

MORPHOLOGICAL ANALYSIS OF TROPICAL BULBS AND
ENVIRONMENTAL EFFECTS ON FLOWERING AND BULB DEVELOPMENT OF
Habranthus robustus AND *Zephyranthes* spp.

By

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by

Camila Brito Paula

This document is dedicated to my husband and to my parents in Brazil.

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TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS	iv
LIST OF TABLES	vii
LIST OF FIGURES	viii
ABSTRACT	xv
CHAPTER	
1 INTRODUCTION	1
2 LITERATURE REVIEW	6
Aerial Organs and Tissues	8
Underground Tissues	8
Taxonomy and Origin of Geophytes	9
Geophytes Growth and Development.....	9
Dormancy	10
Flowering Process.....	12
Anatomy and Physiology of Flower Initiation	14
Factors Affecting Flower Initiation	17
Photoperiod	18
Light quality and quantity	18
Temperature	19
Vernalization	20
Flower Initiation Process in Bulbous Plants.....	21
Flower Bulb Cultivation	21
Flower Bulb Forcing.....	22
Tropical Bulbs and Amaryllidaceae	24
<i>Hippeastrum</i> spp.....	25
<i>Scadoxus multiflorus</i> – Blood Lily	26
<i>Agapanthus africanus</i> – African Lily	27
<i>Habranthus robustus</i> and <i>Zephyranthes</i> spp. – Rain Lilies.....	28
3 BULB MORPHOLOGY	31
Comparative Study	31

	Materials and Methods	31
	Results and Discussion	33
	Bulb type and size	33
	Leaf arrangement and morphology	37
	Floral initiation	41
	Meristematic region.....	48
	General anatomical and morphological arrangement.....	55
	Experiment 1	60
	Materials and Methods	61
	Results	61
4	ENVIRONMENTAL EFFECTS – FERTIGATION FREQUENCY AND FERTILIZER RATES ON FLOWERING IN <i>Habranthus robustus</i> AND <i>Zephyranthes</i> spp.	64
	Experiment 1	67
	Materials and Methods	67
	Results and Discussion	69
	Experiment 2.....	84
	Materials and Methods	84
	Results and Discussion	86
5	ENVIRONMENTAL EFFECTS – LIGHT LEVELS ON FLOWERING AND BULB DEVELOPMENT IN <i>Habranthus robustus</i> AND <i>Zephyranthes</i> SPP.....	93
	Materials and Methods	94
	Experiment 1	94
	Experiment 2	96
	Results and Discussion	97
	Experiment 1	97
	Experiment 2	100
6	CONCLUSIONS	113
	LIST OF REFERENCES	119
	BIOGRAPHICAL SKETCH	127

LIST OF TABLES

<u>Table</u>	<u>page</u>
3-1 Tropical geophytes used in the morphological studies	32
3-2 Geophyte size and characteristics of plants examined	34
3-3 Leaf size of plants examined	39
3-4 Relationship between leaf and flower formation, and number of flowers per inflorescence of plants examined	43
4-1 Mean bulb size and weight prior to experiment	85
5-1 Photometric readings and temperatures at three locations / treatments	96
5-2 Rainfall monthly summary in inches for Gainesville area in 2004 and 2005 according to the Florida Automated Weather Network	97

LIST OF FIGURES

<u>Figure</u>	<u>page</u>
3-1 From left to right <i>Zephyranthes</i> , <i>Habranthus</i> , <i>Hippeastrum</i> , <i>Scadoxus</i> bulbs, and immature <i>Agapanthus</i> rhizome..	35
3-2 Sections of <i>Zephyranthes</i> bulbs.....	35
3-3 Sections of <i>Habranthus</i> bulbs..	36
3-4 Sections of <i>Hippeastrum</i> bulbs..	36
3-5 Sections of <i>Scadoxus</i> bulbs ..	36
3-6 Longitudinal sections of an <i>Agapanthus</i> rhizome..	37
3-7 <i>Hippeastrum</i> leaf arrangement ..	39
3-8 <i>Habranthus</i> leaf arrangement.....	39
3-9 <i>Zephyranthes</i> leaf arrangement..	40
3-10 <i>Agapanthus</i> leaf arrangement.....	40
3-11 <i>Scadoxus</i> leaf arrangement.....	40
3-12 Longitudinal sections of a <i>Hippeastrum</i> bulb.	43
3-13 Sections of <i>Habranthus</i> bulbs ..	43
3-14 Sections of <i>Zephyranthes</i> bulbs.....	44
3-15 Cross section of a <i>Habranthus</i> bulb.....	44
3-16 Longitudinal section of a <i>Habranthus</i> bulb.....	45
3-17 <i>Habranthus</i> bulb with three flower stalks ..	45
3-18 Development of a <i>Habranthus</i> flower.....	46
3-19 Sections of <i>Scadoxus</i> bulbs ..	46

3-20	Flower stalk emerged and pseudo-stem arising from a <i>Scadoxus</i> bulb.....	47
3-21	Sections of <i>Agapanthus</i> rhizomes..	47
3-22	Photomicrograph of the meristematic region of a <i>Hippeastrum</i> bulb.....	50
3-23	Photomicrograph of the meristematic region of a <i>Hippeastrum</i> bulb.....	50
3-24	Photomicrograph of the meristematic region of a <i>Habranthus</i> bulb.....	51
3-25	Photomicrograph of the meristematic region of a <i>Habranthus</i> bulb.....	51
3-26	Photomicrograph of the meristematic region of a <i>Zephyranthes</i> bulb.....	52
3-27	Photomicrograph of the meristematic region of a <i>Zephyranthes</i> bulb.....	52
3-28	Photomicrograph of the meristematic region of a <i>Scadoxus</i> bulb.....	53
3-29	Photomicrograph of the meristematic region of a <i>Scadoxus</i> bulb.....	53
3-30	Photomicrograph of the meristematic region of an <i>Agapanthus</i> rhizome.....	54
3-31	Photomicrograph of the meristematic region of an <i>Agapanthus</i> rhizome.....	54
3-32	Longitudinal section of a <i>Hippeastrum</i> bulb showing its general anatomy and morphology..	55
3-33	Longitudinal section of a <i>Hippeastrum</i> bulb showing its general anatomy and morphology..	55
3-34	Longitudinal section of a <i>Zephyranthes</i> bulb showing its general anatomy and morphology..	56
3-35	Longitudinal section of a <i>Zephyranthes</i> bulb.....	56
3-36	Sections of <i>Habranthus</i> bulbs	57
3-37	Longitudinal section of a <i>Scadoxus</i> bulb showing its general anatomy and morphology..	57
3-38	Longitudinal section of a <i>Scadoxus</i> bulb showing its general anatomy and morphology	58
3-39	Longitudinal section of an <i>Agapanthus</i> rhizome showing its general anatomy and morphology.....	59
3-40	Longitudinal section of an <i>Agapanthus</i> rhizome showing its general anatomy and morphology.....	59

3-41	Number of leaves and flowers produced by <i>Habranthus</i> bulbs in 2005	63
3-42	Number of leaves and flowers produced by <i>Zephyranthes</i> bulbs in 2005	63
4-1	<i>Habranthus</i> bulbs during fertigation experiment with different plastic tags in different color distinguishing the three treatments.....	68
4-2	<i>Habranthus</i> bulbs being weighed after completion of experiment	69
4-3	Number of flowers of <i>Habranthus robustus</i> bulbs in year 2 as affected by fertigation frequency.	74
4-4	Number of leaves of <i>Habranthus robustus</i> bulbs in year 1 as affected by fertigation frequency.	74
4-5	Number of offsets of <i>Habranthus robustus</i> bulbs in year 1 as affected by fertigation frequency.	75
4-6	Bulb size of <i>Habranthus robustus</i> in year 1 as affected by fertigation frequency...75	
4-7	Total weight of <i>Habranthus robustus</i> bulbs in year 1 as affected by fertigation frequency.....	75
4-8	Bulb weight of <i>Habranthus robustus</i> in year 1 as affected by fertigation frequency.....	76
4-9	Number of flower buds of <i>Habranthus robustus</i> bulbs in year 1 as affected by fertigation frequency.	76
4-10	Number of leaves of <i>Habranthus robustus</i> bulbs in year 2 as affected by fertigation frequency.	76
4-11	Number of offsets of <i>Habranthus robustus</i> bulbs in year 2 as affected by fertigation frequency.	77
4-12	Bulb size of <i>Habranthus robustus</i> in year 2 as affected by fertigation frequency...77	
4-13	Total bulb weight of <i>Habranthus robustus</i> in year 2 as affected by fertigation frequency.....	77
4-14	Bulb weight of <i>Habranthus robustus</i> in year 2 as affected by fertigation frequency.....	78
4-15	Number of flower buds of <i>Habranthus robustus</i> bulbs in year 2 as affected by fertigation frequency.	78
4-16	Total number of flowers on <i>Habranthus</i> and <i>Zephyranthes</i> bulbs from July to December 2004	79

4-17	Number of flowers of <i>Zephyranthes</i> spp. bulbs in year 1 as affected by fertigation frequency	79
4-18	Number of flowers of <i>Zephyranthes</i> spp. bulbs in year 2 as affected by fertigation frequency.	80
4-19	Number of leaves of <i>Zephyranthes</i> spp. bulbs in year 1 as affected by fertigation frequency.	80
4-20	Number of offsets of <i>Zephyranthes</i> spp. bulbs in year 1 as affected by fertigation frequency.	81
4-21	Bulb size of <i>Zephyranthes</i> spp. in year 1 as affected by fertigation frequency.	81
4-22	Total fresh weight of <i>Zephyranthes</i> spp. bulbs in year 1 as affected by fertigation frequency.	81
4-23	Bulb weight of <i>Zephyranthes</i> spp. in year 1 as affected by fertigation frequency.	82
4-24	Number of flower buds of <i>Zephyranthes</i> spp. bulbs in year 1 as affected by fertigation frequency.	82
4-25	Number of leaves of <i>Zephyranthes</i> spp. bulbs in year 2 as affected by fertigation frequency.	82
4-26	Number of offsets of <i>Zephyranthes</i> spp. bulbs in year 2 as affected by fertigation frequency.	83
4-27	Bulb size of <i>Zephyranthes</i> spp. in year 2 as affected by fertigation frequency.	83
4-28	Total fresh weight of <i>Zephyranthes</i> spp. bulbs in year 2 as affected by fertigation frequency.	83
4-29	Bulb weight of <i>Zephyranthes</i> spp. in year 2 as affected by fertigation frequency.	84
4-30	Number of flower buds of <i>Zephyranthes</i> spp. bulbs in year 2 as affected by fertigation frequency	84
4-31	Data points, regression lines, equations and coefficient of determination of number of leaves of <i>Habranthus</i>	88
4-32	Data points, regression lines, equations and coefficient of determination of number of offsets of <i>Habranthus</i>	88
4-33	Data points, regression lines, equations and coefficient of determination of bulb size of <i>Habranthus</i>	89
4-34	Data points, regression lines, equations and coefficient of determination of total fresh bulb weight of <i>Habranthus</i>	89

4-35	Data points, regression lines, equations and coefficient of determination of fresh bulb weight of <i>Habranthus</i> .	89
4-36	Data points, regression lines, equations and coefficient of determination of number of flower buds of <i>Habranthus</i> .	90
4-37	Data points, regression lines, equations and coefficient of determination of number of leaves of <i>Zephyranthes</i> .	90
4-38	Data points, regression lines, equations and coefficient of determination of number of offsets of <i>Zephyranthes</i> .	90
4-39	Data points, regression lines, equations and coefficient of determination of bulb size of <i>Zephyranthes</i> .	91
4-40	Data points, regression lines, equations and coefficient of determination of total fresh bulb weight of <i>Zephyranthes</i> .	91
4-41	Data points, regression lines, equations and coefficient of determination of fresh bulb weight of <i>Zephyranthes</i> .	91
4-42	Data points, regression lines, equations and coefficient of determination of fresh bulb weight of <i>Zephyranthes</i> .	92
5-1	Plants under three different treatments full sun	96
5-2	Number of flowers of <i>Habranthus robustus</i> bulbs in year 2 as affected by light levels.	102
5-3	Number of leaves of <i>Habranthus robustus</i> bulbs in year 1 as affected by light levels.	103
5-4	Number of offsets of <i>Habranthus robustus</i> bulbs in year 1 as affected by light levels.	103
5-5	Bulb size of <i>Habranthus robustus</i> in year 1 as affected by light levels.	103
5-6	Total weight of leaves of <i>Habranthus robustus</i> bulbs in year 1 as affected by light levels.	104
5-7	Bulb weight of <i>Habranthus robustus</i> in year 1 as affected by light levels.	104
5-8	Number of flower buds of <i>Habranthus robustus</i> bulbs in year 1 as affected by light levels.	104
5-9	Root condition of <i>Habranthus</i> bulbs, under different treatments, after completion of experiment 1.	105

5-10	Number of leaves of <i>Habranthus robustus</i> bulbs in year 2 as affected by light levels.....	105
5-11	Number of offsets of <i>Habranthus robustus</i> bulbs in year 2 as affected by light levels.....	105
5-12	Bulb size of <i>Habranthus robustus</i> in year 2 as affected by light levels.....	106
5-13	Total weight of <i>Habranthus robustus</i> bulbs in year 2 as affected by light levels. .	106
5-14	Bulb weight of <i>Habranthus robustus</i> in year 2 as affected by light levels.	106
5-15	Number of flower buds of <i>Habranthus robustus</i> bulbs in year 2 as affected by light levels.	107
5-16	Number of flowers of <i>Zephyranthes</i> spp. bulbs in year 1 as affected by light levels.....	107
5-17	Number of flowers of <i>Zephyranthes</i> spp. bulbs in year 2 as affected by light levels.....	108
5-18	Number of leaves of <i>Zephyranthes</i> spp. bulbs in year 1 as affected by light levels.....	108
5-19	Number of offsets of <i>Zephyranthes</i> spp. bulbs in year 1 as affected by light levels.....	108
5-20	Bulb size of <i>Zephyranthes</i> spp. in year 1 as affected by light levels.	109
5-21	Total weight of <i>Zephyranthes</i> spp. bulbs in year 1 as affected by light levels.	109
5-22	Bulb weight of <i>Zephyranthes</i> spp. in year 1 as affected by light levels.....	109
5-23	Number of flower buds of <i>Zephyranthes</i> spp. bulbs in year 1 as affected by light levels.....	110
5-24	Number of leaves of <i>Zephyranthes</i> spp. bulbs in year 2 as affected by light levels.....	110
5-25	Number of offsets of <i>Zephyranthes</i> spp. bulbs in year 2 as affected by light levels.....	110
5-26	Bulb size of <i>Zephyranthes</i> spp. in year 2 as affected by light levels.	111
5-27	Total weight of <i>Zephyranthes</i> spp. bulbs in year 2 as affected by light levels.	111
5-28	Bulb weight of <i>Zephyranthes</i> spp. in year 2 as affected by light levels.....	111

5-29 Number of flower buds of *Zephyranthes* spp. bulbs in year 2 as affected by light levels.....112

Abstract of Thesis Presented to the Graduate School
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By

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Morphologies of *Hippeastrum x hybridum*, *Habranthus robustus*, *Zephyranthes* spp, *Scadoxus multiflorus*, and *Agapanthus africanus* were compared and contrasted. The first three species were true tunicate bulbs with similar shapes and distinct sizes, leaves emerged alternately from the center of the bulb, flower buds were formed alternately at the apical meristem (in a line in bulb cross section), and there were four leaves between each flower formed. *Scadoxus* was a true tunicate bulb with a thick rhizomatous structure at the base, thick scales, leaves arising in a pseudostem and flower buds formed centrally at the apical meristem. Its size is equivalent to *Hippeastrum* bulbs. *Agapanthus* is a rhizome with leaves arising alternately from lateral meristems, and flower buds formed centrally at the apical meristem.

Habranthus and *Zephyranthes* had distinct patterns of leaf production. *Habranthus* bulbs had fewer leaves emerging during flowering compared to *Zephyranthes*, which had a greater number of leaves throughout the entire year.

The responses of *Habranthus robustus* and *Zephyranthes* spp. to fertigation frequencies and fertilizer rates were examined. Experiment 1 tested fertigation frequencies of twice a week, once a week and every other week in both species. Regimens of once or twice a week were effective for flowering of both species. All bulb development factors investigated increased as fertigation increased in *Habranthus* and *Zephyranthes*, except for number of offsets on both species and number of leaves in *Zephyranthes*.

Experiment 2 tested bulb development responses when both species were fertilized with 20-10-20 at rates of 0, 75, 150, 300 ppm N. *Habranthus* bulbs treated with 75 and 150 ppm N had the greatest number of leaves and flower buds, and were larger and heavier, but bulbs treated with 300 ppm had more offsets. *Zephyranthes* bulbs treated with 150 ppm N had the greatest number of leaves, offsets and flower buds; bulbs treated with 300 ppm N were largest. Bulb weight was similar in bulbs treated with 75, 150 or 300 ppm N.

The responses of *Habranthus robustus* and *Zephyranthes* spp. to light levels of full sun, 30% and 60% shade were examined. Results demonstrated that both *Habranthus* and *Zephyranthes* flowered for a longer period under full sun and 30% shade than 60% shade but plants had more flowers under 30% shade. All bulb development factors investigated increased as light level increased in both species.

From this study it was concluded that preferred conditions for both species were fertigation of twice a week using fertilizer rate of 150 ppm N under full sun.

CHAPTER 1 INTRODUCTION

Bulbous plants are plants with a self-contained and highly developed food-storage mechanism that allows them to live underground. These plants are found all around the world; however the principal areas that are natural common habitats of a high percentage of bulbous plants are between 23° North and 45° South latitudes (Du Plessis and Duncan, 1989) in the Mediterranean, South Africa, Middle East and the Pacific seaboard of North and South America (Bryan, 1989).

An enormous number of flower bulb genera and species are found in nature, and they provide material for a wide range of potential ornamental use. The diversity of flower color, form, size, habitat and desirable growing conditions of bulbous plants rivals most other forms of vegetation. They can be used in the landscape, as borders and in flower beds, in containers outdoor and indoor and as cut flowers in indoor arrangements.

Historically bulbs were introduced in Europe almost 400 years ago (Bryan, 1989). *Agapanthus africanus*, Dur et. Schinz (1893) from South Africa was introduced in England in 1629. *Amaryllis belladonna* was introduced to Europe in the late 17th century (Traub, 1958a) and the genus *Hippeastrum* in the beginning of the following century (Tjaden, 1979).

Although no registries exist, it is likely that *Amaryllis belladonna* was originally collected in South Africa at the time of the spice and slave trade – late 15th century and early 16th century, possibly due to its abundance, coastal distribution, floral attributes and commercial value. The slave trade and sugar cane production played a major role in

the distribution of *A. belladonna* around Europe explaining why it is still commonly found in the Canary Islands, Madeira, Spain, Italy, and the Azores, which were main sugar cane growing areas.

During the 1500's, European plant explorers searched the world recording new species of plants using botanical illustrations. One of the earliest and best known illustrations in Europe was of *Tulipa bononiensis*, a species of bulb that would become extensively used, appreciated and commercialized. The Dutch botanist Carolus Clusius, head of the University of Leiden's Hortus Botanicus, the first botanical garden in Western Europe, received several tulip bulbs and seeds from Turkey and started a collection at the end of the 16th century. Clusius bred the tulips and produced new color variations, but he was mostly interested in its scientific importance and possibly medicinal uses for the bulbs. However, people in Holland were already interested in the flowers as money-makers for the developing ornamental floral trade, and some of Clusius' tulips were stolen from his gardens. That was the beginning of the famous "Tulipomania" (Cremers, 1973).

