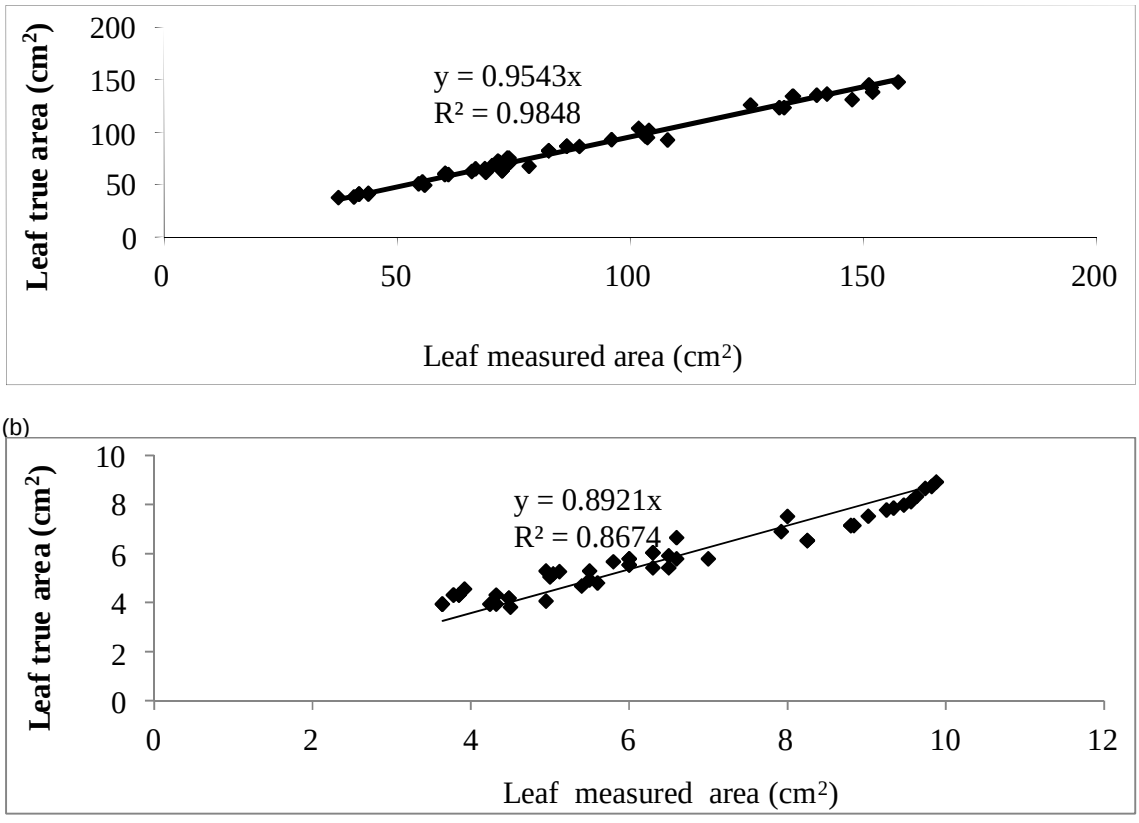


Fig 1: Measurement of leaf area constant for (a) the common hyacinth, and (b) the lily.

2.2.2 INFLORESCENCE CHARACTERISTICS

Inflorescence characteristics were measured in terms of inflorescence length, inflorescence diameter, inflorescence stalk diameter, peduncle length and number of florets. Inflorescence height was recorded as the distance from the soil surface level of each hyacinth plant to the tip of the inflorescence. In the lily, it was measured as the distance from soil surface to the tip of the tallest flower. In hyacinth, inflorescence length was taken as the inflorescence height minus the length of the stalk holding the inflorescence. Peduncle length or the length of the flower stalk was measured in the lily as the length from the point of attachment of the flower from the shoot to the base of the flower. Inflorescence stalk diameter was measured in hyacinth as the growth in girth of the stalk holding the inflorescence that is, it was a measure of thickness of the inflorescence stalk. Similarly, inflorescence diameter was recorded as a measure of inflorescence thickness before the opening of the florets, and this was measured as the growth in girth of the inflorescence in hyacinth. All these parameters were recorded using a ruler but the number of florets was recorded by counting them after they were fully opened.

2.2.3 BULB FRESH MASS

The fresh mass of bulbs was recorded with an electronic weighing balance as the mass of the bulbs prior to planting. At harvest, gain in mass weight was simply measured as the harvest mass less the initial fresh mass at planting.

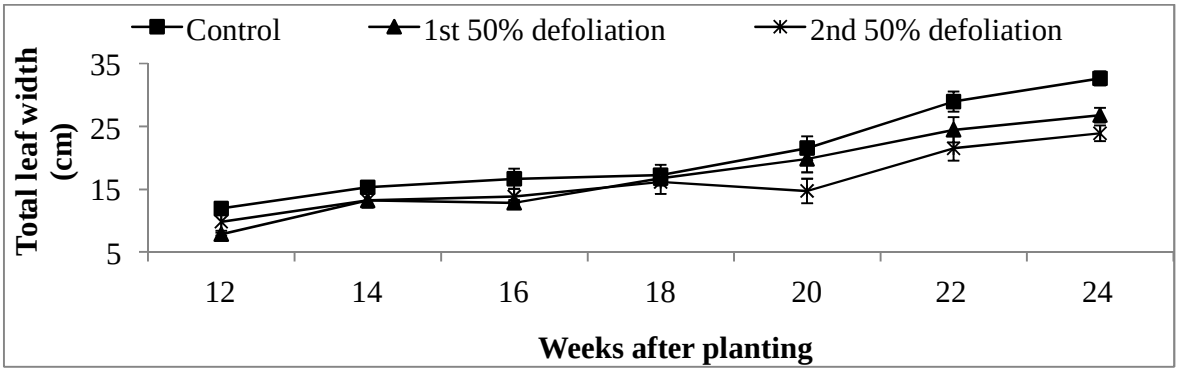
2.2.4 CHLOROPHYLL MEASUREMENT AND PHOTOSYNTHETIC CHARACTERISTICS

Leaf chlorophyll concentration was measured with a SPAD chlorophyll meter (Minolta SPAD-502) that gives a relative index of leaf concentration. The instrument was first calibrated and clipped to three points that is the lower part, the middle portion and towards the tip of the leaf whose chlorophyll content was desired. In hyacinth, the first three leaves from outside were considered whilst in the lily, six leaves from different positions of the plant were involved, that is two from the lower part of the shoot, two from the middle section and two from the topmost part of the shoot system of each plant. Averages were computed for each plant prior to the analysis of this data. Using the infrared gas analyser (Ciras-1 PP Systems), photosynthetic rate and stomatal conductance were determined between the hours of 12:00 and 15:00 at the prevailing solar radiation. A known area from the leaves used for chlorophyll measurement was clipped with the cuvette of the IRGA, and measurements were made once the leaves had acclimatised to the conditions.

3. RESULTS

3.1 HYACINTH

Both the 50 and 100% defoliation treatments were detrimental to plant growth as both treatments reduced leaf growth because plants whose leaves were removed as a result of defoliation had lower leaf area values as compared to those from the control (Figs 2 and 3). Leaf regrowth ability decreased with increased severity of defoliation because bulbs subjected to 50% leaf removal produced plants with generally higher leaf area values than those subjected to the 100% treatment. Thus at 24 weeks after planting, total leaf area values of plants belonging to the control, 1st 50% defoliation and 2nd 50% defoliation were 679.02 cm^2, 527.23 cm^2 and 377.41 cm^2, respectively, whilst values for the 1st and 2nd 100% defoliations were 408.22 cm^2 and 230.50 cm^2, respectively. Plants subjected to either the 50 or 100% leaf removal also had a reduction in leaf chlorophyll concentration because chlorophyll content values of defoliated plants were reduced relative to those from the control (Fig 4). In general, the 100% leaf removal treatment reduced chlorophyll content more than did the 50% defoliation especially at 2-3 weeks after defoliation. In general, all defoliated plants, later recovered in chlorophyll development at 24 weeks after planting. Plants whose leaves were completely removed (100%) at 14 weeks after planting recorded slightly but significantly higher values of inflorescence height and length than those from the control at 22 weeks after planting (Fig 5). However, plants from the 50% defoliation treatments had inflorescence height and length values that were not significantly different from the control. Moreover, both the 50 and 100% defoliation treatments reduced fresh mass of bulbs at harvest (Fig 6) but the latter had a more detrimental effect on this parameter than did the former. The pattern of distribution exhibited by bulb fresh mass at harvest followed a similar trend as that of leaf area.