Throughout the early 1600's tulips were widely traded in the market and their prices were extremely high. In 1624, one tulip type was sold for 3000 guilders per bulb, the equivalent of US \$1,500.00 nowadays. Since then the Dutch have built one of the best organized bulb production and export businesses in the world. In 2001, over nine billion flower bulbs were produced in Holland, and about 80% were exported. According to the Netherlands Flower Bulb Information Center, the United States is the biggest importer of Dutch bulbs.

Tulips and other spring blooming bulbs are still closely associated with the Netherlands; however bulb production is not exclusive to that area. The world flower bulb industry produces a wide variety of high quality bulbs adapted to many climatic zones that are marketed either as cut flowers, flowering potted plants or landscape plants. Today's bulb industry is firmly established in areas of the world where the growers can duplicate by various cultural practices the environmental factors required for floral initiation and development. The demand for bulb crops is high, and the potential exists for greater production and sales of these crops (Johnson et al., 1995).

Florida is the second largest floriculture producing state in the US with over \$650 million in sales according to USDA, making floriculture a vital part of Florida's agricultural economy. Its hot and humid summers and rare frost occurrences during winter provide an ideal scenario for a varied selection of bulbous plants.

The tropical bulb market is practically non-existent in Florida due to production and market problems. Many tropical bulbs grow slowly, some have viral problems, and many consumers are not sure how to grow them. However, there is a large selection of bulbs suitable for Florida and other regions in the US in USDA Hardiness Zones 9, 10 and 11 that produce great spring and summer color. South Florida's climate is favorable for growing most of the tropical and subtropical bulbs. Examples of suitable tropical bulbs for most of Florida include: African Lily, or Lily of the Nile (*Agapanthus africanus*), Amaryllis (*Hippeastrum* spp.), Spring Calla Lily (*Zantedeschia* spp.), Peruvian Daffodil (*Ismene narcissiflora*), and Rain Lilies (*Habranthus* and *Zephyranthes*) (Black et al., 1990).

It is important to increase our research concerning flower bulbs, particularly subtropical and tropical bulbs, in order to identify and understand cultural factors of as many genera as possible. This will increase the number of bulbous plants that can be economically produced for the ornamental market. However, to be economically competitive, these plants should be profitable to produce and market, multiply under a wide variety of soil and climatic conditions, adapt to mechanical handling, tolerate air pollution, resist periods of drought, and tolerate low to moderate nutritional status.

The present study addressed some of these issues and was designed to provide growers with improved methodology and guidelines for the commercial production of two genera of tropical bulbs - *Habranthus robustus* (Herb , Lodd. 1831) and *Zephyranthes* spp. (Herb., 1821). The genera *Habranthus* and *Zephyranthes* belong to the Amaryllidaceae family and are known as Rain Lilies since they bloom several times during a season, usually following rainfalls. Limited information is available in the horticultural literature on cultural practices and commercial production of these two genera (especially of *Habranthus*) and their ability to adapt and develop under Florida's climatic conditions. Increased knowledge of these factors could result in the plants becoming important commercial crops in Florida.

This study was designed to determine the effect of environmental factors of light levels, drought stress, and the cultural practices of irrigation frequency and fertilization on flowering response of *Habranthus robustus* and *Zephyranthes* spp. Specific objectives of this study were 1) to perform morphological evaluations on *Habranthus robustus* and *Zephyranthes* spp. bulbs, comparing those with other species of tropical bulbous plants; 2) to evaluate environmental effects on flowering responses for *Habranthus robustus* and

Zephyranthes spp.; and 3) to develop commercial production and cultural information for *Habranthus robustus* and *Zephyranthes* spp.

CHAPTER 2 LITERATURE REVIEW

Geophyte, from the Greek geo for earth and phyton for plant; is a term that refers to plant species with specialized underground storage organs that accumulate food reserves, nutrients and moisture for seasonal growth and development. This group of plants includes both monocotyledonous and dicotyledonous species (Bryan, 1989) and is collectively referred to as “flower bulbs” (Halevy, 1990; Rees, 1985).

Geophytes can be separated into four groups – true bulbs, corms, tubers and rhizomes. Although they are morphologically different, the underground portions of all types of geophytes perform the same basic function – storage. A key factor used to classify geophytes is the precise origin and nature of the tissue that serves as the primary storage tissue (De Hertogh and Le Nard, 1993). Despite morphological differences, all geophytes share a common characteristic: they have a self-contained, highly developed food-storage mechanism.

True bulbs have a shortened stem, with a basal plate, one or more apical meristems, enclosed flower buds, adventitious roots initials, several layers of fleshy scales and a protective tunic that envelops the bulb. The scales are modified leaves (enlarged leaf bases) and function as the primary storage tissue in true bulbs. The tunic protects the bulb from drying and mechanical injuries (De Hertogh and Le Nard, 1993).

Bulbs can be either tunicate or non-tunicate depending on the origin of their scales. Concentric layers of scales form tunicate bulbs, such as in *Tulipa*, *Hippeastrum*, and

Narcissus. Non-tunicate bulbs do not develop concentric or scaly layers of scales, such as *Lilium* (Black et al., 1990).

Small underground bulbs are either called bulblets or offsets, if they occur at the periphery of the mother bulb. Small aerial bulbs that occur in either the leaf axils or in the floral parts are called bulbils. Most true bulbs are monocotyledonous, such the genera *Allium*, *Amaryllis*, *Haemanthus*, *Habranthus*, *Lilium*, *Nerine*, *Tulipa* and *Zephyranthes* (Bryan, 1989).

Rhizomes are horizontal, thickened, branching storage stems which grow below or along the surface of the soil. Typically, shoots (above ground) and roots (on the lower surface) arise at right angles from the cross stem. They are monocotyledonous (*Agapanthus*, *Canna* and *Clivia*), and dicotyledonous (some *Anemone* and *Achimenes*).

Corms are solid masses of stem tissue with an enlarged basal plate, distinct nodes and internodes, and adventitious root initials, enclosed by several dry, papery scale-like leaves. They are protected against injury and water loss by dry leaf bases that are similar to the tunic that encloses true bulbs. Corms are easily distinguished from true bulbs by the absence of visible storage rings when crossly sectioned and by having the basal plate as the primary storage organ. Small corms are called cormlets or cormels. Most corms reproduce by annual replacement and are monocotyledonous; examples include *Crocus*, *Freesia* and *Gladiolus* (Bryan, 1989).

Tubers consist basically of enlarged underground stem tissue with a root primordia developing basally and one or more apical shoot meristems (buds) on the underground stem. These buds (also called eyes) arise from the nodes and they are arranged in the same spiral pattern characteristic as buds on an aerial stem. Tubers are covered with a

tough skin and do not have scales as in true bulbs. Another distinction from true bulbs is the absence of a basal plate and protective tunic. They occur in both monocotyledonous (*Caladium*, *Gloriosa* and some *Zantedeschia*) and dicotyledonous (*Anemone* and *Eranthis*) genera (Bryan, 1989).

Aerial Organs and Tissues

Geophytes exhibit a wide variety of flowers, stems and leaves (Bryan, 1989). Their flowers can be single, double, semi-double or multiflowered, depending on the number of petals. According to Du Plessis and Duncan (1989) they can be hysteroanthous (leaves appear after flowers), proteranthous (leaves appear before flowers) or synanthous (leaves and flowers appear simultaneously). Floral development can be determinate (number of flowers do not increase after first flower is opened) or indeterminate (number of flowers can increase after first flower is opened). Stems can be leafed or leafless. Plants can be multi-stemmed or single-stemmed. Additionally, geophytes can be classified as either evergreen or deciduous according to their leaf persistence throughout the year.

Underground Tissues

Three morphological characteristics are commonly used to describe flowering bulb root systems: branching habit, presence or absence of root hairs and contractile root habit. Although most higher plants produce branched root systems (Whittington, 1969), several ornamental flowering bulbs do not. No branching has been observed for several genera such as *Allium*, *Crocus*, *Hyacinthus*, *Muscari*, *Narcissus*, and *Tulipa* (Kawa and De Hertogh, 1992). It is generally assumed that all plant roots have root hairs, but this is not true for some ornamental flower bulbs such as *Crocus flavus* (De Munk and De Rooy, 1971).

Contractile roots play a major role in positioning bulb crowns and storage organs at a proper soil depth for optimal growth and survival of the species. Corms and true bulbs commonly reposition themselves in the ground via contractile roots. This mobility of the underground plant organs occurs because of the activity of the contractile roots in response to light and temperature (De Hertogh and Le Nard, 1993). Of the bulbs used in their study, Theron and De Hertogh (2001) reported that *Hippeastrum*, *Agapanthus* and *Zephyranthes* have contractile roots, while *Scadoxus* did not have contractile roots. *Habranthus* was not used in their study.

Rhizomes secure an optimal position by the growing activity of their shoots tips, as reported by Pütz (1998) who found that *Hemerocallis fulva* rhizomes were able to adjust their own soil depth by elongating the root axis and not via root contraction.

Taxonomy and Origin of Geophytes

The three most important plant families containing geophytes are Amaryllidaceae, Iridaceae and Liliaceae. Most tropical bulbs, and those used in this study, belong to the family Amaryllidaceae. Bryan (1989) summarized the origin of many geophytes and stated that they mainly occur between the 23° to 45° North and South latitudes, this includes the Mediterranean, South Africa, Middle East and the Pacific seaboard of North and South America.

Geophytes Growth and Development

Geophytes must reach a certain physiological stage before they are capable of flowering; this can take less than a year or as long as six years (De Hertogh and Le Nard, 1993). In several species the ability to flower is directly related to the size of the geophytic organ, which varies from species to species. *Hippeastrum* for example, flowers when bulbs reach a circumference of approximately 20 cm (6 cm in diameter), *Scadoxus*

flowers when the geophytic organ circumference is 15 cm (4.5 cm in diameter), while *Eucharis* bulbs need to attain a circumference of 3 to 5 cm (1 cm in diameter) before flowering occurs (Theron and De Hertogh, 2001).

A number of factors affect growth, development, and flowering in bulbs. These include their native habitat and related microclimate parameters such as temperature range, rainfall, sun irradiation, photoperiod, altitude, moisture, soil type and nutritional status. With the exception of some equatorial areas that have fairly uniform environments, geophytes are often exposed to a wide range of climatic conditions during their growth cycle (De Hertogh and Le Nard, 1993).

Among environmental factors that affect bulb growth and development, the most important ones are temperature, light and moisture. These three factors are manipulated to force bulbs, since they act directly on rooting, flower development, shoot elongation, and bulbing (bulb elongation). Temperature is the major external factor that controls growth, development, flowering, dormancy and physiological maturity of bulbs. Light intensity and photoperiod also affect several physiological processes, such as photosynthesis, flower abortion and abscission (Bryan, 1989).

Dormancy

Bulbs have developed mechanisms to survive seasonal changes in climatic conditions such as low or high temperatures and drought. Under adverse conditions many bulbs enter a dormant period, in which they do not exhibit any visible external growth. Le Nard (1983) stated that the period of dormancy mainly corresponded to the period of bulbing, when the bulb enlarged. However, De Hertogh and Le Nard (1993) defined it as a complex and dynamic physiological, morphological and biochemical state during which

there are no apparent external changes or growth. Internally, however, many physiological and/or morphological events may occur.

Roughly, species that go dormant are deciduous as they lose their leaves during adverse periods (winter or seasonal dry periods) and those that do not go dormant are evergreen (they keep their leaves all year round). Examples of evergreen bulb genera include *Agapanthus*, *Amaryllis* and *Clivia*. Different genera respond differently to this period of dormancy and have also distinct requirements to break dormancy. Yet, temperature and moisture are the two major factors used to affect bulb dormancy (Le Nard, 1983).

Some temperate zone bulb species, such as *Tulipa*, *Daffodil* and *Hyacinth*, have cold dormancy requirements; which means they need a critical number of chilling hours in order to bloom the following season (Kamenetsky, 2004). That does not occur in Florida even in the northern areas of the state as most winters are not sufficiently cold. Consequently, temperate zone bulbs are not used in the landscapes, except as annuals, in these areas. Other species, such as *Caladium* and *Zantedeschia*, have warm dormancy requirements, which means they need a period of dry and warm temperature in order to bloom next season (De Hertogh and Le Nard, 1993). North and Central Florida's winters are usually not sufficiently dry or warm for some of these species; however, South Florida's winters are suitable for some of the species.

The existence of a rest or dormant period is very convenient for horticultural practices because it facilitates the handling, storage and transportation of these bulbs. The species used in this study, *Habranthus* spp. and *Zephyranthes* spp, go dormant during the cold season and require very little water during this period. However, not all bulb crops

go through a dormant period. *Hippeastrum* bulbs, for example, do not require a rest period in order to flower, since bulbs can produce inflorescences annually in a greenhouse under conditions of continued irrigation (Haynes et. al, 2001).

Flowering Process

Plants continue to generate new organs even after their embryonic phase, unlike animals. Undifferentiated cells called meristematic cells are responsible for the formation of new organs. The organ produced by the shoot meristem during its post-embryonic phase will depend on the phase of the plant's life cycle, which can be characterized as: juvenile vegetative phase, adult vegetative phase and reproductive phase. During the juvenile phase, the shoot meristem initiates stems, true leaves and axillary buds; and during the adult phase, the shoot meristem can form inflorescences which contain sexual organs. In some plants reproduction is the last of the shoot's phases; in other plants vegetative growth begins on lateral meristems when the apex becomes reproductive. In some other plants the apical meristem remains vegetative and lateral meristems generate reproductive structures (Poethig, 1990).

The transition from producing one organ to another, which is known as phase change, can be either gradual or abrupt. This process, called flower initiation, marks the end of vegetative growth and is a major determinant of plant reproductive success (Poethig 1990).

The flowering process involves five successive stages: induction, initiation, organogenesis, maturation (growth of the floral parts), and anthesis (De Hertogh and Le Nard, 1993). Important aspects of this process are: 1) the signals received by the plant that instigate the process, 2) their transport to the shoot apex, and 3) the changes in the shoot apex during floral differentiation (Evans, 1993).

The successive steps of the flowering process are controlled by several factors and each takes place in a determined period of the growth cycle. Controlling these processes in bulbous plants, as well as other horticultural crops, can promote or retard flowering, prevent flowering or induce flower abortion (De Hertogh and Le Nard, 1993). Promoting or retarding flowering permits out of season and/or year-round commercial flower production. Preventing flowering is necessary for the production of some bulbs, such as *Iris hollandica*. Inducing flower abortion can promote bulb development in some bulb species such as *Tulipa* and *Hippeastrum*. The flowering process can be controlled by applying specific treatments (temperature, moisture, light, or plant growth regulators) to the bulb. However, precise knowledge of bulb periodicity is essential to control flowering (Bryan, 1989).

Flower initiation takes place at different times of the year and at different stages in the development of bulbs. Seven different types of flower initiation have been identified in commercially grown bulbous plants (Hartsema, 1961):

1. Flowers are formed during spring or early summer of the year preceding the one in which they flower (*Narcissus*, *Galanthus*, *Leucojun* and *Convallaria*).
2. Flowers are formed after the end of the assimilation period (*Crocus*, *Hyacinthus*, *Iris reticulata* and *Tulipa*).
3. Flowers are formed some time after new growth matures, in winter or early spring (most *Iris* spp).
4. Flowers are formed during the storage period and complete development after planting (*Begonia tuberosa*, *Dahlia* and *Lilium*).
5. Flowers are formed after replanting in spring (*Galdiolus*, *Anemone* and *Freesia*).
6. Flowers are formed more than a year before flowering (*Amaryllis belladonna* and *Nerine sarniensis*).

7. Flower formation occurs alternatively with leaf formation during the whole assimilation period (*Zephyranthes* and *Habranthus*). In this case, both young developing flower buds and one year-old flower buds are present in the bulb.

Anatomy and Physiology of Flower Initiation

All the aerial parts of a plant (excluding the cotyledons) are produced by the shoot apical meristem. This meristem is formed during embryogenesis and comprises a group of undifferentiated cells that generate different organs and structures such as stems, leaves and flower. The root system of a plant is produced by the root meristem (Poethig 1990).

The shoot apex meristem at a certain point in the growth cycle undergoes a phase change, caused by floral induction in response to exogenous (such as daylength, nutrient status, or temperature) and endogenous (related to internal factors such as plant age and metabolic status) factors, and becomes reproductive producing flower buds instead of leaves. This transition is not irreversible in plants and in some species under certain environmental conditions, leafy shoot formation occurs after flower formation in a phenomenon known as inflorescence reversion (Pouteau et al. 1997).

Three different models have attempted to describe the control of flowering in plants. The first model is known as the “florigen concept” (Evans, 1971) which suggested that substances or signals are transferred across grafts between reproductive “donor” shoots and vegetative “recipients”, and that a flower-promoting hormone called florigen transports them to the shoot apex via the phloem. Chailahjan (1937) suggested that the florigen hormone was produced in leaves under favorable photoperiodic conditions. This model could not be proved, which lead to a second model called nutrient diversion hypothesis. This suggested that external conditions could raise the amount of assimilates moved to the apical meristem, which were responsible for flower induction (Bernier,

1988). A third model, called “multifactorial control model”, proposed that several promoters and inhibitors (including phytohormones and assimilates) were involved in flowering induction; and that flowering would only occur if these were present in the apical meristem in proper concentrations and specific time intervals (Evans, 1995).

Genetic investigations of flowering in several species support the assumption that several factors act together to control flowering. Most of these studies have been done in *Arabidopsis*, and have provided recent advances in better understanding of this process (Guo et al, 1998; Koornneef et al., 1998; Simpson, 2002).

A number of genes are involved in flower initiation, such as the flowering-time, which integrates the signals and act as promoters or repressors of flowering, the meristem-identity, which determines the fate of newly formed primordia (shoot/leaf-, or a flower-primordium), and the organ-identity, which directs the formation of various flower parts (reviewed in Yanofsky, 1995). Peeters and Koornneef (1996) have identified several genes that control the timing of the transition from leaf production to flower production by mutant analysis. There is still much to be learned about the functions of these different genes, however, it has been suggested that some of these flowering-time genes are involved in the partitioning or metabolism/sensing of compounds that might play a part in the endogenous plant signal(s), such as the plant hormone gibberellin, and sucrose concentrations (Nilsson et al. 1998).

There is a small group of plants that can be induced to flower artificially by the application of chemicals. Manochai (2005) tested the application of potassium chlorate (KClO_3) to either the root or the foliage of *Dimocarpus longan* and obtained successful results at all times of the year.

During flower induction and early flower development the apical meristem undergoes several morphological alterations (Tooke and Battey, 2003). Changes in local forces at the surface of the shoot apex have been proposed to play an important role in organogenesis (Fleming et al., 1997), which is the step that follows initiation in the flowering process. Albrechtová et al. (2004) examined the role of these local forces during photoperiodic flower induction in *Chenopodium rubrum*, by measuring the changes in shape of the apical dome, and changes in cell wall properties. The results obtained confirmed that early changes at the surface of the apical meristem affect the process of floral transition. The relative size of the apical meristem has also been proposed as an important factor in the developmental (vegetative/reproductive) switch.