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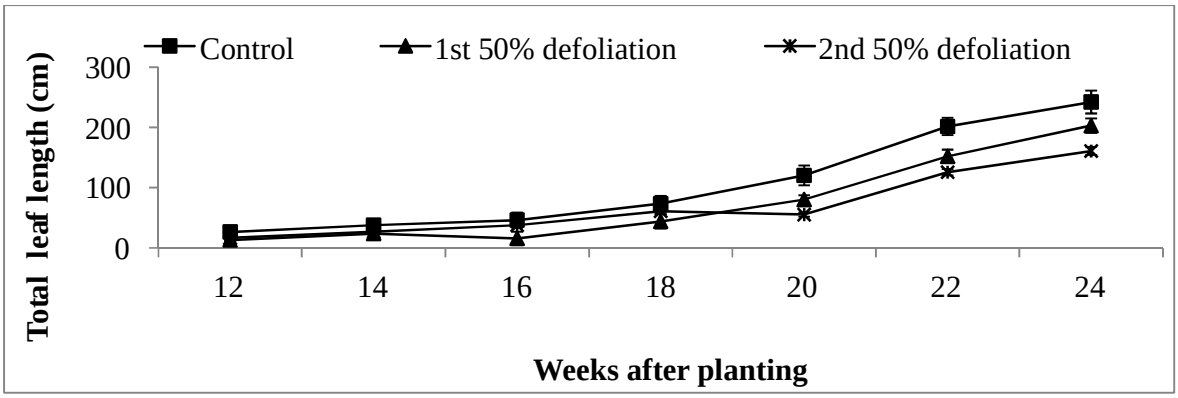

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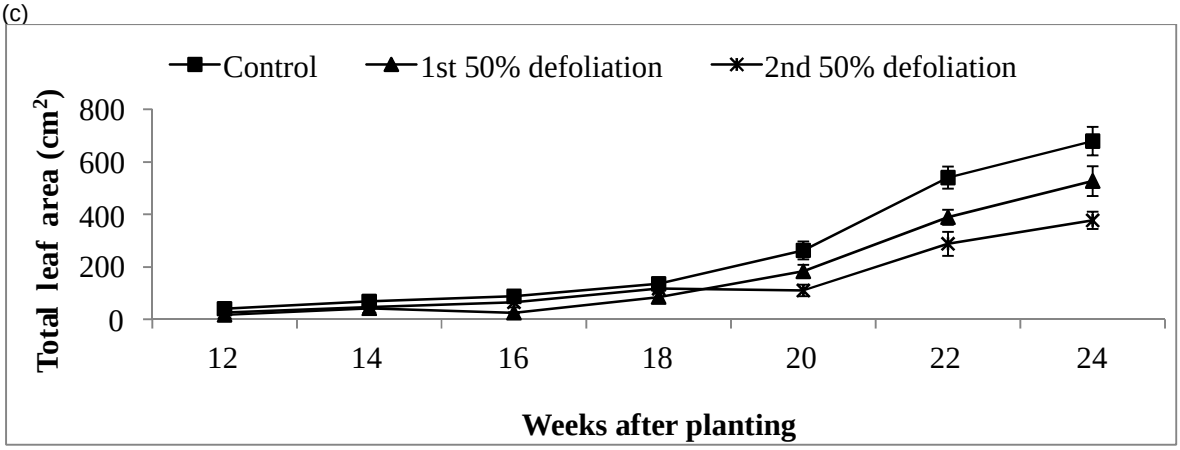
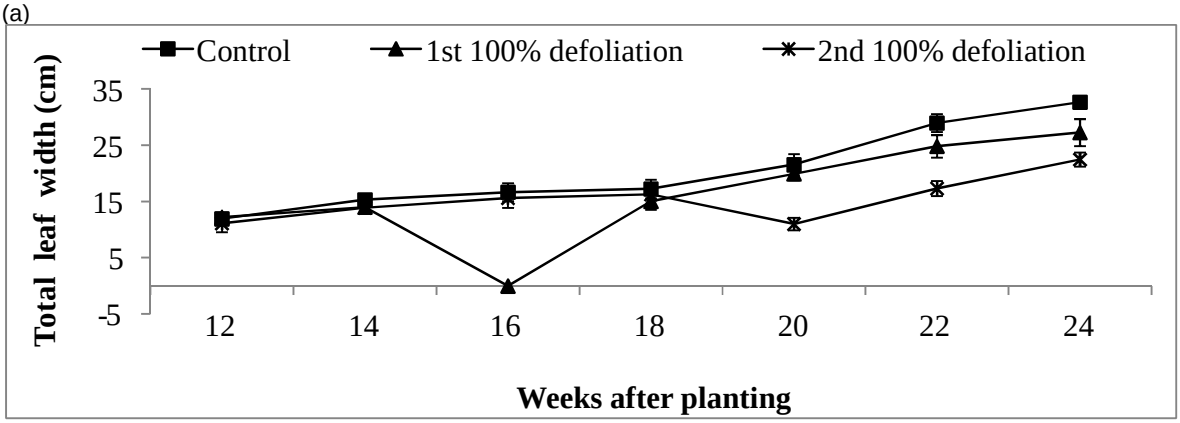


Fig 2: Influence of partial (50%) defoliation on leaf growth: (a) leaf width, (b) leaf length and (c) leaf area of the common hyacinth. Bars represent means ± SE of four replicates. Half of all leaves on each plant were manually removed at 14 and 18 WAP, respectively, representing the 1st and 2nd 50% defoliations.

(a)



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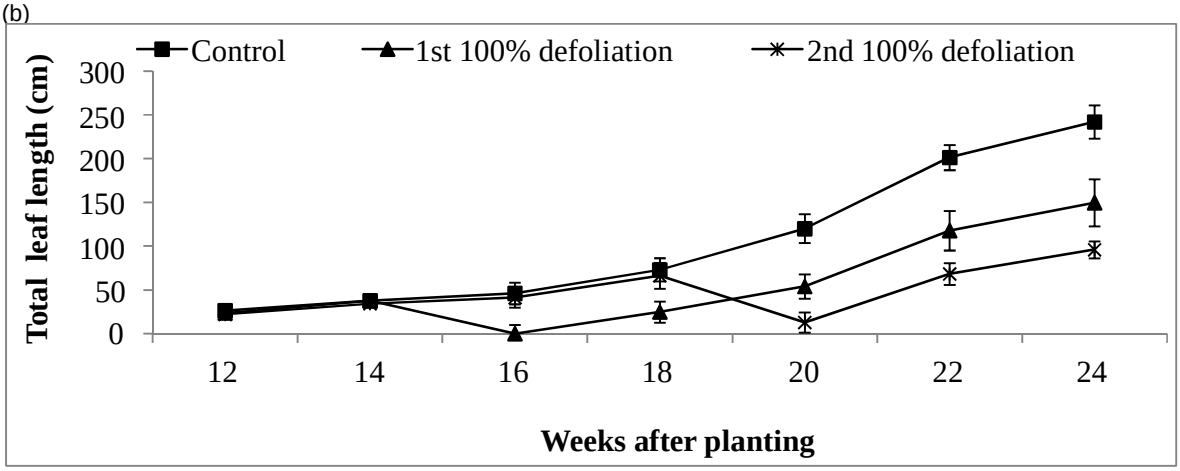