After a signal is received by the plant and transferred to the shoot apex, the meristematic cells begin the process of organogenesis, the formation of tissues by cell differentiation. These tissues mature forming the floral organs. Different species have different mechanisms with which they control the development of their flower organs (stamens, carpels, etc). Most species develop their carpels and stamens simultaneously, but in some species the male flower organs grow first (these are referred to as protandrous flowers) and in others the female organs grow first (and these are referred to as protogynous flowers). A few species like pumpkin (*Cucurbita pepo*) develop male flowers first, next hermaphroditic ones, finally female and at last parthenocarpous flowers (lacking an embryo) that produce seeds agamically, not involving the fusion of male and female gametes, as occurs in sexual reproduction (Evans, 1993).

A flower is considered a modified stem with shortened internodes and bearing modified leaves at the nodes. In essence, a flower is structured as a modified shoot or axis

with an apical meristem that does not continue to grow. A typical flower contains a pedicel (stem) with a torus or receptacle at the end. The four main parts (or whorls) of a flower sit on the receptacle, and they are: the calyx (group of sepals); corolla (group of petals); the androecium (male organs – filaments and anthers); and the gynoecium (female organs – stigma, style, ovary and ovule). Plant species show a wide variety of modifications from this plan (Eames, 1961).

The basic function of flowers is to mediate the union of male and female gametes, in the process called pollination. The period of time during which the flower is fully expanded, functional, and thus allow the pollination process can take place is called anthesis, and it can vary from few hours to weeks. During the maturation phase, most assimilates obtained by the plant are used to develop the floral parts. As soon as the flower is fully expanded and opened, assimilates start to be mobilized and used for seed development, and that is when the process of flower senescence begins (Poethig, 1990).

Factors Affecting Flower Initiation

In some species, the timing of flowering is primarily influenced by environmental factors, which determine the time of year and/or growth conditions that are favorable for sexual reproduction and seed maturation. These factors include photoperiod (day length), light quality (wave length), light quantity (photon flux density), temperature, vernalization (exposure to a defined number of hours below a critical temperature), and nutrient and water availability (Halevy, 1990).

Some species are not very sensitive to environmental variables and these appear to flower in response to endogenous factors such as plant size (bulbs are an example of that) or number of vegetative nodes. Flowering can also be induced by stresses such as nutrient deficiency, drought, and overcrowding. This response enables the plant to produce seeds,

which lay dormant until the return of favorable environmental factors (Levy and Dean, 1990).

Photoperiod

Photoperiod is defined as the length of time a plant is exposed to light and/or darkness within a 24-hour period. Flower induction, initiation and/or development of many plant species are greatly affected by photoperiod and can be synchronized during the year by manipulating night length (Garner and Allard, 1920). According to Thomas and Vince-Prue (1997), plants with photoperiodic flowering responses are divided into five groups according to the amount of light/darkness they require: short-day (SD) plants, long-day (LD) plants, day-neutral (DN) plants, intermediate-day plants, and ambiphotoperiodic-day plants. Short- and long-day plants can also be subdivided into: obligate or qualitative, and facultative or quantitative. Photoperiodic responses are often interspecific and can vary within cultivars of a species (Martson and Erwin, 2005). In most plants the amount of darkness is what determines initiation; a night break (or addition of extra light during the dark period) can inhibit or promote flowering (Evans 1993).

Rees (1985) reported that *Hippeastrum* bulbs have no response to photoperiod regarding flowering. However, De Hertogh and Gallitano (2000) determined that photoperiod, as well as temperature, affect leaf size in the 'Apple Blossom' cultivar of *Hippeastrum*.

Light quality and quantity

There are two different plant behaviors related to light quality: light dominance and dark dominance. Light dominants are plants that are susceptible to changes in the spectral

distribution during the light period. Dark dominants are plants that need uninterrupted dark periods in order to flower (Fankhauser and Chory, 1997).

Flower initiation and time to flower in LD plants are related to light quality and to the timing of light treatments in the photoperiod (Thomas and Vince-Prue, 1997). Pringer and Cathey (1960) examined the effects of different types of light on *Petunia* flowering and concluded that they flower 2 to 3 weeks earlier if exposed to incandescent light (containing red and far-red light) than when exposed to fluorescent light (which has no far-red light).

Red light appears to be effective earlier in the photoperiod for LD plants, while far-red light seems to be important in the flower inductive response later in the photoperiod for LD plants, which according to Thomas and Vince-Prue (1997) is different from SD plants. Studies made by Vince (1965) in *Lolium temulentum* showed that red light used for 8 hr at the beginning or at the end of the photoperiod induced flowering, but when it was used at the beginning it promotes stronger flowering.

Temperature

In bulbous plants, temperature is the major external factor controlling growth, development and flowering (promoting or delaying it). Temperature also affects bulb dormancy in some genera and the physiological maturity of the bulbs (Bryan, 1989).

Doorduyn and Verkerke (2002) investigated bud development and flowering of *Hippeastrum* under 15 to 25°C and observed that at higher temperatures larger bulbs with more leaves developed, but the percentage of bulb dry matter decreased. In *Scadoxus*, temperature affects not only flowering but also bulb development. The optimal temperature to overcome dormancy of *Scadoxus* bulbs is 10 to 15°C, which is low enough to injure several other species (Bryan, 1989).

Flower formation does not occur in *Amaryllis belladonna* at 9°, 13° or 31°C, and the optimal temperature for flower initiation on this species appears to be 17°C. However, for non-planted *Amaryllis belladonna* bulbs, the optimal temperature for flower formation is 23°C (reviewed in Theron and De Hortogh, 2001).

Mori and Sakanishi (1989) demonstrated that for *Agapanthus*, flowering occurred when plants were continuously grown at 10° or 15°C; in contrast, flowering was inhibited when plants were grown at 20°C or higher from September onward. They also found that flowering could be accelerated by growing plants at a minimum of 20°C after the end of November in combination with a 16-hour photoperiod.

Hartsema (1961) reported that flower formation of *Zephyranthes rosea* occurred at 13° to 18°C and flowering occurred at 22°C, with soil moisture being important. No flowering occurred at 30°C. In *Zephyranthes candida* inflorescences were formed in spring and when plants with at least two previously formed inflorescences were subjected to 10°, 15°, 23° or 30°C in October, earliest flowering occurred on plants exposed to 23°C (Hartsema, 1961).

Vernalization

Vernalization is a period of cold temperature treatments that accelerates flowering in some plant species. Many biennial (two-year) plants require a temperature below a critical level for a definite time period before flowering can occur. Plants can either have an obligate or quantitative vernalization period. Obligate vernalization refers to plants that require cold temperatures for a period of time in order to flower. Quantitative vernalization refers to plants that do not require cold temperatures to flower but start their flowering period earlier under cold temperatures. Additionally, there are plants that do not respond to cold temperatures (reviewed in Yan and Wallace, 1995).

Flower Initiation Process in Bulbous Plants

Most true bulbs have a sympodial branching system (superposed branches) and at flower initiation a growing point is formed laterally in the apex. This growing point develops a certain number of leaves before an inflorescence develops, alternating flower and leaf formation throughout the entire growth period (Hartsema, 1961). The flower/inflorescence emergence is delayed compared to leaf emergence thus leaves and flower/inflorescence above ground have a difference of one generation between them, and the inflorescence appears to be lateral to leaves (De Hertogh and Le Nard, 1993).

Blaaum (1931) described the general flowering process in true bulbs and according to his studies bulbs undergo the following stages: I) the meristem is vegetative and produces leaves; II) the last leaf and new growing point are formed; III) a certain number of leaves are formed; IV) then the flower/inflorescence meristem is formed; followed by flower and floral parts formation. More recently, De Munk and Van der Hulst (cited in Theron and De Hertogh, 2001) have described the flowering process as: Stage I) vegetative; Stage II) formation of spathe; Stage III) beginning of flower initiation; Stage IV) flower development and anthesis; Stage V) flower senescence and vegetative growth.

Theron and De Hertogh (2001) showed that *Hippeastrum* bulbs initiate the flowering process in the spring, the differentiation period lasts from 18 to 24 months and anthesis occurs in the spring.

Flower Bulb Cultivation

Field production of bulbous crops occurs where soil and climate have advantageous characteristics. A large bulb industry developed in the Northwest region of the United States because soils usually do not freeze enough to damage the bulbs and abundant rainfalls create favorable growing conditions for them. Mild temperatures and abundant

moisture favor the production of bulbs having a multi-year production cycle. In more severe climates, such as the Midwest and Northeast, tender bulbs must be removed from the soil in the fall and stored during the winter (Johson et al., 1995).

Some bulbs grow well in light sandy or gravelly-type soils. However, most bulbs grow best in loams with high organic matter content. Generally, bulbs do not grow well in water-logged or heavy clay soils (Johson et al., 1995).

The majority of bulbous crops are planted in the early fall; however, some varieties are planted during the spring, such as *Gladiolus*, *Gloxinia* and *Begonia*. The bulblets remain in the ground for 1 to 3 years until they reach harvestable size. Some tender species require “lifting” or removal from the soil in the fall to avoid freeze damage (Johson et al., 1995).

The harvesting process is usually done mechanically, using methods similar to those used in onion production. Bulbs are lifted from the soil and deposited onto a belt-conveyor that moves them into the harvester, which shakes the bulbs to loosen and separate the soil. After harvesting, bulbs are sorted, graded, and damaged bulbs are discarded (Johson et al., 1995).

Flower bulbs present several different growth habits and when cultivated under growing conditions much different than their native habitat, they may drastically change their growth and flowering habit. For example, *Ornithogalum*, which is a deciduous perennial, becomes an evergreen when grown in the tropics, does not go dormant, blooms constantly, and does not produce bulbs (Halevy, 1990).

Flower Bulb Forcing

Forcing is defined as the regulation of bulb growth and development under greenhouse controlled environmental conditions (De Hertogh, 1977). True bulbs, as well

as corms, rhizomes, and tubers can be forced. According to De Hertogh (1977), in order to succeed using this process a grower must fully understand: a) the origin and morphology of the species, b) the production and growth cycle of the species, and c) the influence of various environmental factors on the development of the species.

The complete forcing system has been divided into four distinct phases: I) production, II) programming, III) greenhouse and IV) marketing. The exact programming of temperatures and times varies from species to species and might not be applicable to all cultivars of all species. The complete process should be based on marketing time and bulbs should finish the process at proper stage of development (De Hertogh, 1974).

The basic bulb production cycle initiates when bulbs are harvested, sorted and graded (according to their circumference measurements). The process continues with the storage of bulbs in warm temperatures to fully develop the floral organs. In the fall, the bulbs are planted, kept moist and under temperatures low enough to promote flowering and bulbing. In spring, the floral stalk elongates and the plant flowers. Some species require the removal of flowers, to increase bulb size (De Hertogh, 1977).

Successful forcing of flowering bulbs in a greenhouse is based on seven factors: temperature (the most important), watering, light, fertilization, ventilation, sanitation, and pest control. Forcing can be either accelerated or delayed by manipulating these factors (De Hertogh, 1996).

Hippeastrum bulbs can be forced for either fresh cut flowers or flowering potted plants. The key factors for forcing *Hippeastrum* bulbs are: 1) use bulbs larger than 20 cm in circumference (6 cm in diameter), 2) remove the bottom half of the roots, 3) cure the bulbs for 10 days at 17° to 23°C, 4) store the bulbs at 9° to 13°C for at least 8 weeks

before planting, 5) package bulbs to avoid roots drying out if transported, 6) plant bulbs in well-drained planting medium, 7) use bottom heat of 22°C in the greenhouse (reviewed in Theron and De Hertogh, 2001).

Tropical Bulbs and Amaryllidaceae

Most tropical bulbs, and in particular those used in this study, belong to the family Amaryllidaceae, which is a very diverse family with species on almost all continents and under various climatic conditions (Meerow and Snijman, 1998).

Amaryllidaceae classification includes the following:

Kingdom:	Plantae
Subkingdom:	Tracheobionta (Vascular plants)
Superdivision:	Spermatophyta (Seed plants)
Division:	Magnoliophyta (Flowering plants)
Class:	Liliopsida (Monocodiledoneous)
Subclass:	Liliidae
Order:	Liliales / Amaryllidales / Asparagales
Family:	Amaryllidaceae

According to Watson and Dallwitz (1992) the family Amaryllidaceae comprises approximately 60 genera and 800 species. Some of the important horticultural crops are *Amaryllis*, *Clivia*, *Crinum*, *Eucharis*, *Haemanthus*, *Hippeastrum*, *Hymenocallis*, *Lycoris*, *Narcissus*, *Nerine*, *Scadoxus* and *Zephyranthes*.

The two most recent formal classifications of the Amaryllidaceae family are those of Müller-Doblies and Müller-Doblies (1996) and Meerow and Snijman (1998).

Hyacinthaceae, is also considered a related family, however Agavaceae, Hypoxidaceae,

Haemodoraceae or Alstroemeriaceae with which Amaryllidaceae is sometimes associated, are not considered related families.

Plants in the Amaryllidaceae family have distinct habits, however most of them are perennial, bulbaceous and have contractile roots. Leaves are mostly deciduous and simple, with entire lamina, entire margins and parallel venation. Flowers may be solitary or produced on different types of inflorescences. Bulbous plants in this family have thickened underground storage organs which enable them to survive unfavorable environmental conditions and may also function as propagative units (reviewed by Theron and De Hertogh, 2001).

Halevy (1990) demonstrated that when flower bulbs are produced under growing conditions that are dissimilar to their indigenous environments, their growth habit can be altered. Therefore, it is important to understand the effects of temperature, light, nutrition, growth regulators, and other environmental factors on bulb growth, development and the flowering process, to significantly expand the horticultural usage of the Amaryllidaceae family (Theron and De Hertogh, 2001).

***Hippeastrum* spp.**

The name *Hippeastrum* comes from the Greek *hippeus*, meaning knight and *astron* meaning star. *Hippeastrum* is an important genus of the Amaryllidaceae family which comprises about 70 species, such as *H. argentinum*, *H. aulicum*, *H. barbatum*, *H. correiense*, *H. elegans*, *H. evansiae*, *H. leopoldii*, *H. miniatum*, *H. morelianum*, *H. pardinum*, *H. psittacinum*, *H. puniceum*, *H. reginae*, *H. reticulatum*, *H. rutilum*, *H. stylosum*, *H. vittatum*, and *H. reticulatum* (Rees, 1985). There are more than 300 cultivars and most of the horticulturally important ones were bred by Ludwig, Warmenhove and

van Meeuwen in the Netherlands and by HADECO (Barnhoorn) in South Africa (Read, 2004).

Hippeastrum can be considered a tropical plant by origin as it is indigenous to Central and South America, being centered in Brazil and Peru, and distributed from Mexico to Argentina (De Hertogh and Le Nard, 1993). *Hippeastrum* is commercially known as Amaryllis, however, the true Amaryllis (*A. belladonna*) originated in South Africa and it is not widely used. There are several differences between them such as the presence of a solid scape and the absence of scales between the filaments in *A. belladonna* (Goldblatt, 1984).

Hippeastrum spp has large and showy flowers with many bright colors (red, pink, orange, white or bi-colored) consisting of several flower types: trumpet-flowered, belladonna types, reginae types, leopoldii types, miniatures, doubles, and orchid-flowered. They are grown mainly as potted plants or as cut flowers, but they can also be grown in the landscape in subtropical and tropical areas (Schulz, 1954).

The bulb has a sympodial branching system, which means that the terminal bud dies or ends in an inflorescence, and growth of sympodial shoots continues from lateral buds. At flowering initiation, a lateral growing point is formed on the side of the apex. It develops in a sequence of four leaves and an inflorescence. Bulblets are initiated in the axils of senescing bulb scales in the outer parts of the bulb and they produce nine leaves before initiating the first inflorescence (reviewed in Theron and De Hertogh, 2001).

***Scadoxus multiflorus* – Blood Lily**

The genus *Scadoxus* contains 9 species: *S. cinnabarinus*, *S. cyrtanthiflorus*, *S. longifolius*, *S. membranaceus*, *S. multiflorus*, *S. nutans*, *S. pole-evansii*, *S. pseudocalus*, and *S. puniceus* (Friis and Nordal, 1976). *Scadoxus* is closely related to *Haemanthus*;

they were treated as a single genus at one time but were divided by Friis and Nordal (1976). The major differences between *Scadoxus* and *Haemanthus* are related to their geophytic organs, growth habits, and number and shape of their leaves (Snijman, 1984).

Scadoxus multiflorus is one of the most horticulturally relevant species in the genus, its name derived from *doxus* meaning glory or splendor, and *multiflorus* referring to many flowers (Jackson, 1990). *Scadoxus multiflorus* is endemic to southern and central Africa and was established by Rafinesque (1836). This species includes three subspecies: *katherinae*, *longitubus* and *multiflorus*, and the major differences between the subspecies are height of the plants, length of the perianth tubes and the extent of the perianth segments (Du Plessis and Duncan, 1989).

***Agapanthus africanus* – African Lily**

The genus *Agapanthus* was established by L'Heritier (1788). The name *Agapanthus* is derived from the Greek *agapé* that means love and *anthos* that means flower (Snoeijer, 2004). It was placed in the Liliaceae family, later moved to the Amaryllidaceae family. *Agapanthus* is endemic to southern Africa and the first species collected - *Agapanthus africanus* was described in 1679 by the name *Hyacinthus africanus tuberosus*, which is sometimes still referred to as *Agapanthus umbellatus* (Leighton, 1965).

Agapanthus is a variable genus, all species are rhizomatous with similar appearances. Botanists consider it difficult to classify them into distinct species. Plessis and Duncan (1989) identified about 10 species indigenous to Southern Africa.

Agapanthus africanus is a summer-flowering evergreen species, with its perennial geophytic organ a rhizomatous rootstock with contractile roots. Flowers are formed in an umbel inflorescence on a leafless scape. Mori and Sakanishi (1989) observed that *A.*

africanus meristem was vegetative in October, flower initiation began in November and flower differentiation occurred in December.

***Habranthus robustus* and *Zephyranthes* spp. – Rain Lilies**

Habranthus robustus was established by Herbert and Loddiges (1831), and *Zephyranthes* spp. was established by Herbert (1821). The name *Habranthus* comes from the Greek habros, meaning graceful and anthos meaning flower, and *Zephyranthes* comes from the Greek, zephyros meaning "the west wind" and anthos, meaning flower. These two groups of summer-flowering small bulbs of the Amaryllidaceae family are native to the southeastern United States, Central and South America (Hume, 1935; Traub, 1958 b).

The genus *Habranthus* contains about 40 species, and among the horticulturally important are *H. tubispathus* and *H. robustus*, which is native to Brazil (Read, 2004). The *Zephyranthes* genus contains about 60 species and the most horticulturally important are *Z. candida* Herb and *Z. grandiflora* Lindl, but other commercially grown species include: *Z. andersonii* Baker, *Z. atamasco* (L.) Herb, *Z. drummondii*, *Z. primulina* T.M. Howard & S. Ogden, *Z. rosea* Lindl, and *Z. citrina* Baker. There are several named cultivars derived from interspecific crosses (Van Scheepen, 1991).

Habranthus and *Zephyranthes* geophytic organs are perennial bulbs covered with a dark tunica, contractile roots, deciduous leaves with sheathing basis and linear blades, and isolated flowers (Theron and De Hertogh, 2001).

Habranthus robustus flowers are very similar to those of *Zephyranthes* and *Habranthus* have at times been included in the genus *Zephyranthes* because of that. Both are commonly called "rain lilies" because of their tendency to bloom after rain periods (Fellers, 1996).

Habranthus robustus is often called *Zephyranthes robusta* incorrectly, which adds to the confusion between it and *Zephyranthes grandiflora*. The very subtle differences between genera are based on spathe characters, position of flowers, symmetry of corolla, insertion of anther filaments, number and length of filaments, and number of seeds per locule in capsule (Fernández-Alonso & Groenendijk, 2004).

Zephyranthes flowers point straight up and have equal length stamens, while *Habranthus* flowers point upward but at an angle and have stamens of different lengths; these characteristics are commonly used to separate the two genera. Additionally, *Habranthus* flowers tend to have zygomorphic flowers (bilaterally symmetrical), while *Zephyranthes* are actinomorphic flowers (radially symmetrical). The flowers of *Habranthus* are clearly distinguished by filaments of 4 different lengths and always longer than the perianth tube. *Zephyranthes* flowers are declinate and distinguished by filaments of two very similar lengths (Fernández-Alonso & Groenendijk, 2004).

Zephyranthes and *Habranthus* can also be distinguished by the shape of their seed. *Zephyranthes* seeds tend to be more D-shaped or wedge shaped while those of *Habranthus* are more openly obliquely winged. These two genera are also distinguished phylogenetically as, *Zephyranthes* apparently have 2-3 different origins according to nrDNA spacer sequences (Meerow et al, 2000).

The differences between *Habranthus* and *Zephyranthes* are not readily apparent to most growers and consumers but the two groups of bulbs seem to have different flowering periods and re-blooming characteristics. The results of this study will contribute to a better understanding of these species and their cultural differences. This

study will also help growers determine which species grow best at different times of the year and maximize seasonal sales and facilitate their commercialization.

CHAPTER 3 BULB MORPHOLOGY

Geophytes were defined by Raunkier (1934) as plant species with specialized underground storage organs that accumulate food reserves, nutrients and moisture for seasonal growth and development. They are usually collectively called “flower bulbs” and can be separated into four groups: true bulbs (tunicate and non-tunicate), corms, tubers and rhizomes. Although morphologically different, all types of geophytes perform the same basic function, storage of photosynthates.

Most geophytes have a shortened stem, a basal plate, one or more apical meristems, enclosed flower buds, adventitious root initials, several layers of fleshy scales (modified leaves), and a protective tunic. The size of storage organs vary tremendously among species (Proches et al., 2006), as well as their leaf arrangements and flower formation. Some genera, including *Tulipa* and *Narcissus* (Caldwell and Wallace, 1955) have been extensively examined. However, only limited information is available in the literature concerning morphology of other tropical bulbs.

This portion of the present study was designed to compare and contrast the morphology and flower formation of *Hippeastrum hybridum*, *Scadoxus multiflorus* and *Agapanthus africanus*, and compare them to *Habranthus robustus* and *Zephyranthes* spp, which were species used in the subsequent phases of this study.

Comparative Study

Materials and Methods: The five species of tropical bulbous plants listed on table 3-1 were grown under same conditions, dissected by freehand sections, stained with

Safranin, and examined during mature and immature stages of development. Digital images and drawings were produced to determine similarities and differences in morphology and floral development of the five species examined.

Table 3-1 – Tropical geophytes used in the morphological studies:

Species	Common Name	Family	Source
<i>Hippeastrum hybridum</i> .	Amaryllis	Amaryllidaceae	Agristarts, Inc.
<i>Scadoxus multiflorus</i>	Blood Lily	Amaryllidaceae	Agristarts, Inc.
<i>Agapanthus africanus</i>	Agapanthus	Alliaceae	Agristarts, Inc.
<i>Habranthus robustus</i>	Rain Lily	Amaryllidaceae	UF stock
<i>Zephyranthes</i> spp.	Rain Lily	Amaryllidaceae	UF stock

Seventy two plugs of *Hippeastrum hybridum*, *Scadoxus multiflorus* and *Agapanthus africanus* were obtained from Agristarts Inc. in Apopka, Florida during the first week of March 2004. *Habranthus robustus* and *Zephyranthes* hybrids bulbs were obtained from University of Florida stock where they had been grown in ground beds for a year prior to the beginning of this study. The *Zephyranthes* hybrids used in this study were: *Z.* ‘Paul Niemi’, *Z.* ‘Jo Ann’s Trial’ and *Z.* ‘Fadjar’s Pink’, which were hybridized by Fadjar Marta in Jakarta, Indonesia.

All geophyte plugs and *Habranthus* and *Zephyranthes* bulbs were transplanted into 15 cm plastic pots using sphagnum peat based Fafard No. 2 soilless growing medium (Agawam, MA) consisting of 70% Canadian sphagnum peat, 10% perlite and 20% vermiculite. Plants were placed in a greenhouse (which provided 11% shade), natural photoperiod and a temperature range of 31/24°C (day/night). From planting through establishment all pots were irrigated every other day with 250ml of water, except *Hippeastrum* which was watered daily with same amount of water. After establishment (first week of April), plants were fertigated twice a week with 250ml of water containing

Peters Professional 'Florida Special' water soluble fertilizer 20N-4.7P-16.6K (Scotts Co., Marysville, OH) with N at 150 mg L⁻¹. Plants were grown in the greenhouse for ten months.

From June to November 2005, a series of freehand sections of the four species of bulbs and *Agapanthus* rhizomes were made. The sections were mounted in glycerin and stained with Safranin for 24 hours to facilitate the observation of specific tissue components. Sections were examined with a Wild M5 dissecting scope and light microscopy images were obtained with a Zeiss Tessovar with an Rts Contax camera attachment.

Freehand sections of the meristematic regions of the five species studied were mounted in glycerin (but not stained) and light microscopy images were obtained with a Nikon Labophot-2 microscope and a Nikon E4500 digital camera attached to it. Drawings, based on observations of numerous freehand sections, were made to demonstrate the general anatomy and morphology of each of the five species examined.

Results and Discussion

Bulb type and size: Observations and measurements made in this study revealed that *Zephyranthes* and *Habranthus* bulbs were similar in shape but that *Zephyranthes* bulbs were smaller than *Habranthus* bulbs. Mature *Zephyranthes* bulbs were approximately 6 cm tall with a diameter of about 6 cm, while mature *Habranthus* bulbs were approximately 8 cm tall with a diameter of about 8 cm. Both bulb genera were covered with a fine, papery dark brown tunica. *Hippeastrum* bulbs were covered with a fine, papery dark brown tunica and were similar to *Zephyranthes* and *Habranthus* in shape but were larger, as mature bulbs were approximately 12 cm tall with a diameter of about 12 cm (Table 3-2 and Figure 3-1). *Zephyranthes*, *Habranthus* and *Hippeastrum*

form true tunicate bulbs, with concentric layers of modified leaves called scales (Figures 3-2, 3-3 and 3-4).

Scadoxus geophytic organs were true bulbs formed by concentric layers of scales (approximately 6 cm tall when mature) with a thick (4 cm tall) rhizomatous structure at their base and covered by a fine, papery dark brown tunica (Figure 3-5). Scales of *Scadoxus* were thicker (0.5 cm) than scales of *Zephyranthes*, *Habranthus* and *Hippeastrum* which averaged about 0.2 cm in thickness.

Agapanthus geophytic organs were rhizomes and did not have layers, scales or a tunica as did the other four previous studied species (Figure 3-6). A mature *Agapanthus* rhizome was approximately 20 cm long with a diameter of approximately 10 cm (Table 3-2).

Table 3-2 – Geophyte size and characteristics of plants examined

Genera	Geophytic organ	Height (cm)	Diameter (cm)	Scales present	Tunica present
<i>Hippeastrum</i>	True bulb	12	12	Yes	Yes
<i>Habranthus</i>	True bulb	8	8	Yes	Yes
<i>Zephyranthes</i>	True bulb	6	6	Yes	Yes
<i>Scadoxus</i>	Bulb/rhizome	10	12	Yes	Yes
<i>Agapanthus</i>	Rhizome	-	10	No	No

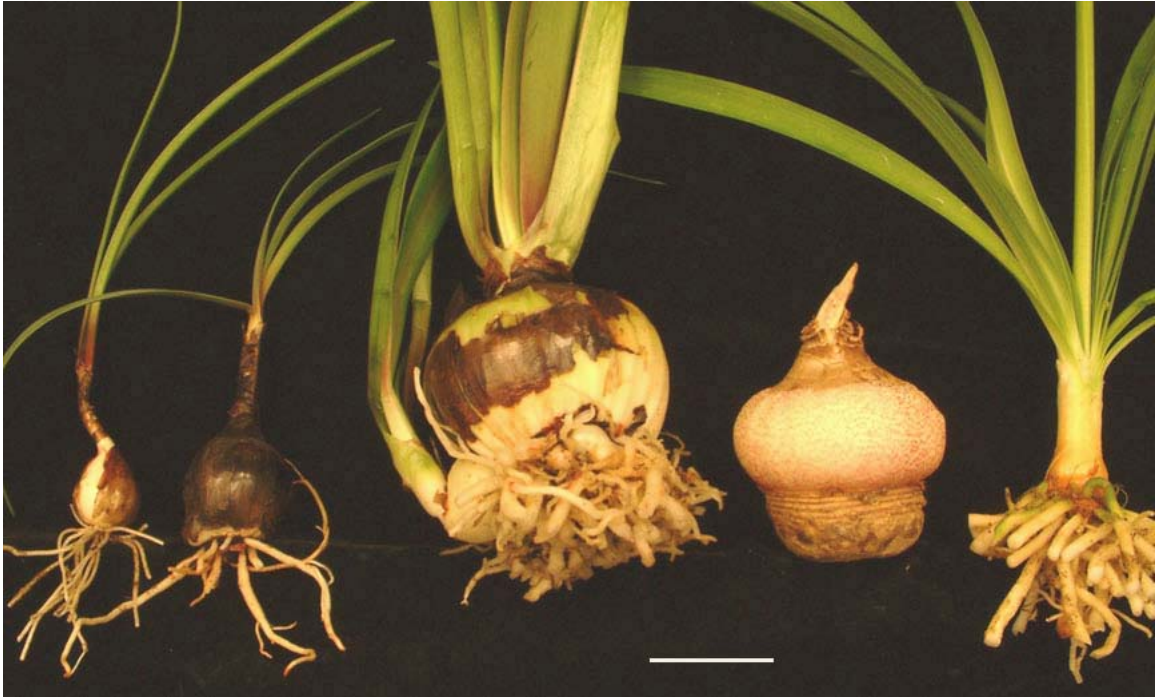


Figure 3-1: From left to right *Zephyranthes*, *Habranthus*, *Hippeastrum*, *Scadoxus* bulbs, and immature *Agapanthus* rhizome. *Bar* = 10 cm.

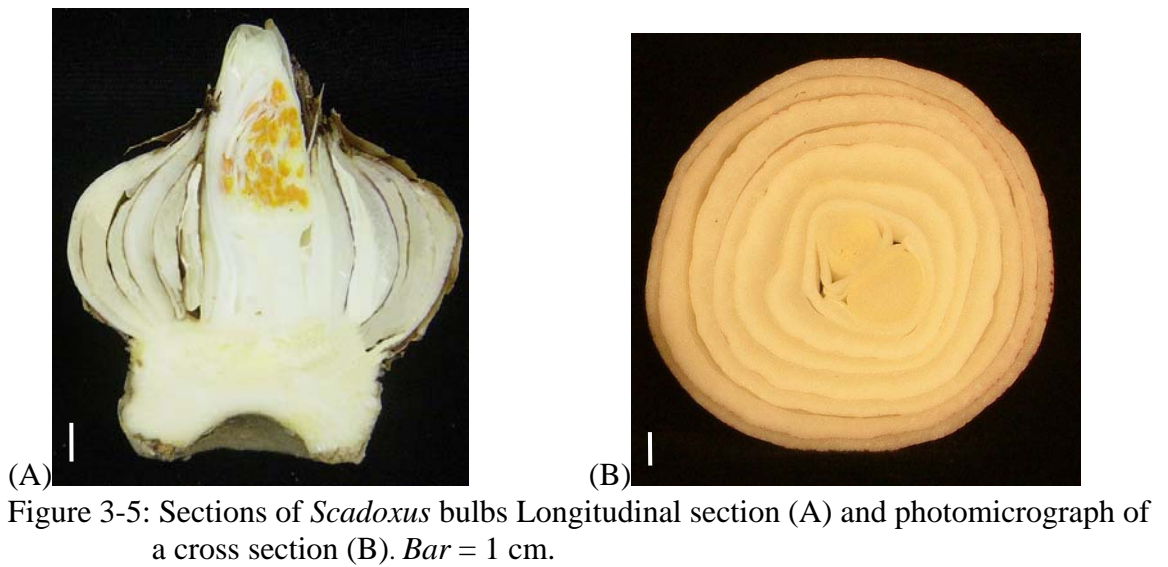
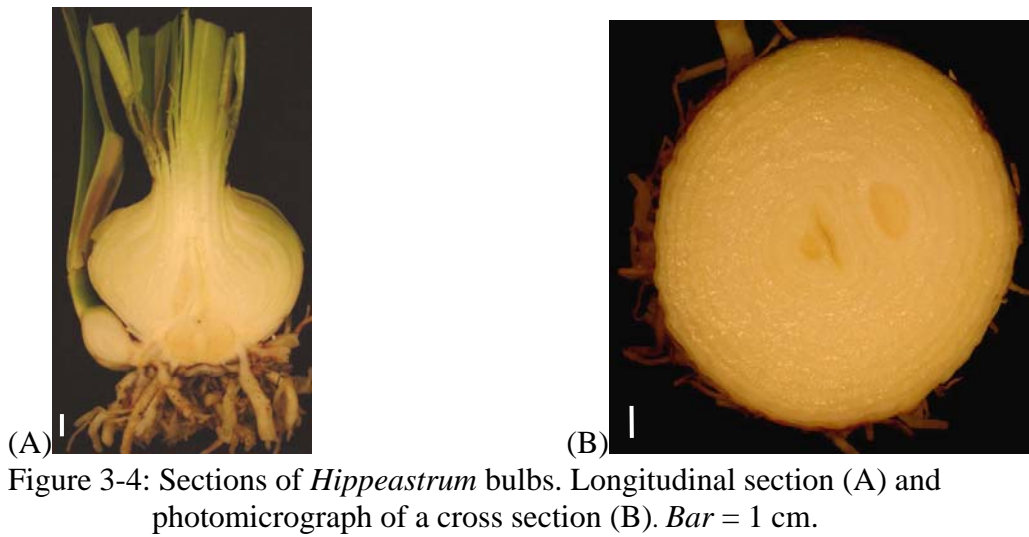
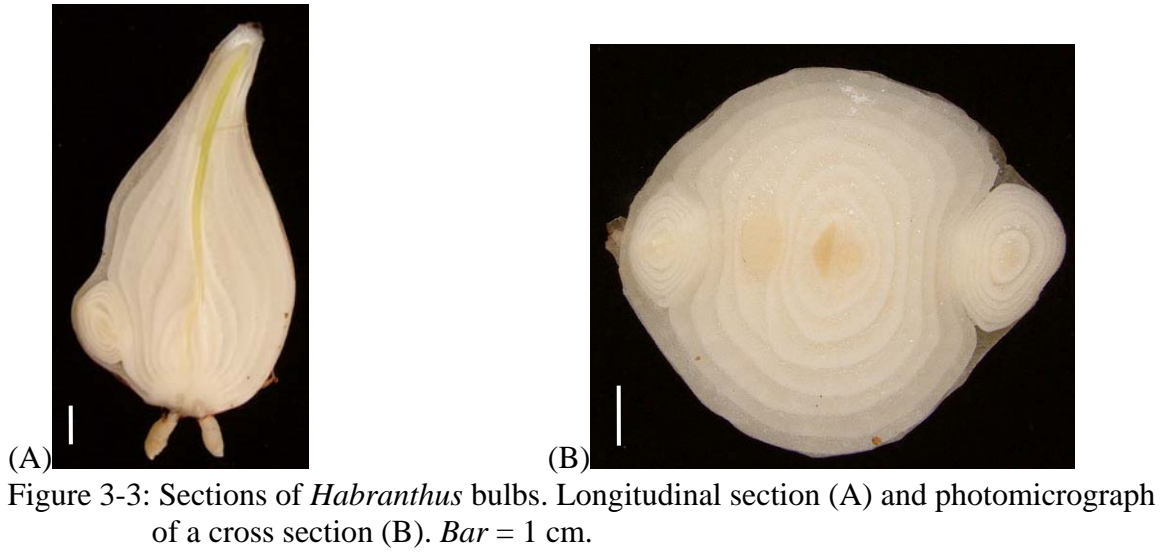


(A)



(B)

Figure 3-2: Sections of *Zephyranthes* bulbs. Longitudinal section (A) and photomicrograph of a cross section (B). *Bar* = 1 cm.



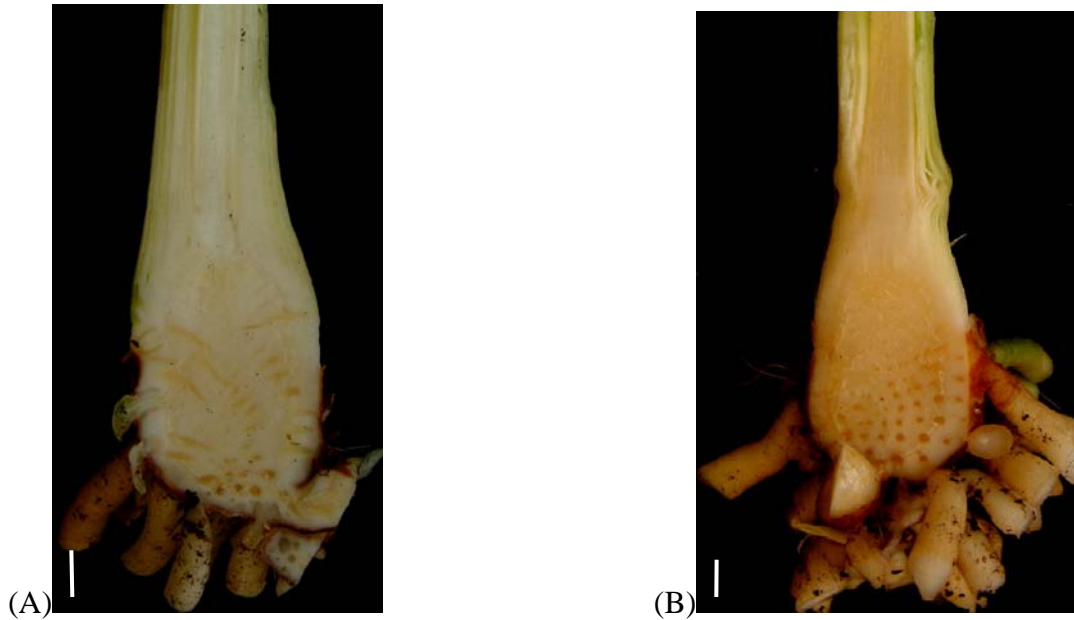


Figure 3-6: Longitudinal sections of an *Agapanthus* rhizome. Bar = 1 cm.

Leaf arrangement and morphology

Hippeastrum, *Habranthus* and *Zephyranthes* bulbs had similar leaf arrangements and leaf morphologies. Leaves were perennial, basal, simple, linear, glabrous, with entire margins and parallel venation. They emerged from the center of the bulb, with leaves two-ranked as the blade of each new leaf emerged 180° from the previous leaf, thus older leaves were always on the outside and younger leaves on the inside of the leaf cluster (Figure 3-7, 3-8 and 3-9). Each leaf was composed of a photosynthetic leaf blade and a non-photosynthetic storage leaf base (scale), which thickened during the growth cycle forming true bulbs.