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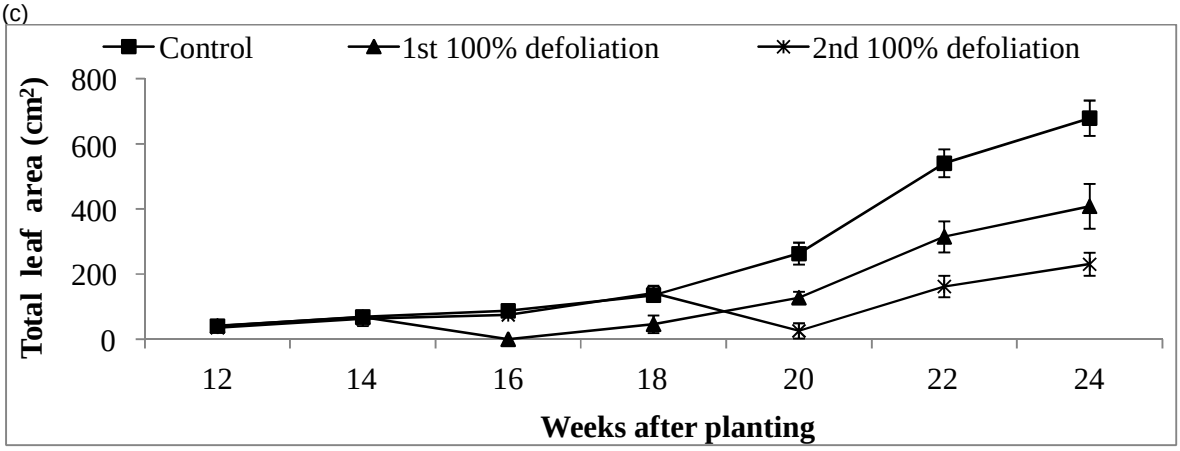
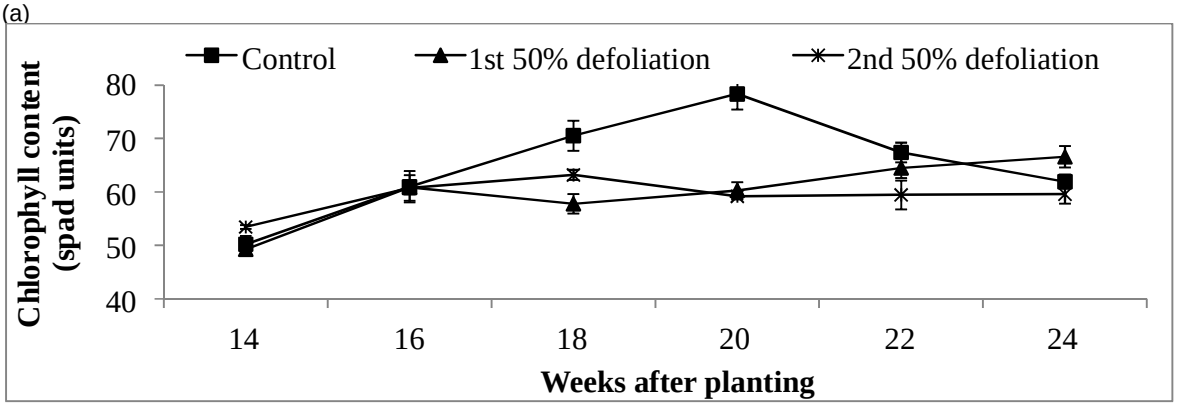


Fig 3: Influence of complete (100%) defoliation on leaf growth: (a) leaf width, (b) leaf length and (c) leaf area of the common hyacinth. Leaf removal was conducted at 14 and 18 WAP, respectively, for the 1st and 2nd 100% defoliation respectively. The error bars represent means ± SE of four replicates.

(a)



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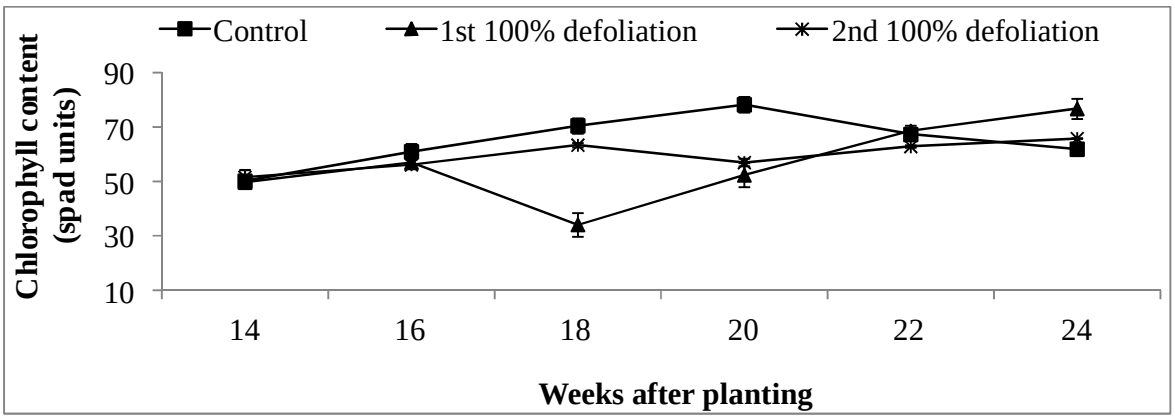
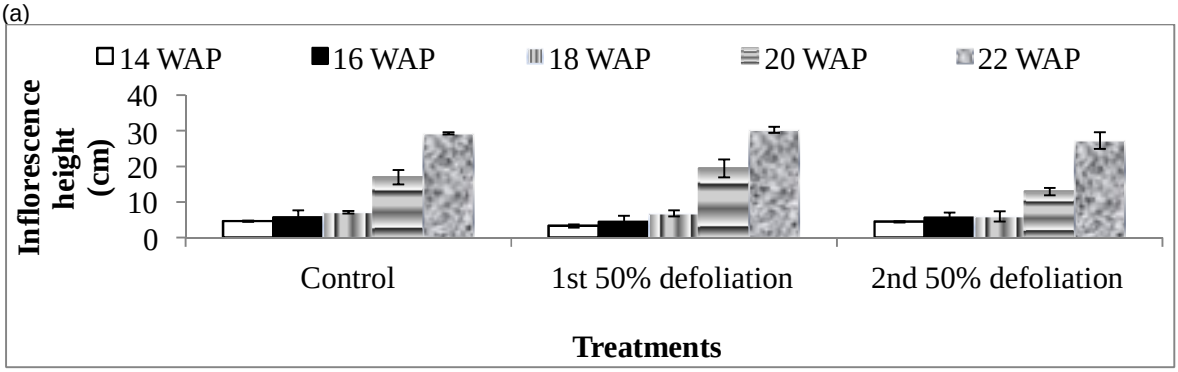


Fig 4: Influence of (a) partial (50%), and (b) complete (100%) defoliations on chlorophyll content of the common hyacinth. Three sections (lower portion, middle part and towards the tip) of each leaf in a plant were considered for measurement. Bars represent means ± SE of four replicates.

(a)



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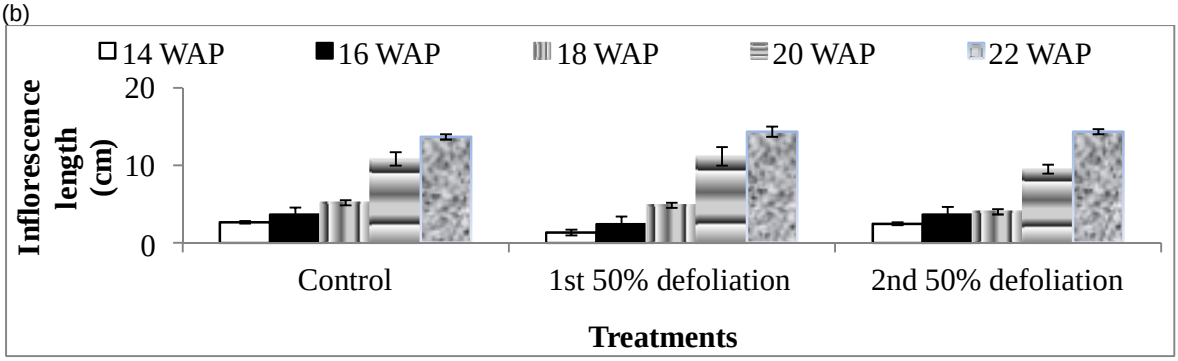

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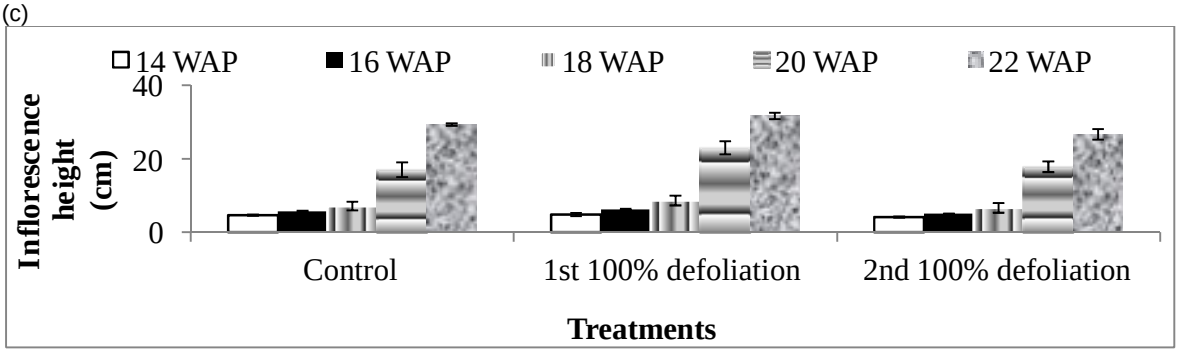

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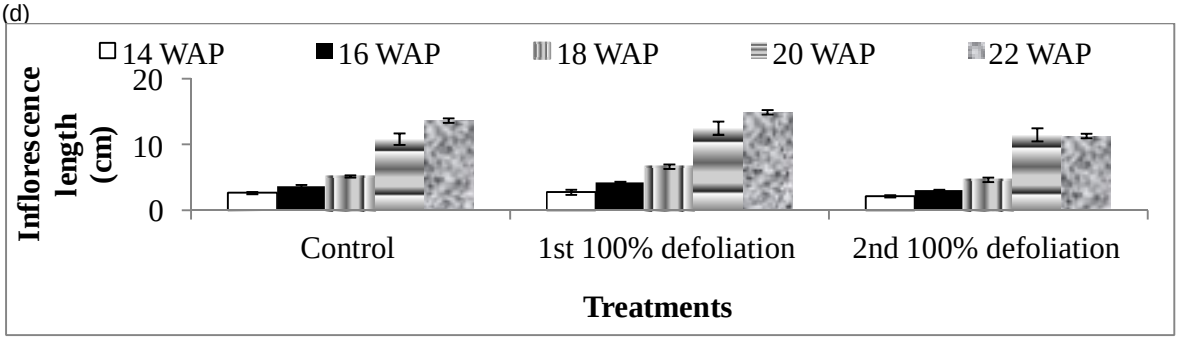
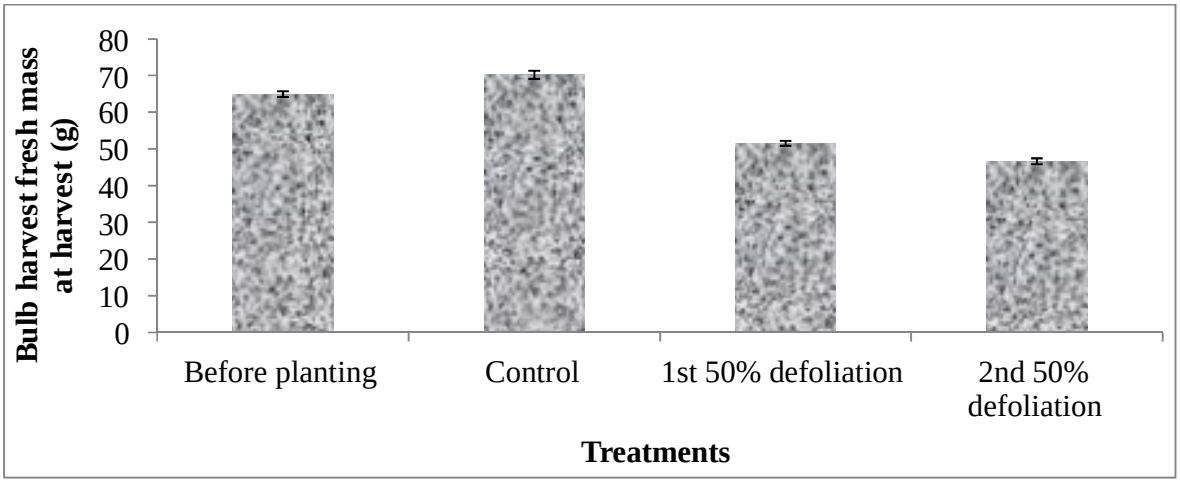


Fig 5: Influence of partial defoliations (a) on inflorescence height, and (b) inflorescence length; Influence of 100% defoliation on (c) inflorescence height, (d) inflorescence length, of the common hyacinth. Bars represent means ± SE of four replicates.

(a)



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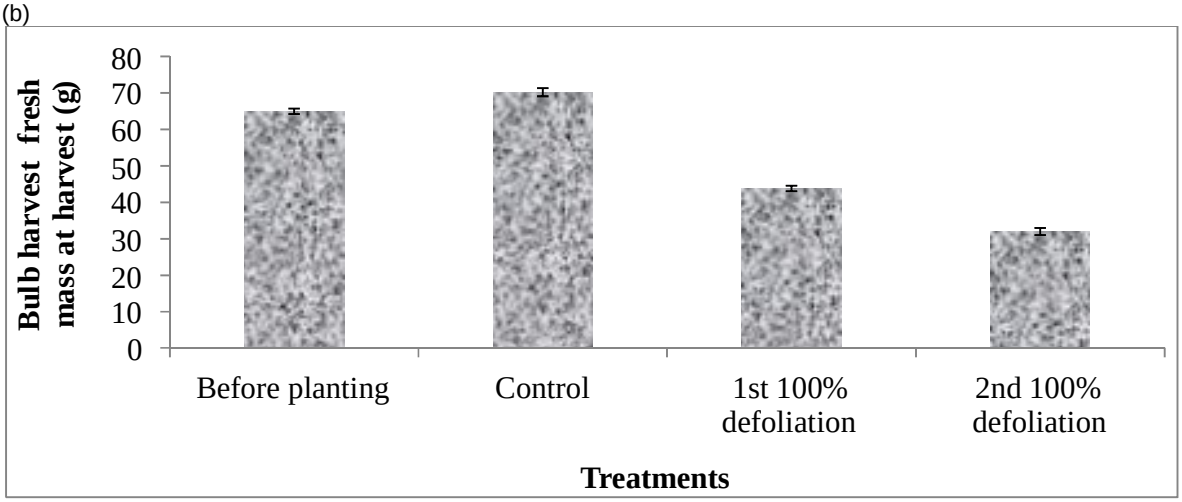
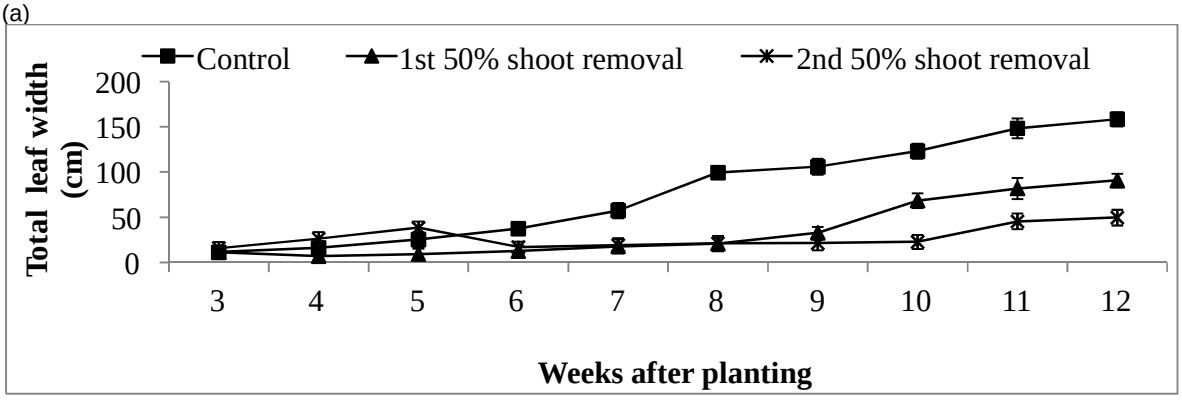