Jones and Emsweller (1936) stated that each new leaf of *Allium cepa* developed on the side of the apical meristem opposite to the preceding blade by an upward growth of tissue surrounding the apical meristem. We observed that *Hippeastrum*, *Habranthus* and *Zephyranthes* leaf production occurred in a similar process. According to Mann (1960) *A. cepa* bulbs contain leaves that are morphologically distinct from each other, and

Kamenetsky (1994) classified them according to their function: protective, storage and assimilation.

Black et al. (1990) described *Hippeastrum* leaf blades as being up to 60 cm long and up to 5 cm wide. We observed that *Habranthus* leaf blades were 10 to 20 cm long and 1.5 to 2 cm wide; while *Zephyranthes* blades were 10 to 20 cm long and 1 cm wide. As part of this study, a determination of number of leaves produced weekly for a period of one year of *Habranthus* and *Zephyranthes* bulbs was made (Figures 3-41 and 3-42).

Agapanthus rhizomes have simple, linear, perennial glabrous leaves with entire margins and parallel venation. Leaf blades were up to 50 cm long and approximately 4 cm wide. Leaf arrangement was alternate but we observed that the leaves did not emerge from the center as they did in *Hippeastrum*, *Habranthus* and *Zephyranthes*, but from the lateral sides of the rhizome (one at a time). Thus, the older leaves were external to inner new leaves. Another distinction between *Agapanthus* and *Hippeastrum*, *Habranthus* and *Zephyranthes* bulbs was that leaf bases did not thicken and form scales, but remained thin and papery (Figure 3-10 C).

Scadoxus leaves were shorter, wider and thinner than leaves of *Hippeastrum*, *Habranthus*, *Zephyranthes* and *Agapanthus*, and they had a distinct oblong shape, prominent mid-ribs, undulating leaf margins, and leaf blades were 30 to 40 cm long and 9 to 13 cm wide. *Scadoxus* leaf arrangement was distinct from the previous four species. The first two leaves emerged singularly and were distinctly different from subsequent leaves. After the first two leaves senesced, a cluster of leaves arose from the center of the bulb all at once. They were held together by a structure called a pseudo-stem (a false stem formed by the sheathing and overlapping of the leaf bases – Figure 3-11 C).

Table 3-3 – Leaf size of plants examined

Species	Leaf blade length (cm)	Leaf blade width (cm)
<i>Hippeastrum</i>	Up to 60	5
<i>Habranthus</i>	10 to 20	1.5 to 2
<i>Zephyranthes</i>	10 to 20	1
<i>Scadoxus</i>	30 to 40	9 to 13
<i>Agapanthus</i>	Up to 50	4

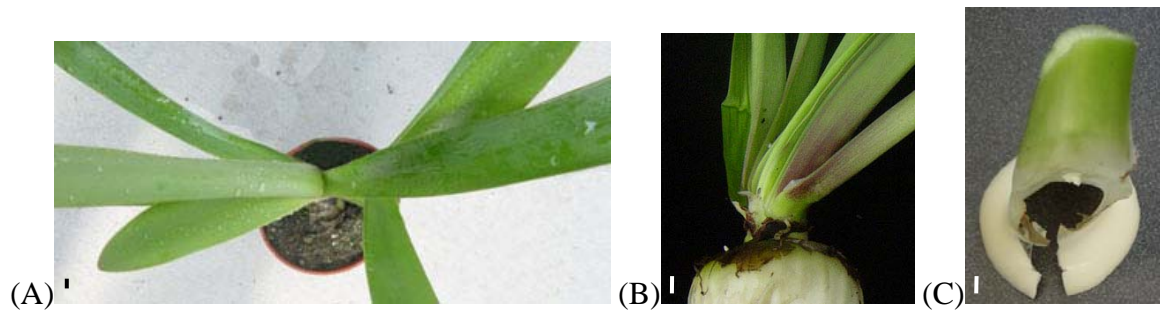


Figure 3-7: *Hippeastrum* leaf arrangement. From top (A), side (B) and individual leaf with continuous leaf base / scale (C). Bar = 1 cm.

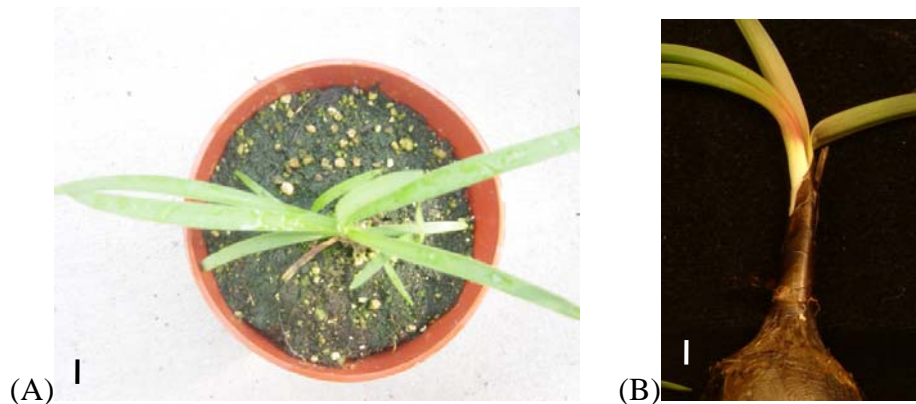
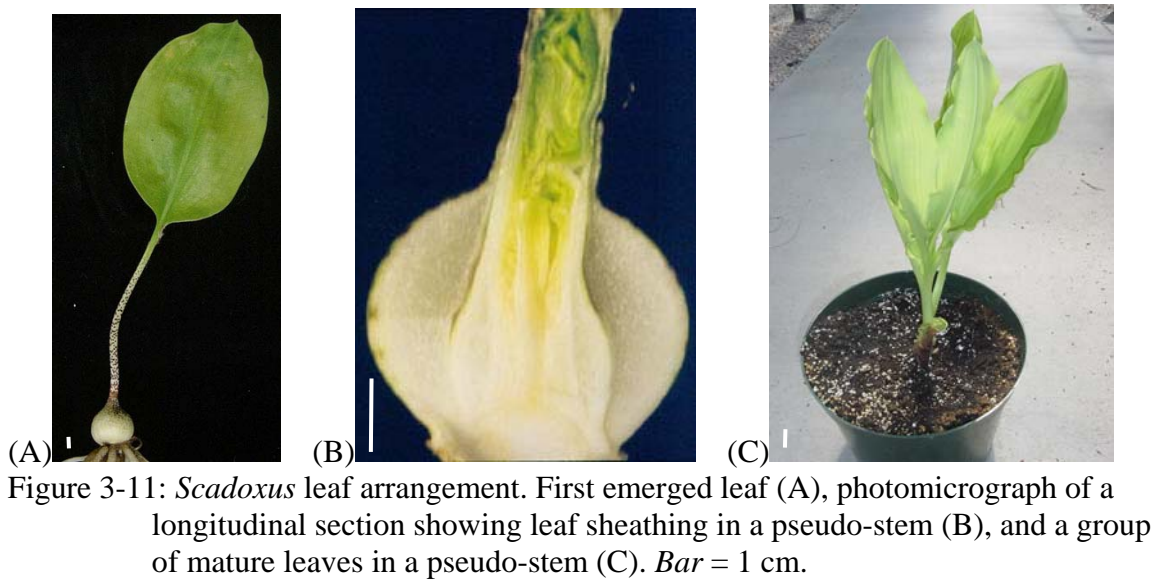
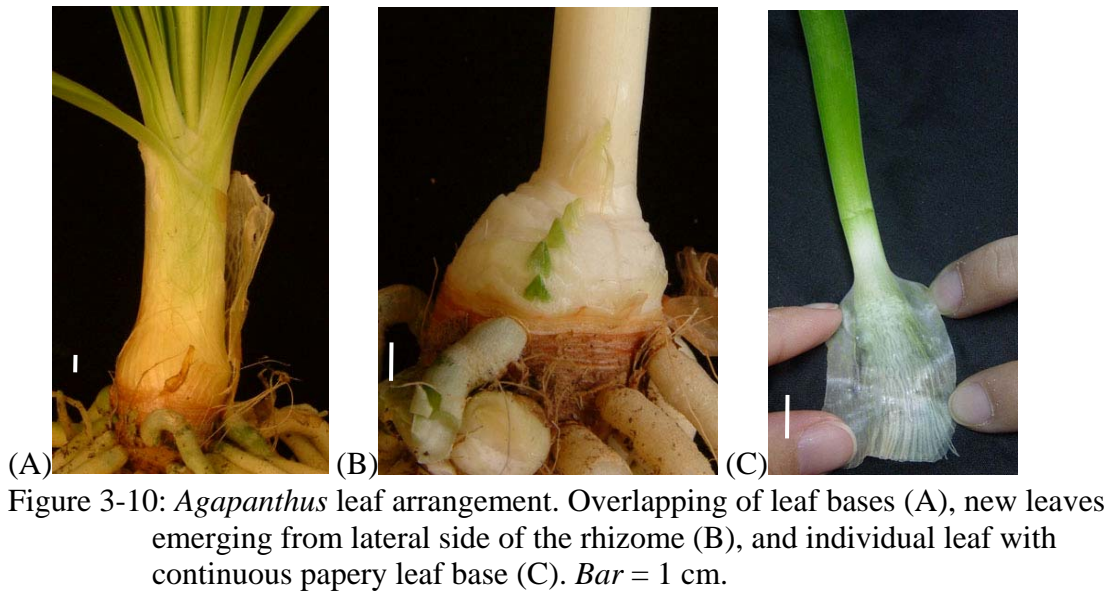
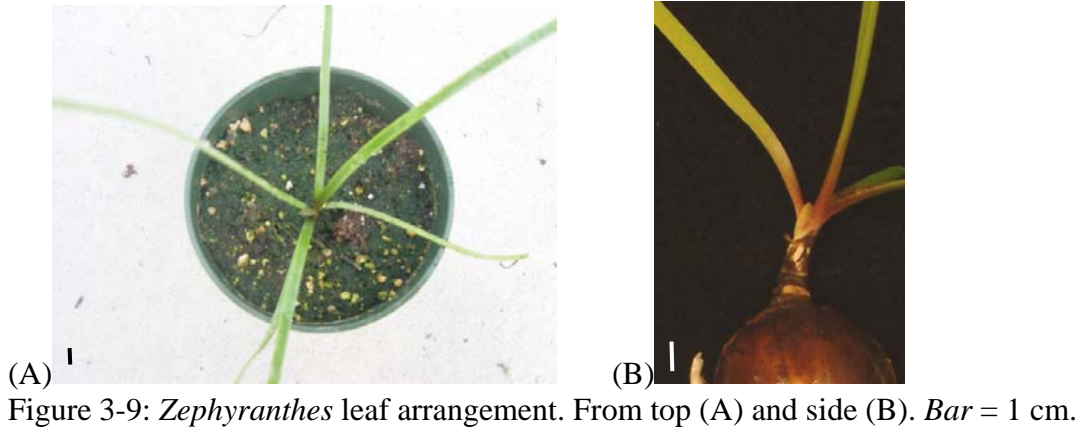


Figure 3-8: *Habranthus* leaf arrangement. From top (A) and side (B). Bar = 1 cm.



Floral initiation

Free hand cross sections of the bulbs used in this study revealed that floral bud formation was similar in *Hippeastrum*, *Habranthus* and *Zephyranthes* bulbs (Figures 3-12, 3-13 and 3-14). Flower buds were formed centrally in the apical meristem, and were initiated during the bulb's vegetative growth but did not emerge until the bulb reached a critical size. The elongation of flowering scapes occurred after the formation of 3 to 4 leaves on these species. We observed that flower buds were produced alternatively from each side of the meristem and formed a cross line in cross section (Figure 3-15). Since the apical meristem was constantly active (except during dormant periods) the older flower buds were located on the outer part of the bulb, identical to the leaf development pattern of these three species (Figure 3-16).

The average number of leaves initiated prior to inflorescence initiation depends upon the species in Amaryllidaceae bulbs. Hartsema and Leupen (1942) found that 11 leaves were initiated before floral initiation in *Amaryllis belladonna* and 8 in *Nerine bowdenii*; while there were 4 in *Hippeastrum hybridum* (Blaauw, 1931), 15 in *Scadoxus multiflorus* (Peters, 1971), 7 to 8 in *Leucojun aestivum* L. (Luyten and Van Waveren, 1938), 5 in *Lycoris radiata* and 10 in *Lycoris squamigera* (Mori and Sakanishi, 1977). We observed that there were 4 leaves formed between each inflorescence in both *Habranthus* and *Zephyranthes* bulbs (Table 3-4).

In *Allium cepa*, which is similar to *Hippeastrum*, *Habranthus* and *Zephyranthes*, the first stages in the development of the leaf and inflorescence primordia in the meristematic region are similar and an inflorescence bract is indistinguishable from a leaf blade, as both are protected by an involucre and a series of bracts (Jones and Emsweller, 1936).

Hippeastrum flowers are produced in groups of 2 to 6 in an umbel inflorescence and are attached to a hollow scape (around 50 cm tall) that can appear singly or more than one at the same time. A mature bulb produces about 12 leaves and 3 to 4 scapes per season. Inflorescences in *Habranthus* and *Zephyranthes* possess only one flower in most cases (rarely 2 flowers) attached to a hollow scape. We observed that a mature bulb can produce up to 4 scapes at the same time (figure 3-17). Both *Habranthus* and *Zephyranthes* bulbs can flower several times during one season, their flowers last for 2 to 3 days and leaves may or not be present during flowering. Throughout this study it was observed that it takes four days for a *Habranthus* flower to transition from visible flower bud to an open flower (Figure 3-18).

In *Scadoxus* bulbs, flower buds and pseudo-stems are formed side by side at the apical meristem (Figure 3-19), one of each per season. The inflorescence scape which is a spherical umbel (25 cm in diameter) consisting of up to 200 flowers, emerges first and then the foliage held by a solitary pseudostem emerges (Figure 3-20). The inflorescence lasts for 1 to 2 weeks, while the pseudo-stem lasts for a few months. Their flowering season is in late summer to early autumn.

We observed that *Agapanthus* rhizomes did not produce inflorescence and leaves in the same region of the basal plate. Inflorescences were formed in the apical meristem located in the central part of the basal plate while leaves were developed from apical meristems distributed along the lateral sides of the basal plate (Figure 3-21A).

Agapanthus inflorescences are umbels with 8 to 20 flowers held by stiff erect scapes that arise from the center of the rhizome (Figure 3-21B). Inflorescences last for 1 week and flowers appear during summer.

Table 3-4 – Relationship between leaf and flower formation, and number of flowers per inflorescence of plants examined

Species	Leaves between inflorescences	Number of flowers per inflorescence
<i>Hippeastrum</i>	4	2 to 6
<i>Habranthus</i>	4	1 to 2
<i>Zephyranthes</i>	4	1 to 2
<i>Scadoxus</i>	15	Up to 200
<i>Agapanthus</i>	-	8 to 20

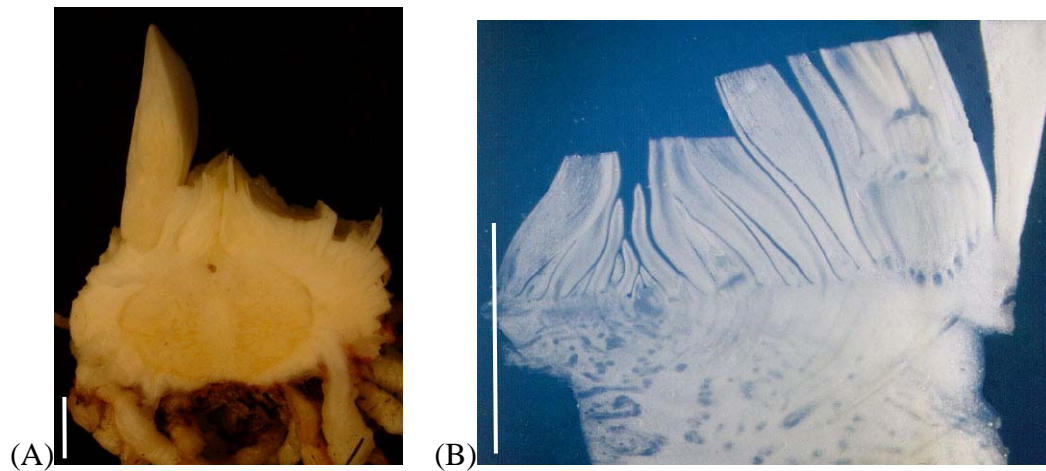


Figure 3-12: Longitudinal sections of a *Hippeastrum* bulb. Free-hand section (A) and photomicrograph (B). *Bar* = 1 cm.

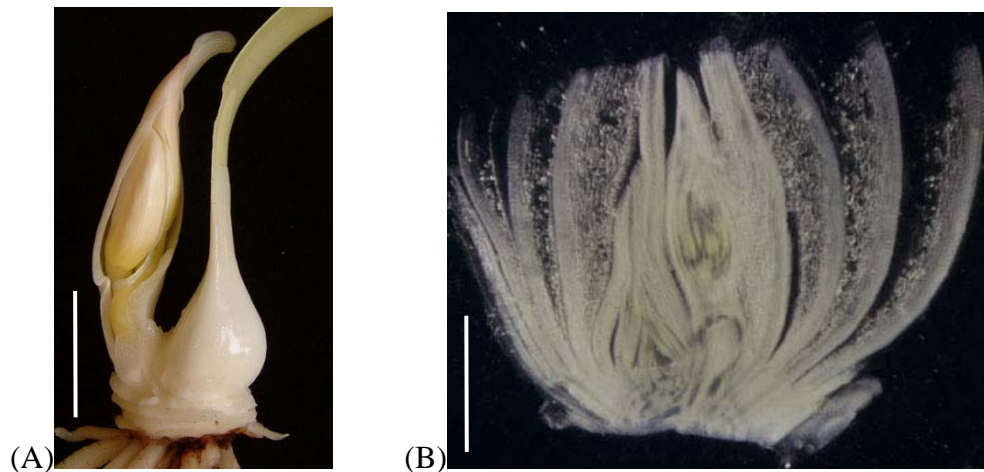


Figure 3-13: Sections of *Habranthus* bulbs. Inner part with outer scales removed (A) and photomicrograph of a longitudinal section (B). *Bar* = 1 cm.

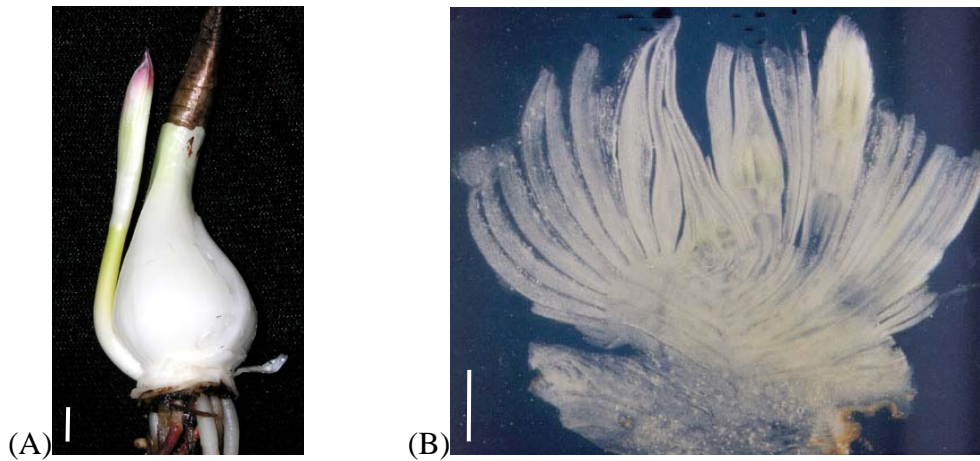


Figure 3-14: Sections of *Zephyranthes* bulbs. Inner part with outer scales removed (A) and photomicrograph of a longitudinal section (B). *Bar* = 1 cm.