Fig 6: Influence of (a) partial defoliation and (b) complete defoliation on fresh weight at harvest of hyacinth bulbs. Bars represent means ± SE of four replicates.

3.1.2 THE LILY

Response of the lily to 50% shoot herbivory, in terms of vegetative regrowth (Figs 7–8) was similar to that of 50 % leaf herbivory of hyacinth. Results from the 100 % shoot removal treatment, however, was quite different from those observed in hyacinth because lily plants from the 1st 100 % shoot removal regime produced leaves with high regrowth capacity such that their total leaf length and area of such leaves at 12 weeks after planting were similar to those of the control plants (Fig 8). Similarly, chlorophyll content, photosynthetic rate and stomatal conductance of plants subjected to the 1st 100 % shoot removal treatment were all significantly higher than those of the control (Figs 9 -10). These parameters, when measured from plants belonging to the 2nd 100 % shoot removal regime, were lower in magnitude relative to those of the control. Gain in bulb fresh weight (Fig 11) also followed a similar trend as those of leaf herbivory of hyacinth.

(a)



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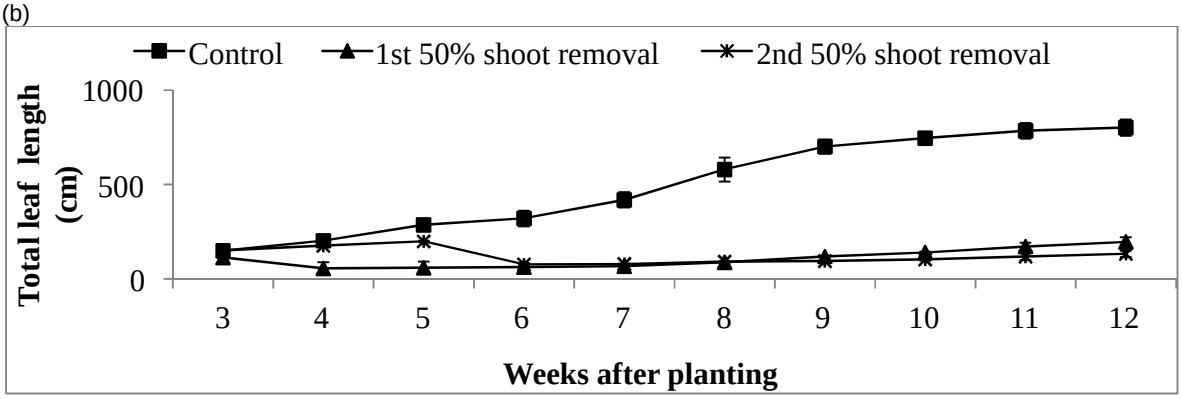

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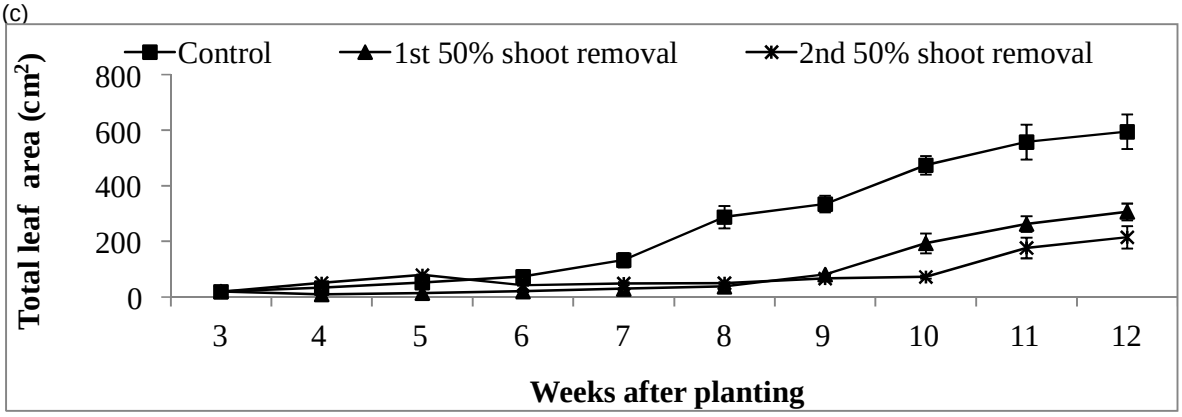
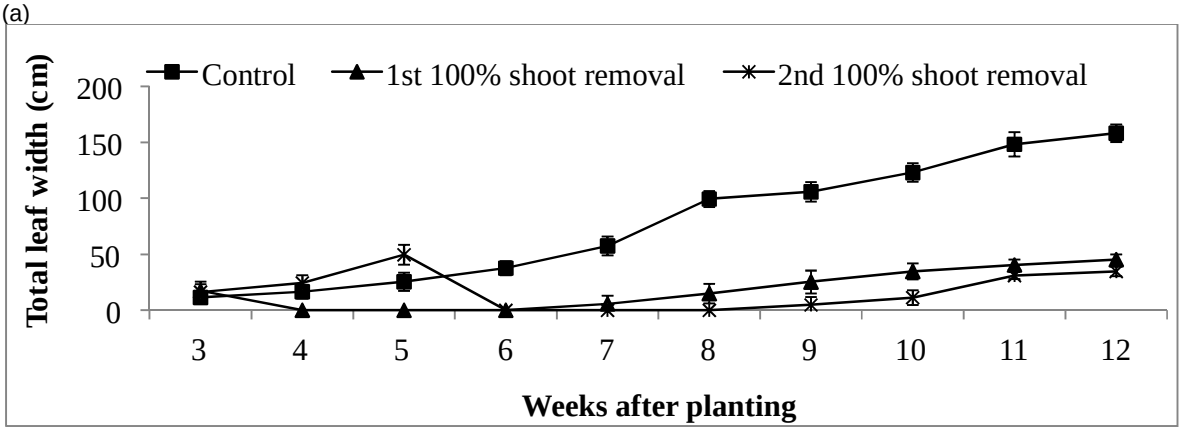


Fig 7: Influence of partial (50%) shoot removal on leaf growth: (a) leaf width, (b) leaf length and (c) leaf area of the lily. At 3 and 5 weeks after planting (WAP), half the shoots system of each plant was manually removed representing 1st and 2nd shoot removal respectively. Error bars represent means ± SE of four plants.

(a)



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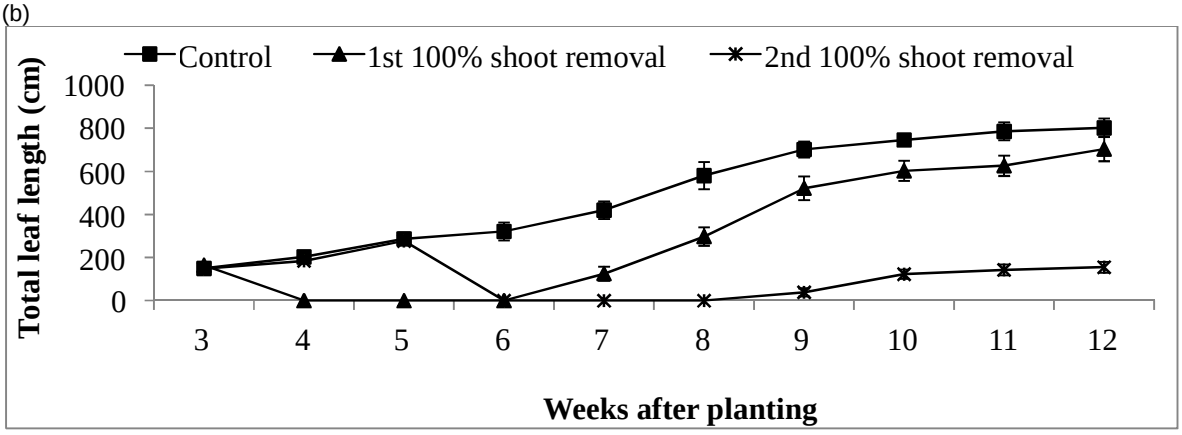

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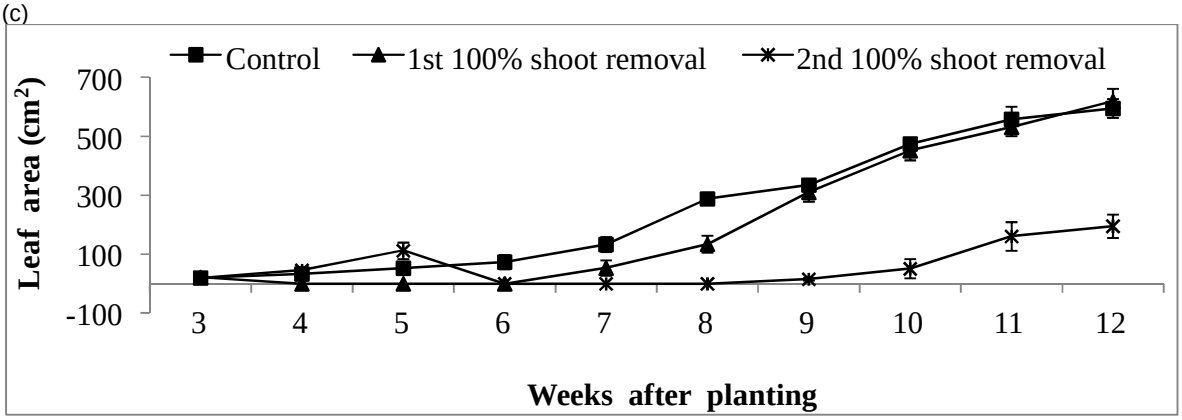

Fig 8: Influence of complete (100%) shoot removal on leaf growth: (a) leaf width, (b) leaf length and (c) leaf area of the lily. At 3 and 5 WAP, the whole shoots system of each plant was manually removed representing 1st and 2nd shoot removal respectively. Error bars represent means ± SE of four plants.

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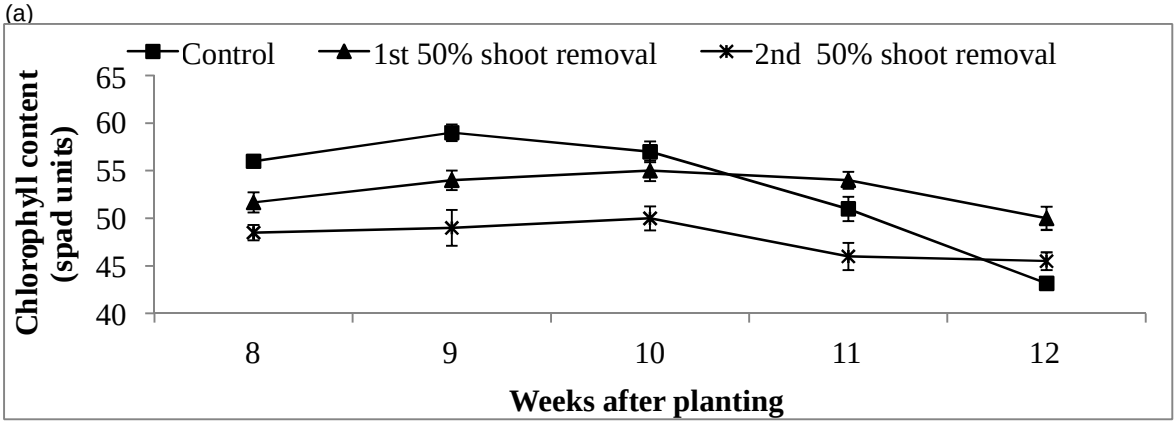

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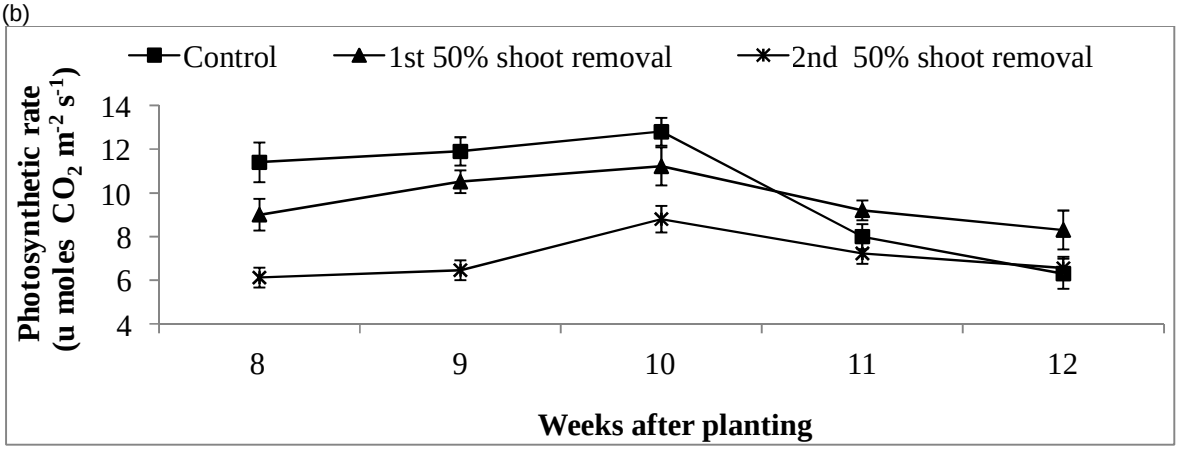