Figure 3-15: Cross section of a *Habranthus* bulb (stained with Safranin), showing the alignment of flower buds. *Bar* = 1 cm.



Figure 3-16: Longitudinal section of a *Habranthus* bulb (stained with Safranin), showing flower buds. *Bar* = 1 cm.



Figure 3-17 *Habranthus* bulb with three flower stalks. *Bar* = 10 cm.

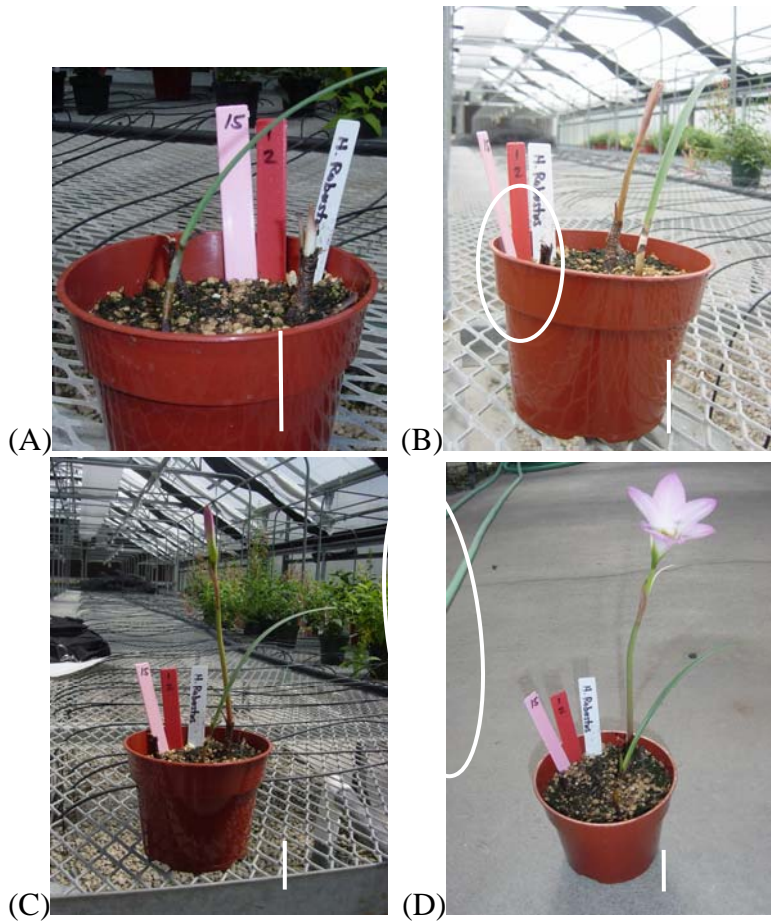


Figure 3-18 Development of a *Habranthus* flower. Flower bud (circled) emerged from soil on day 1 (A), flower stalk elongated (circled) on day 2 (B), flower stalk (circled) elongated on day 3 (C) and open flower on day 4 (D). *Bar* = 5 cm.

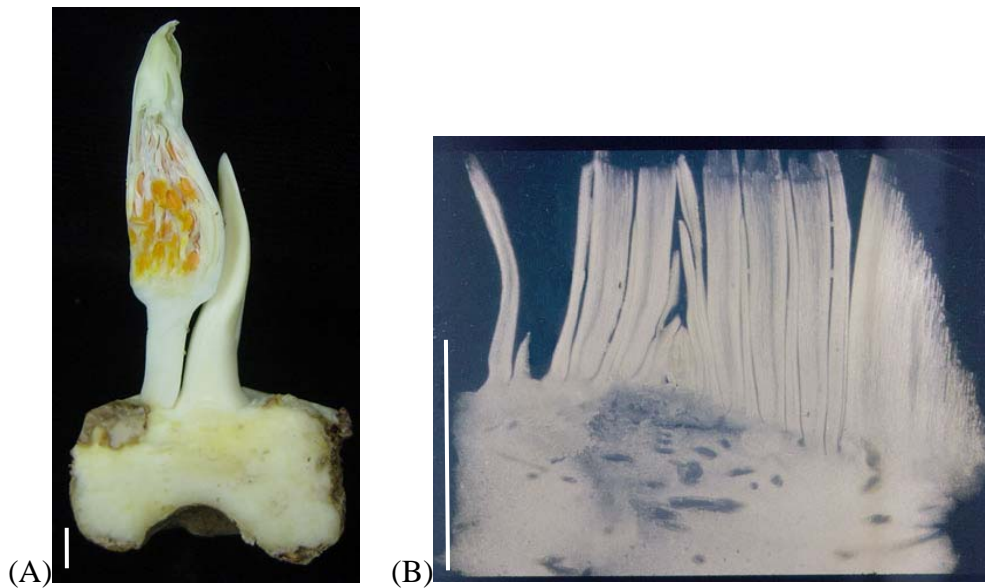
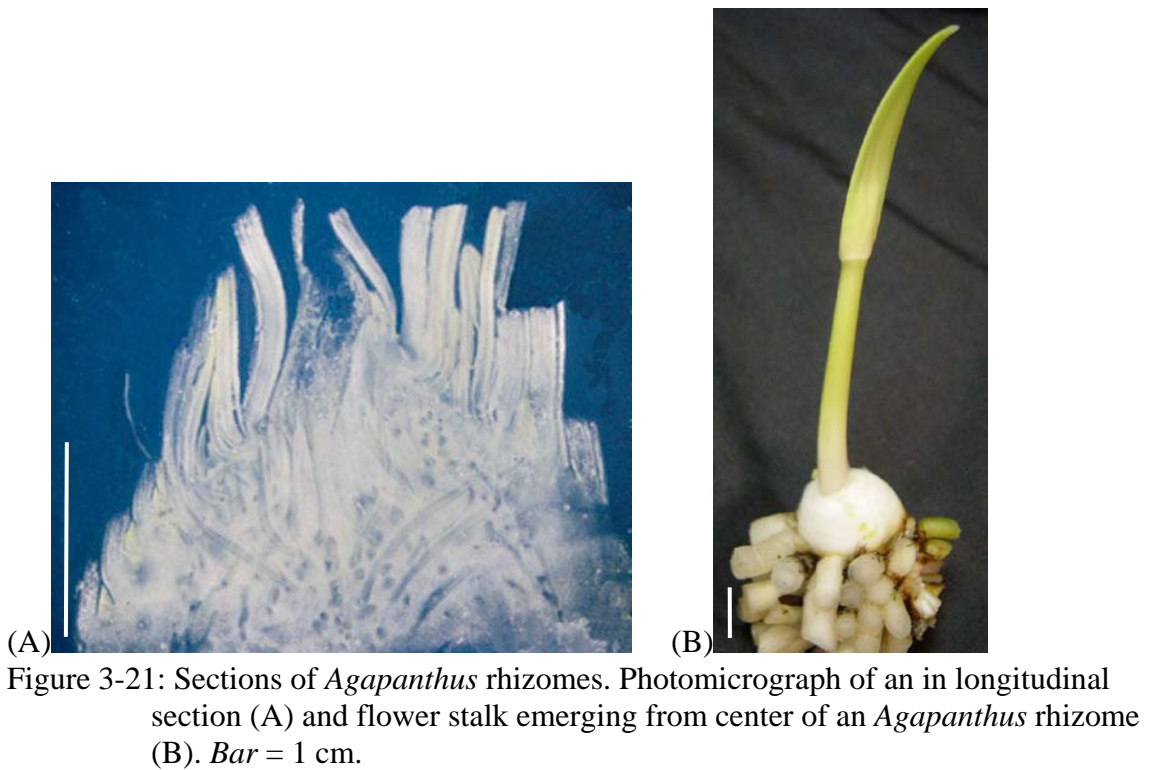


Figure 3-19: Sections of *Scadoxus* bulbs. Inner part with outer scales removed (A) and photomicrograph of a longitudinal section (B). *Bar* = 1 cm.



Figure 3-20: Flower stalk emerged and pseudo-stem arising from a *Scadoxus* bulb. *Bar* = 1 cm.



(A) (B)
Figure 3-21: Sections of *Agapanthus* rhizomes. Photomicrograph of an in longitudinal section (A) and flower stalk emerging from center of an *Agapanthus* rhizome (B). *Bar* = 1 cm.

Meristematic region

The apical meristem consists of a group of undifferentiated cells located at the apex of a shoot or a root that continuously produces new cells. The apical meristem was first observed in 1759 by Caspar Wolff, who recognized it as being the center of organ and cell formation (Tooke and Battey, 2003).

There are four types of meristems: single apical cell or initial (that can be lenticular or tetrahedral), cluster of apical cells, zoned apex and tunica corpus type. The first two types are characteristic of ferns and other lower plants, the third type is characteristic of gymnosperms, and the fourth type occurs in angiosperms. The five species of tropical bulbs studied have the tunica-corporis type of shoot meristem (Dengler, 2002).

Studies of meristems reflect the technology of the time period in which they were conducted. During the 19th and 20th centuries, observational analysis were made on sections of living and preserved tissue, from 1940 to 1970, experimental manipulations were made with microsurgery, radioisotopes, labeling and chimeric analysis. Since 1970, genetic and molecular analyses have been employed to gain information on plant meristems (Tooke and Battey, 2003).

Tulip apices were described by Sass (1944) as a tunica-corporis type, during the vegetative state and flower differentiation. The vegetative apex of the principal axis is deeply buried in the bulb, just above the basal plate, and it is 2 to 3 mm long and 1 to 2 mm wide. The apex is a short dome 100 to 125 μm high and 300 to 375 μm broad and approximately semicircular in longitudinal section. The apical meristem of *Allium cepa* has also been described as a low, circular, dome-shaped mass of cells (Hoffman, 1933).

In tulips, the tunica consists of a single layer of cells, followed by several layers of the corpus. The leaf primordia results from division of cells in the first layers of the corpus and rapidly involve zone three or four cells deep. According to Rees (1972), different plants can have a tunica with more than one layer of cells. That is the case in *Iris*, which possesses a tunica of two layers of cells, and *Lilium candidum*, which has a tunica formed by three layers of cells. This study did not identify the number of cell layers in the tunica of each species but clarified the cellular layout of the apical region in all five species studied.

Hippeastrum, *Habranthus*, *Zephyranthes* and *Scadoxus* bulbs had a similar arrangement and their apical meristematic regions were located in the basal plate, as described for *Allium cepa* (Mason, 1979). The apical meristem and youngest leaf primordia were surrounded by scales (Figures 3-22 to 3-29). Blaauw (1931) found that the first morphological sign of inflorescence initiation in *Hippeastrum* bulbs was a slight increase in the size of the apical meristem.

Agapanthus rhizomes were distinctly different than *Hippeastrum*, *Habranthus*, *Zephyranthes* and *Scadoxus*, as they had a centrally located apical meristem responsible for flower formation and several lateral meristems located on the sides of the rhizome, which were responsible for leaf production (Figures 3-30 and 3-31).

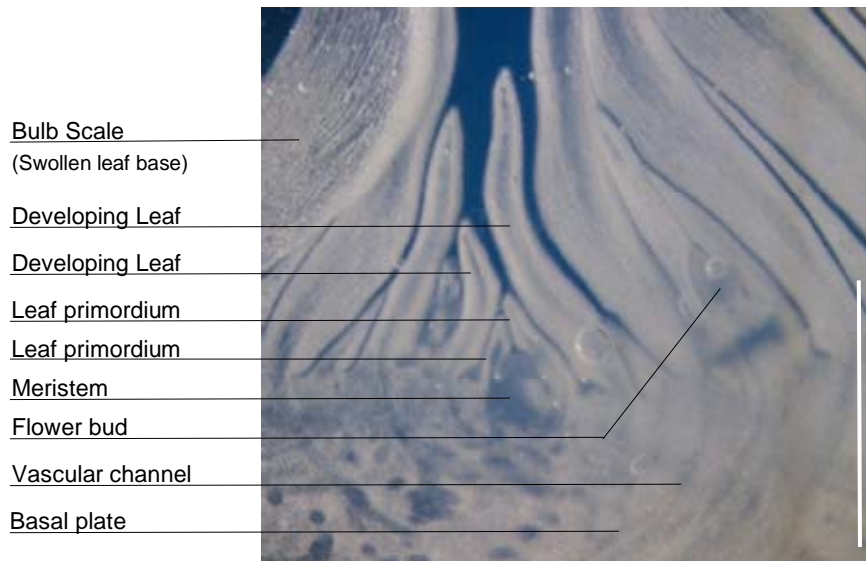


Figure 3-22: Photomicrograph of the meristematic region of a *Hippeastrum* bulb. Bar = 1 cm.

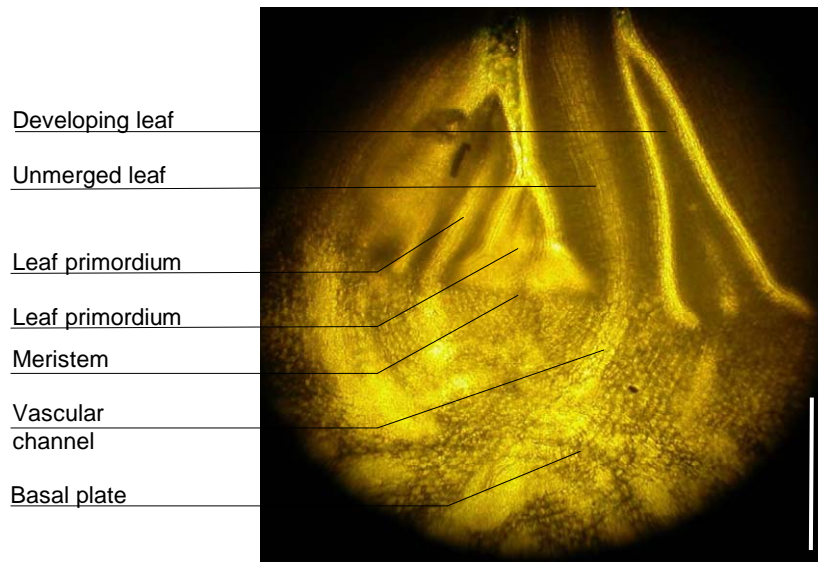


Figure 3-23: Photomicrograph of the meristematic region of a *Hippeastrum* bulb. Bar = 1 cm.



Figure 3-24: Photomicrograph of the meristematic region of a *Habranthus* bulb. *Bar* = 1 cm.

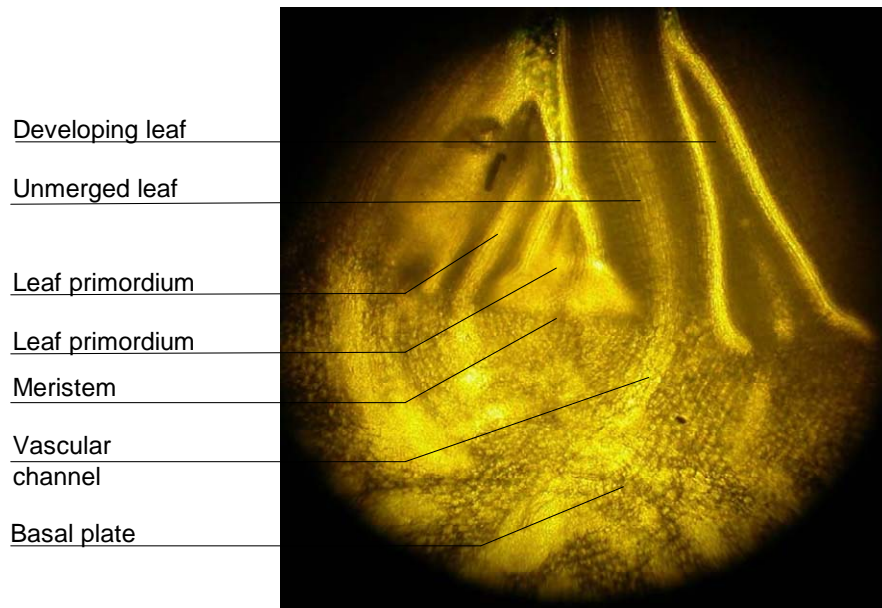


Figure 3-25: Photomicrograph of the meristematic region of a *Habranthus* bulb. *Bar* = 1 cm.

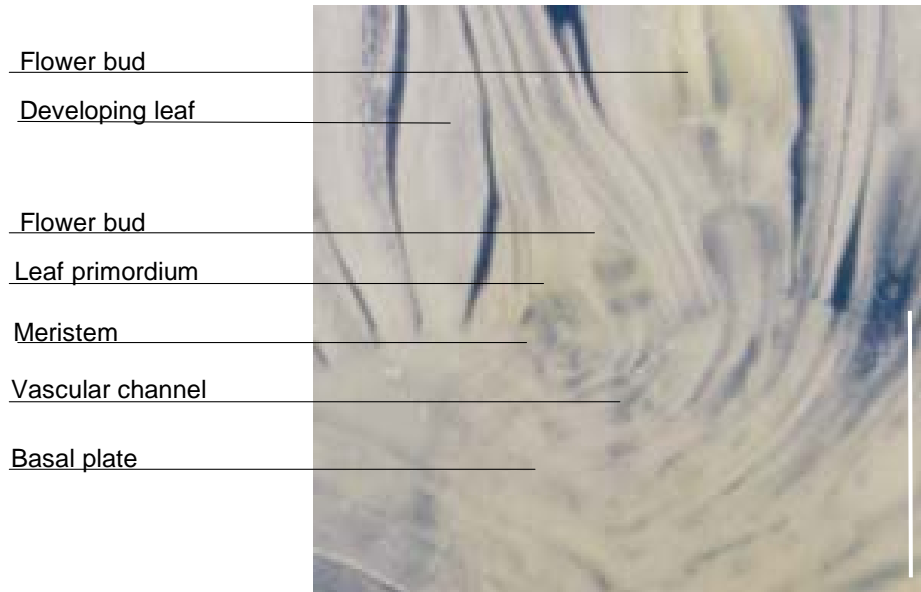


Figure 3-26: Photomicrograph of the meristematic region of a *Zephyranthes* bulb. *Bar* = 1 cm.

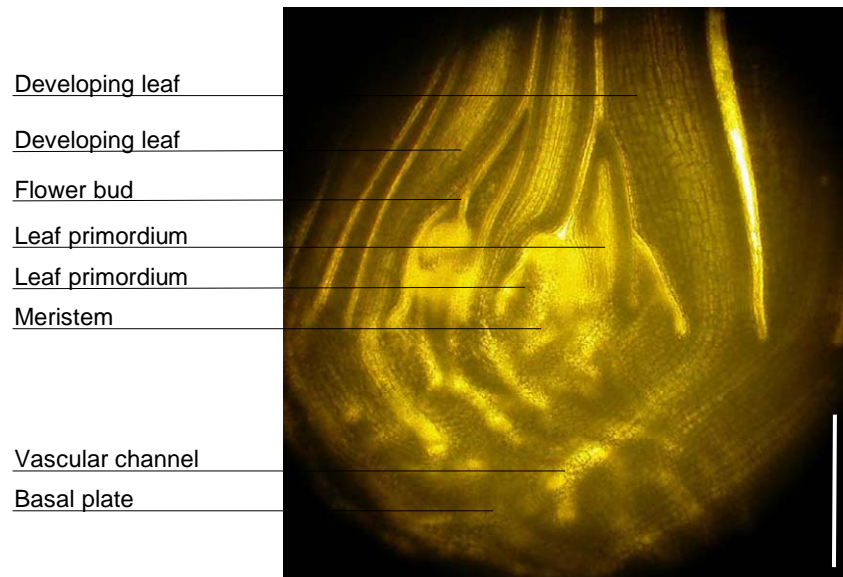


Figure 3-27: Photomicrograph of the meristematic region of a *Zephyranthes* bulb. *Bar* = 1 cm.



Figure 3-28: Photomicrograph of the meristematic region of a *Scadoxus* bulb. *Bar* = 1 cm.

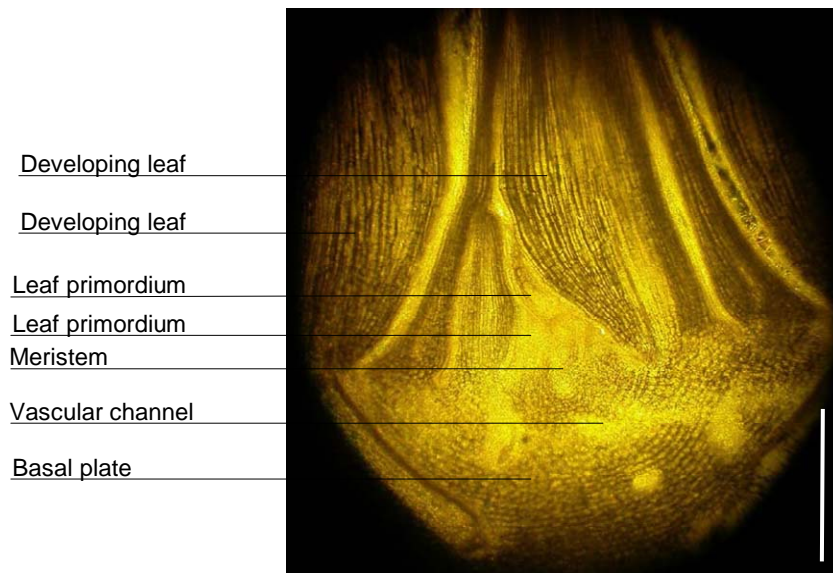


Figure 3-29: Photomicrograph of the meristematic region of a *Scadoxus* bulb. *Bar* = 1 cm.

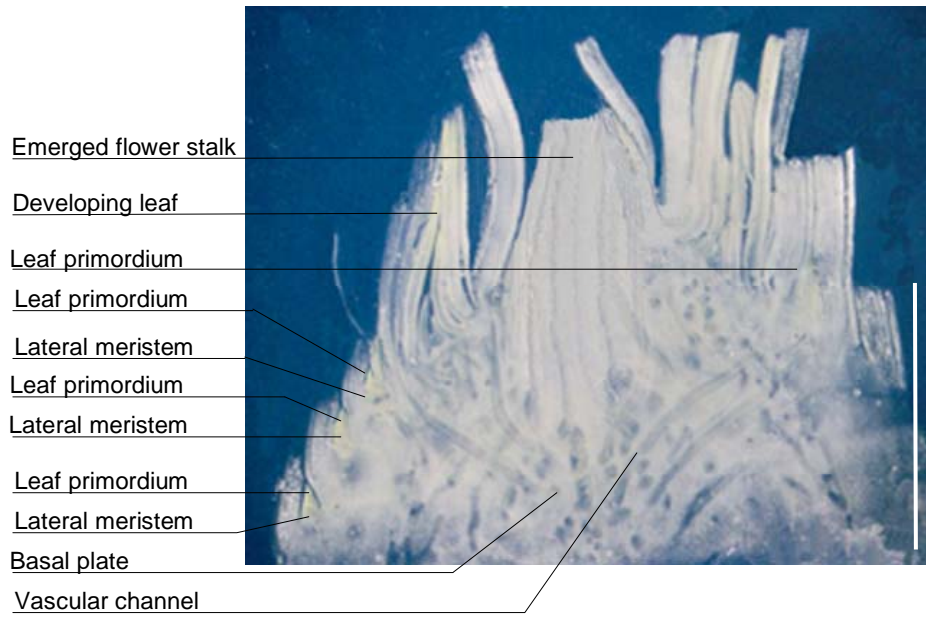


Figure 3-30: Photomicrograph of the meristematic region of an *Agapanthus* rhizome. *Bar* = 1 cm.

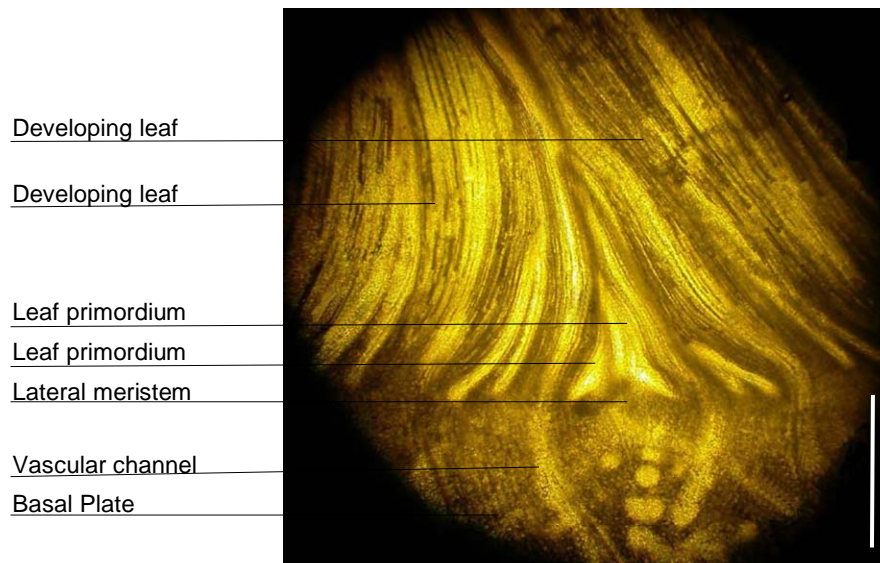


Figure 3-31: Photomicrograph of the meristematic region of an *Agapanthus* rhizome. *Bar* = 1 cm.

General anatomical and morphological arrangement

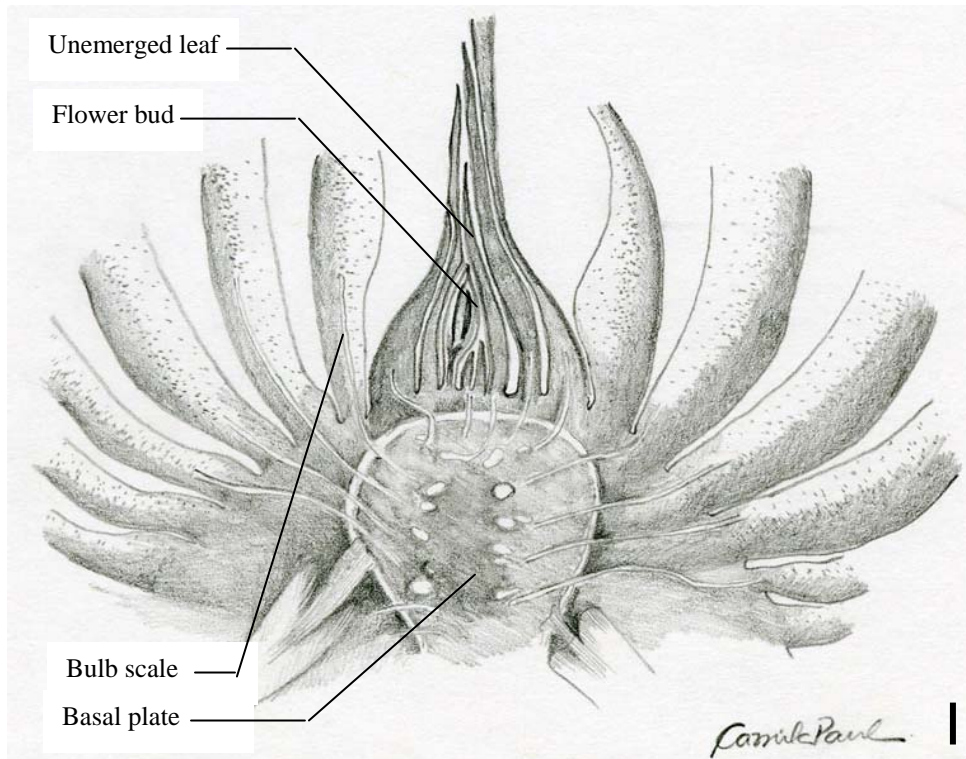


Figure 3-32: Longitudinal section of a *Hippeastrum* bulb showing its general anatomy and morphology. Bar = 1cm.

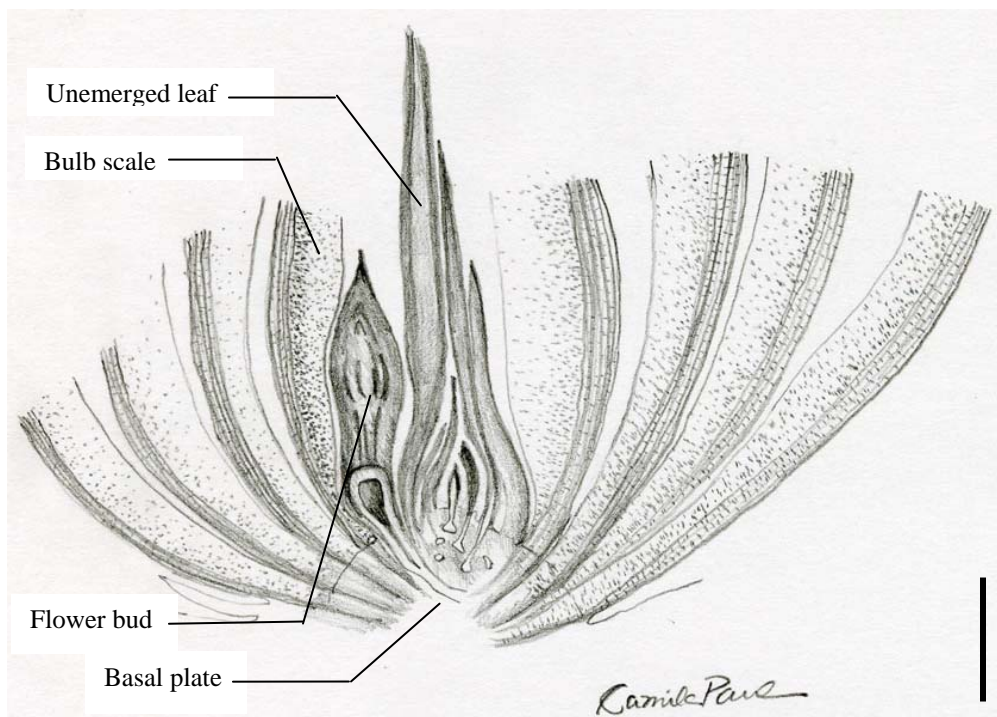


Figure 3-33: Longitudinal section of a *Hippeastrum* bulb showing its general anatomy and morphology. Bar = 1cm.

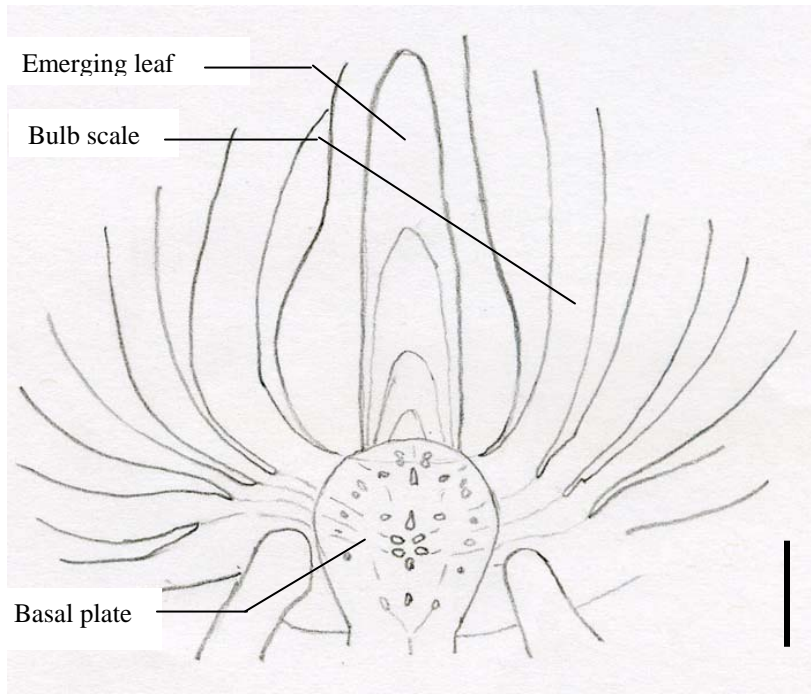


Figure 3-34: Longitudinal section of a *Zephyranthes* bulb showing its general anatomy and morphology. *Bar = 1cm.*

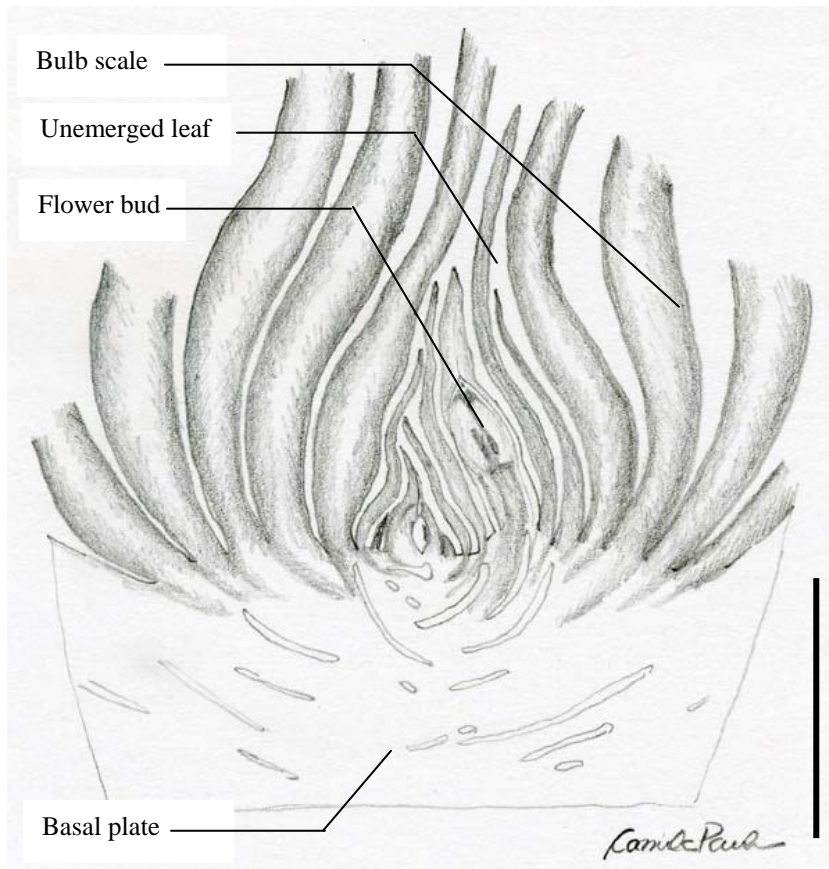
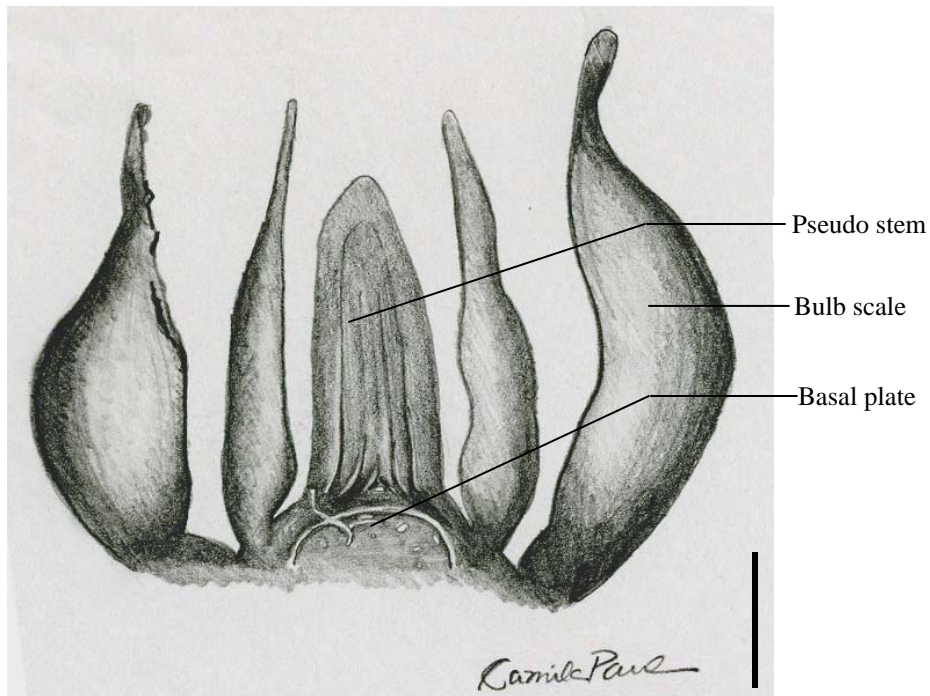
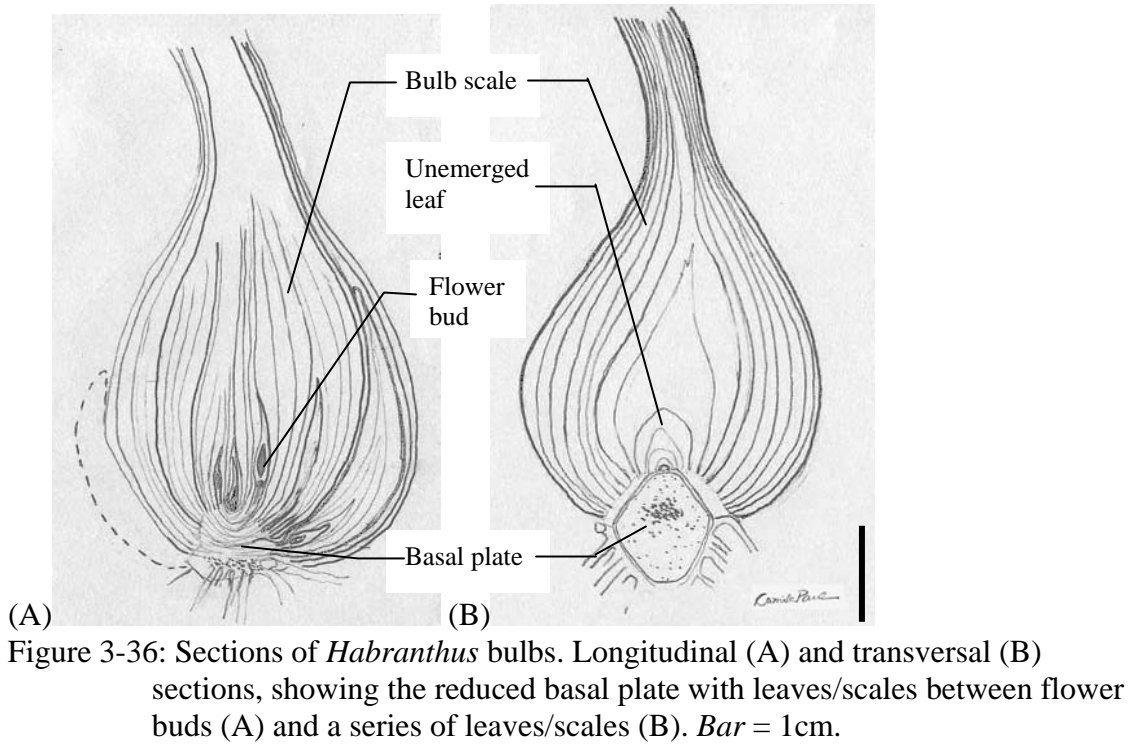