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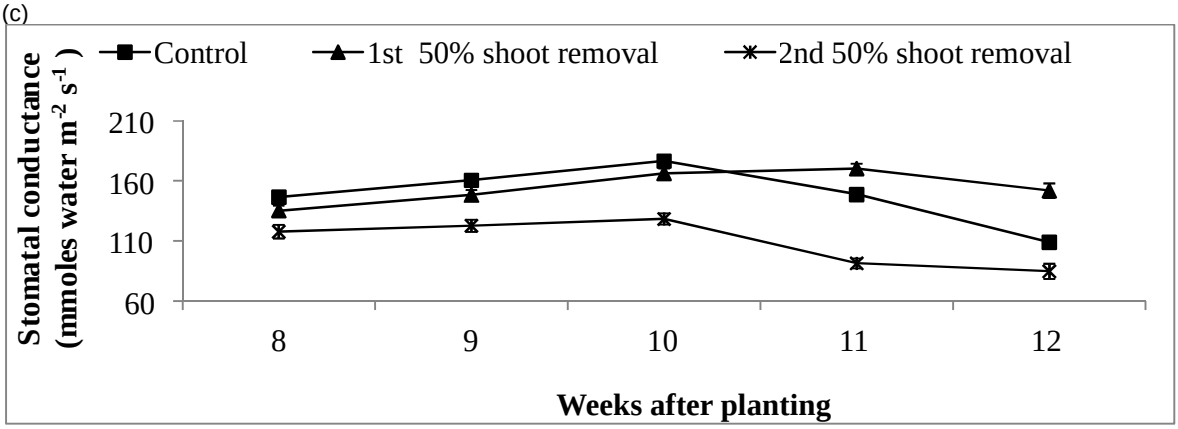
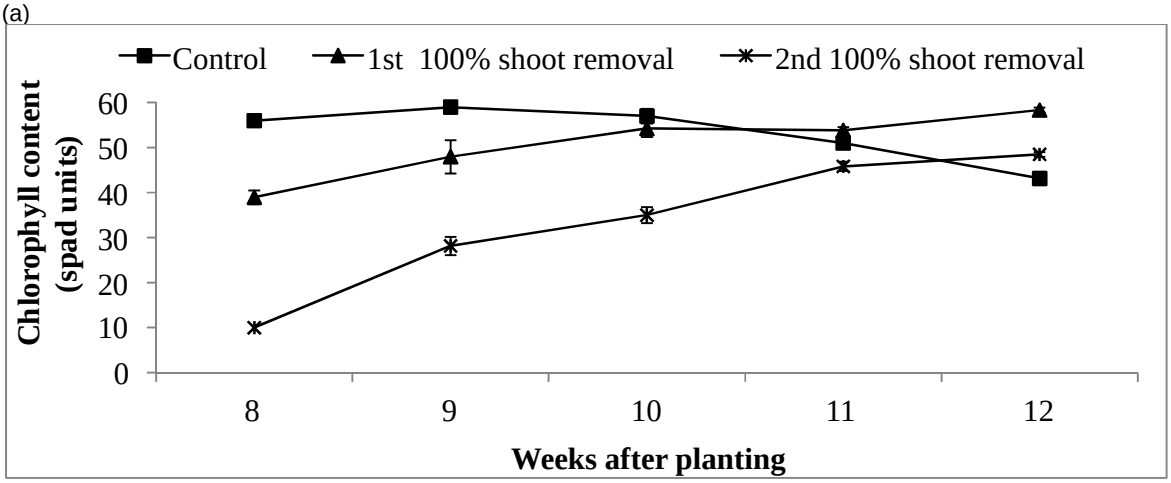


Fig 9: Influence of partial (50%) shoot removal on: (a) chlorophyll content, (b) photosynthetic rate, and (c) stomatal conductance of the lily. Error bars represent means ± SE of four plants.

(a)



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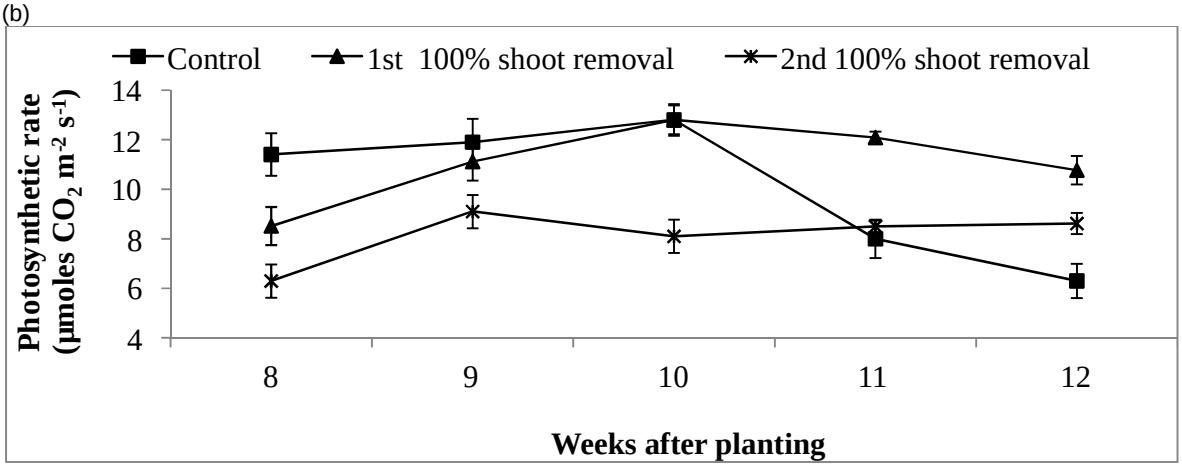


(c)

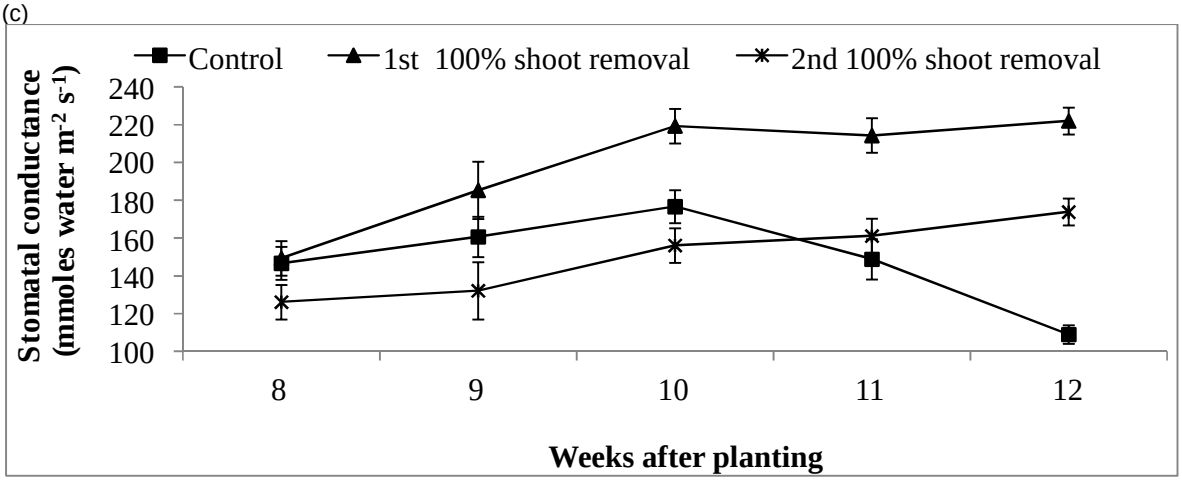
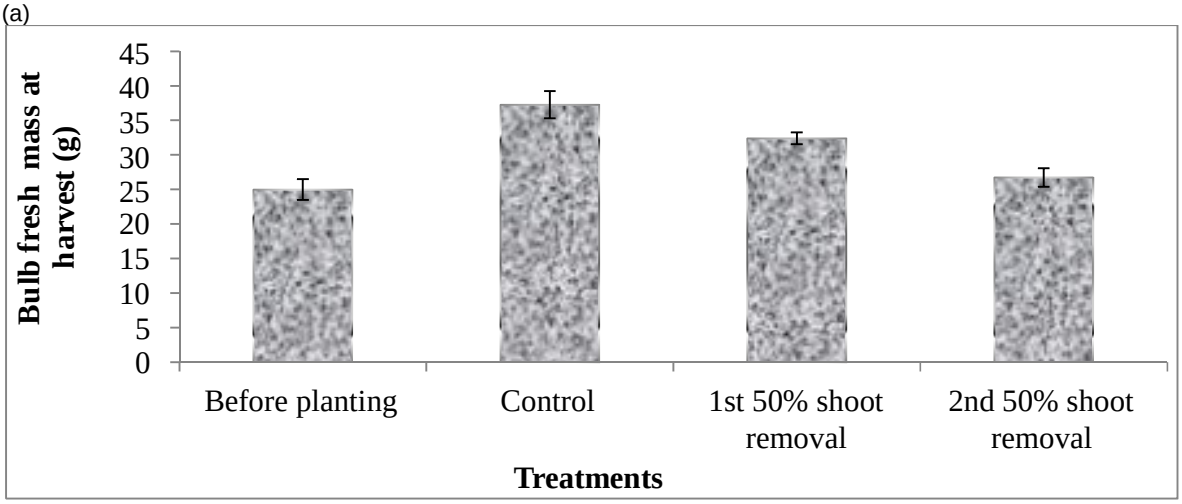


Fig 10: Influence of complete (100%) shoot removal on: (a) leaf chlorophyll content, (b) photosynthetic rate, and (c) stomatal conductance of the lily. Error bars represent means ± SE of four plants.

(a)



(b)

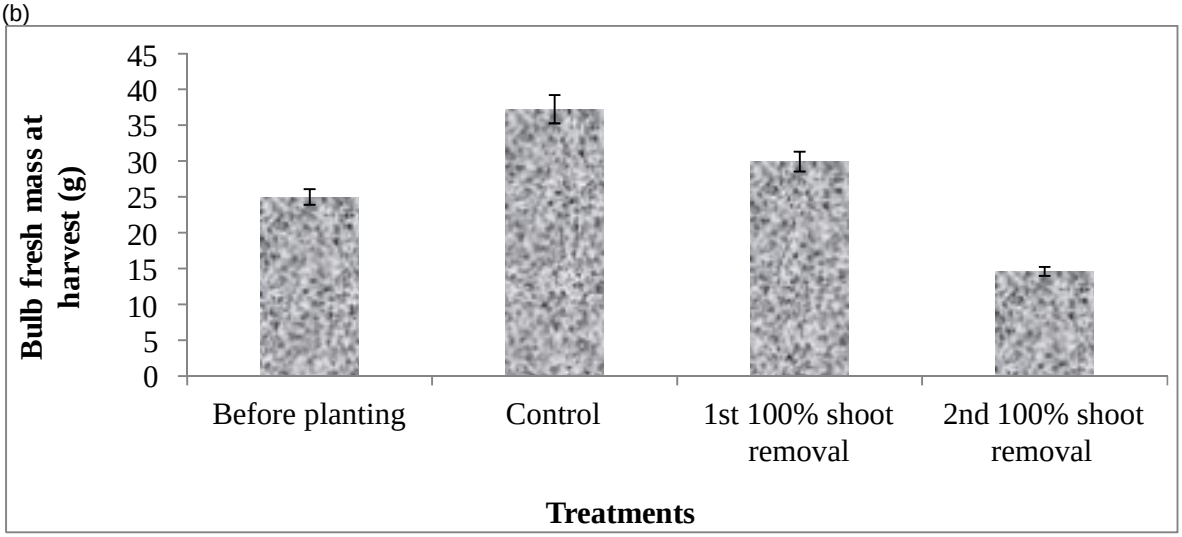


Fig 11: Gain in fresh weight of bulbs at harvest in response to shoot removal of lily. We ight gain in response to (a) partial shoot removal and (b) complete shoot removal. Error bars represent means ± SE of four plants.

4. DISCUSSION

In hyacinth, plants whose leaves were defoliated did not compensate for leaf loss because growth was always reduced whilst flowering was unaffected. Thus once leaves are above ground, any minor or devastating damage to the leaves will not stop the plants from flowering. The plants will continue to flower as they would have done without the damage. Even though complete and partial defoliation in hyacinth were both detrimental to the growth and subsequent development of this flower bulb, plants that were subjected to complete defoliation suffered more reductions in all parameters measured than those that were partially defoliated. In fact, defoliated plants did not only experience reductions in vegetative growth but they also produced bulbs with poor fresh mass at harvest as compared to the control. The defoliated plants experienced a reduction in the size of the leaf canopy and this must have decreased the production of photoassimilates. In general, carbohydrate reserves might have decreased following defoliation due to respiration and regrowth (Carlson, 1966). It was possible that a reduction in root growth occured and the production of leaves must have occurred at the expense of the root system. In general, defoliated plants were placed at a competitive disadvantage relative to their control counterparts in terms of their ability to acquire resources for growth (Caldwell *et al.*, 1987; Louda *et al.*, 1990). Food reserves of defoliated plants might have been used for vegetative growth instead of the reserves being used to enhance productivity. The reserves might have been depleted as a result of refoliation (Rockwood and Lobstein, 1994).

However, in the case of the lily, plants responded to complete herbivory if the damage was exerted at the beginning of their growth. That is, lily plants that were subjected to 100% shoot removal at 3 WAP (1st 100% shoot removal) responded to shoot losses by exhibiting compensatory regrowth of leaves. A number of physiological adjustments must have taken place in these plants in order to overcome the immediate loss of the photosynthetic tissues. In addition, the lily plants subjected to complete shoot herbivory at 3 WAP (1st 100% shoot removal) had higher values of chlorophyll concentration, photosynthetic rate and stomatal conductance than their control counterparts. It is possible that there was a reallocation of food reserves for the production of new but longer leaves in the case of the 100% defoliated lily plant and this reflected in these plants having high total leaf area as compared to those that were not defoliated. These plants had no option but to depend entirely on the mobilisation of stored reserves for regrowth of vegetation and later on current photosynthesis once new leaves were developed. This agrees with the observation that plants sometimes respond to high herbivory levels with a high regrowth as a tolerant mechanism to maintain fitness (Ruiz *et al*., 2002). In general, both hyacinth and the lily plants from the 1st herbivory regimes recorded higher vegetative growth than those from the 2nd herbivory regime. This indicates that the response of plants to herbivory is related to the time at which herbivory occurs. The difference in time interval between the 1st and 2nd herbivory treatments in hyacinth and the lily were 4 and 2 weeks, respectively. In hyacinth, the 1st and 2nd herbivory treatments occurred at 14 and 18 WAP, respectively, whilst in the lily, shoot removal was carried out at 3 and 5 WAP, respectively, for the 1st and 2nd herbivory treatments. The difference in response to herbivory by plants from the 1st

and the 2nd herbivory treatments, therefore, is attributable to the stage of growth of the plant at the time of herbivory, and this is also related to the amount of reserve carbohydrates present in the bulb scales at the time of herbivory. Our earlier studies on carbohydrate metabolism of these species (Manuscript under review) produced evidence that the reserve carbohydrates especially starch content of the bulb scales, decreased after planting. This is because the newly developed organs utilised these reserves for their own growth. In hyacinth, the carbohydrate reserves (starch) of the scales decreased from 0 to 5 months (20 weeks) after planting whilst in the case of the lily bulb, these reserves decreased from 0 to 9 weeks after planting. At the time of the 1st herbivory treatments, the carbohydrate reserves were higher than the reserves at the time of the 2nd leaf or shoot herbivory. Thus, more resources (food reserves) were available to support growth and development during the time of the 1st herbivory than during the 2nd herbivory treatment. Moreover, both hyacinth and lily plants whose leaves or shoots were completely removed suffered higher reductions in growth than those that were partially defoliated and this may be due to the fact that the photosynthetic leaf surfaces of plants from complete defoliation regimes were interfered with, and became more damaged as compared with those that were partially defoliated. This implies that the intensity of herbivory is very important in determining plant's response to that stress.

5. CONCLUSIONS

In hyacinth defoliated plants did not compensate for leaf loss as growth was always reduced but flowering was unaffected. Complete and partial defoliation were both detrimental to the growth and development of the plants, however, complete defoliation was more damaging than partial defoliation. Plants subjected to defoliation did not only experience reductions in vegetative growth but they also produced bulbs with poor fresh mass at harvest as compared to the control because they experienced a reduction in the sizes of the leaf canopy and this must have decreased the production of photo assimilates. Thus in general, leaf removal placed plants at a competitive disadvantage position relative to their control counterparts in terms of their ability to acquire resources for growth. Food reserves of defoliated plants must have been used for vegetative growth instead of the reserves being used to enhance productivity. The lily, however, responded positively to complete leaf herbivory especially if the damage was exerted at the beginning of their growth by exhibiting compensatory regrowth of leaves through the production of unusually long leaves whose total leaf area were similar to that of the undefoliated control. The study revealed that the response of plants to herbivory is related to the time or stage of growth of the plants at the time that herbivory occurs.

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