Figure 3-35: Longitudinal section of a *Zephyranthes* bulb. *Bar = 1cm.*



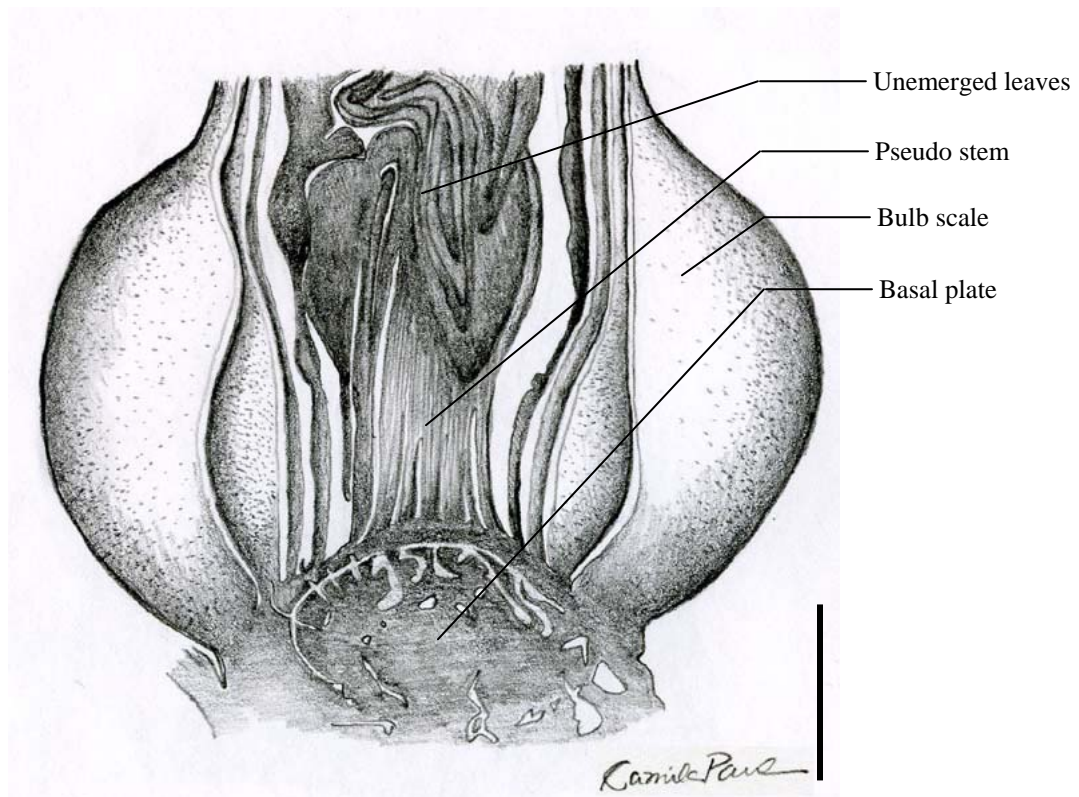


Figure 3-38: Longitudinal section of a *Scadoxus* bulb showing its general anatomy and morphology. *Bar* = 1cm.

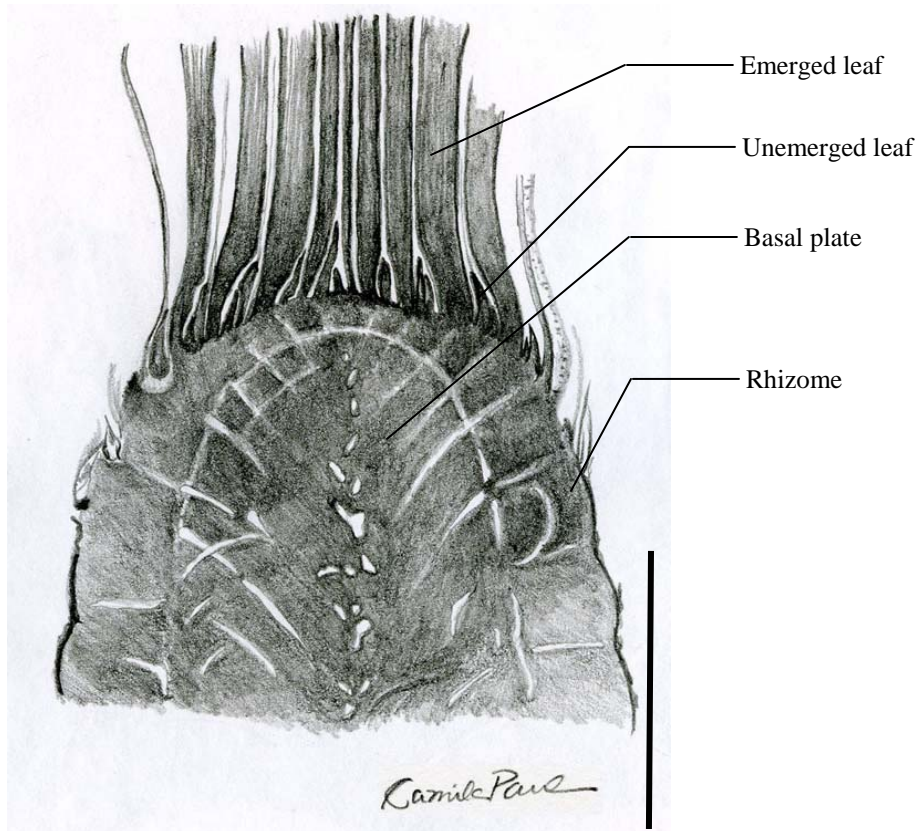


Figure 3-39: Longitudinal section of an *Agapanthus* rhizome showing its general anatomy and morphology. Bar = 1cm.

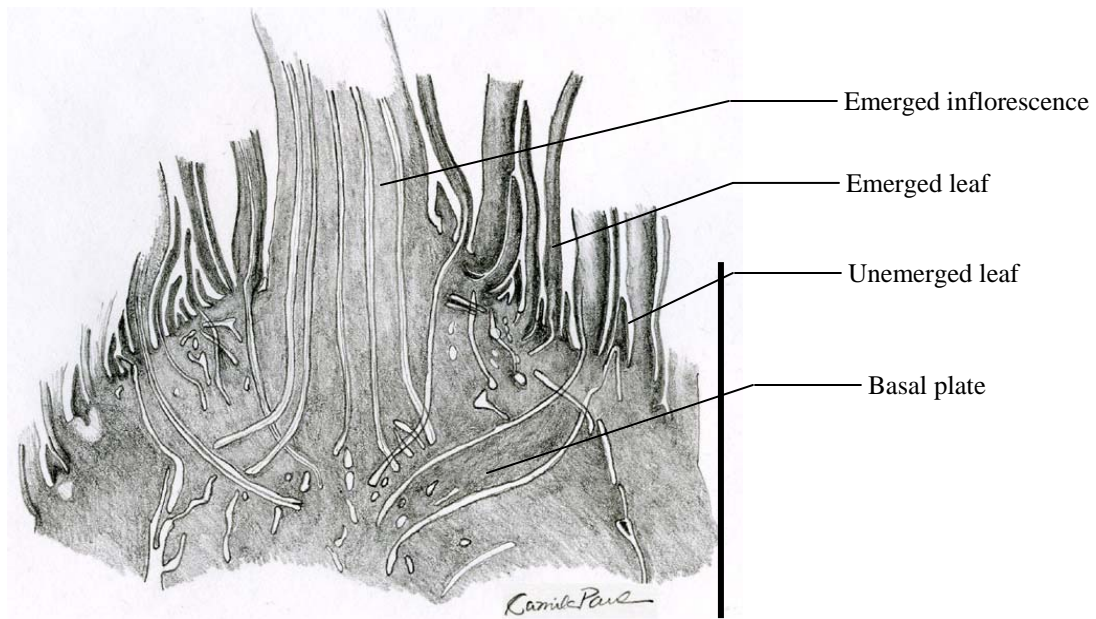


Figure 3-40: Longitudinal section of an *Agapanthus* rhizome showing its general anatomy and morphology. Bar = 1 cm.

Experiment 1

The storage organs of geophytes are able to supply food reserve for rapid leaf growth at the beginning of their growth and reproductive cycle, after cold winters and/or dry seasons (Rees, 1972). In bulbs with hysteranthous leaves (flowers and leaves develop in separate seasons), an accumulation of storage materials is a prerequisite for flowering (Burt, 1970). In bulbs with synanthous leaves, which are present when plants flower, the storage materials provide for early growth of photosynthetic organs and allocation of resources for flowering originate from the storage organ and from existing leaves (Dafni et al., 1981).

Phenological differences can be summarized into two groups based on the speed of leaf development and duration of photosynthetic period. The rapid route is a characteristic of bulbs that produce leaves quickly in order to compensate for a short photosynthetic period or when there is a limiting factor, such as moisture (most common), light or temperature. The slow route is characteristic of bulbs that produce leaves slowly, under long photosynthetic periods or when moisture, light and temperature are not limiting factors (Dafni et al., 1981).

Of the five species used in this morphological study, *Habranthus* and *Zephyranthes* were the least investigated by other researchers, and since these two genera were used in the subsequent phases of this study an experiment was designed to understand their leaf and flower production. *Habranthus* and *Zephyranthes* have perennial storage organs and synanthous leaves. According to Dafni et al. (1981) this type of bulb accumulates more reserves than required for a growth cycle which includes completion of flowering and seed production even if the net production (by existing leaves) is insufficient. Therefore relatively slight differences are expected from year to year in the abundance of flowering.

The following experiment was performed to compare leaf and flower production of *Habranthus* and *Zephyranthes* during a period of one year.

Materials and Methods: On the first week of January 2005, 12 *Habranthus robustus* bulbs and 12 *Zephyranthes* bulbs were planted in 15 cm plastic pots, one bulb per pot, using a sphagnum peat based Fafard No. 2 soilless growing medium (Agawam, MA) consisting of 70% Canadian sphagnum peat, 10% perlite and 20% vermiculite. Plants were placed in a greenhouse with 11% shade, natural photoperiod and a temperature range of 31/24°C (day/night). Plants received 250ml of water and were fertilized at each irrigation with Peters Professional 'Florida Special' water soluble fertilizer 20N-4.7P-16.6K (Scotts Co., Marysville, OH) with N at 150 mg.L⁻¹. Bulbs used in this experiment were obtained from the University of Florida stock and had been grown in ground beds for a year prior the beginning of the experiment.

This experiment was performed from January to December 2005. Data were collected twice a month during the entire year and the number of leaves and flowers present at the moment of data collection were recorded. Data was analyzed by taking the mean number of leaves and flowers per total of bulbs at each observation, using the SAS statistical package version 8.02 (Cary, NC). Results demonstrate the performance of leaf and flower production of these two species during 2005.

Results: *Habranthus* bulbs demonstrated a predictable performance of leaf production with more leaves at the beginning and end of the year when not flowering and a gradual reduction of leaf emergence as flowering season occurred (Figure 3-41). *Zephyranthes* also produced more leaves in the beginning and end of the year, but their flowering season did not coincide with a period of reduced leaf production. In April

Zephyranthes bulbs produced the least number of leaves followed by a gradual increase until August when a slight drop occurred and the flowering season started. Production of leaves increased again until October, when another reduction occurred followed by an increase of leaf emergence until the end of the year (Figure 3-42).

Comparing both figures (3-41 and 3-42) makes it clear that these two species possess distinct patterns of leaf production. *Habranthus* bulbs had fewer leaves emergent when flowering, while leaves of *Zephyranthes* bulbs continued to emerge during flowering. Overall, *Zephyranthes* bulbs had a greater quantity of leaves during the entire year but with oscillations, while *Habranthus* bulbs demonstrated a more uniform progress with a gradual decrease and increase in leaf correlated with the flowering period. This information is valuable for the landscape use of these two species as they generate distinct appearances in a garden; *Zephyranthes* have copious foliage in combination with their flowers and *Habranthus* have few leaves when flowering.

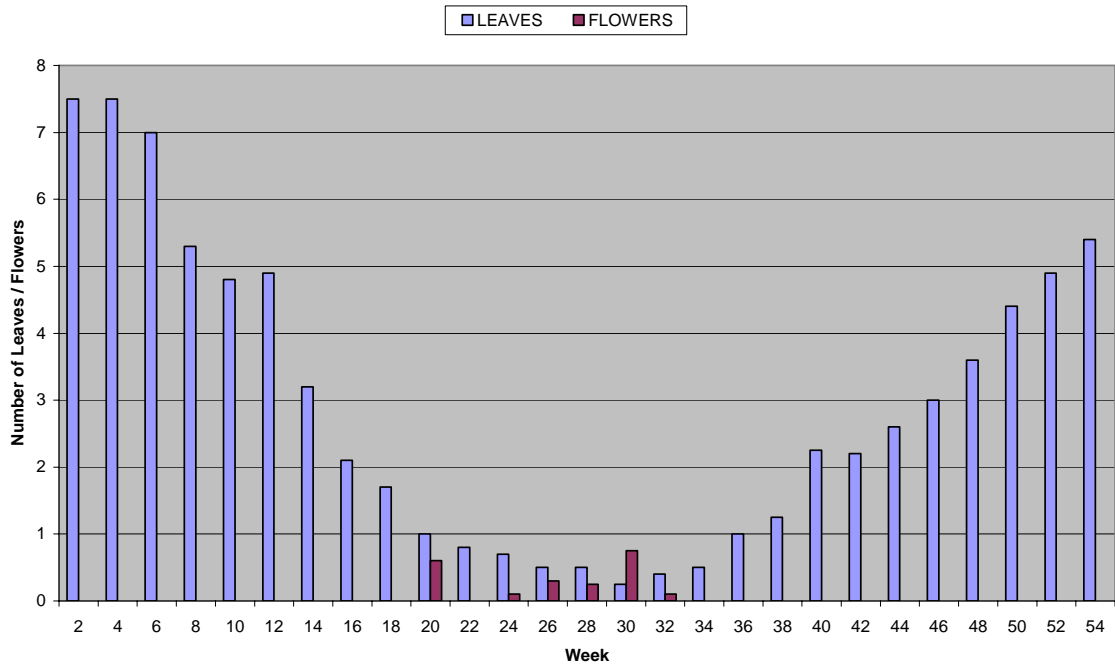


Figure 3-41: Number of leaves and flowers produced by *Habranthus* bulbs in 2005

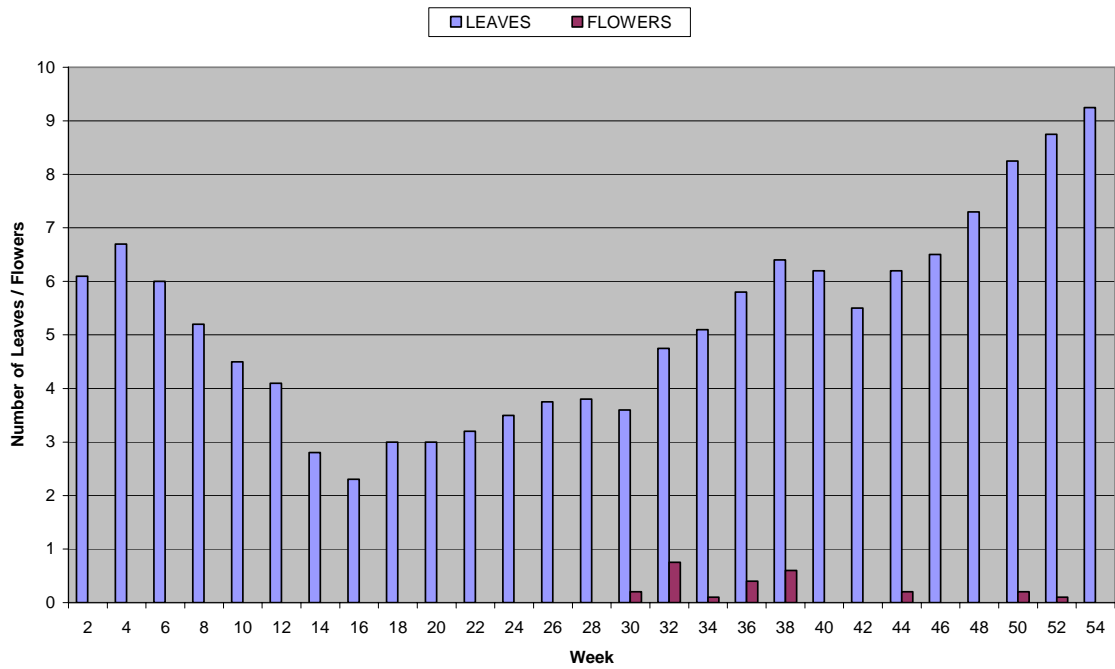


Figure 3-42: Number of leaves and flowers produced by *Zephyranthes* bulbs in 2005

CHAPTER 4
ENVIRONMENTAL EFFECTS – FERTIGATION FREQUENCY AND FERTILIZER
RATES ON FLOWERING IN *Habranthus robustus* AND *Zephyranthes* spp.

The primary goal of a flower bulb grower is to produce true-to-type, essentially disease- and insect-free plants that flower successfully. Proper water management and fertilization are among the critical factors to accomplish that goal.

Most all ornamental bulbs along with onion and garlic (related vegetable crops) are sensitive to water deficit. When the soil is kept relatively moist, root growth is reduced which favors bulb enlargement and consequently flowering, since flower production in bulbs is highly affected by bulb size in several species including *Hippeastrum*, *Habranthus*, *Zephyranthes* (Theron and De Hertogh, 2001). A frequent and light irrigation is commonly practiced on both vegetable and ornamental bulbous crops, while over-irrigation is avoided since it can increase the incidence of several diseases (Hafeez, 1984).

Soil water deficits inhibit leaf expansion, as nutrient uptake is reduced because of reduced transpiration rates (Russel, 1977). In onion, transpiration rates, photosynthesis and growth are lowered by mild water stresses (Begun et al., 1990). Stressed onions often bulb too early, produce small-sized bulbs and have an increased rate of bulb split. All these factors can reduce marketable yields (Hegde, 1986).

The soil moisture requirement of onions is influenced by several factors including cultivar used, soil type and temperature, light levels and other environmental factors. A crop can be grown to maturity under a soil moisture deficit, but higher yields were

associated with irrigation frequencies that eliminated soil moisture deficits (De Lis et al., 1967).

Minimizing the period when leaf and flower tissues are wet by using proper irrigation management reduce moisture and consequently the development of most fungal and bacterial caused diseases. Fertilizer formulations also influence disease development in flower bulb crops since they can alter soil pH, therefore fertigation should be carefully planned in bulb production.

Nutrient requirements for greenhouse and outdoor bulb production can be grouped into four categories according to De Hertogh and Le Nard (1993): 1) bulbs containing sufficient nutrients to produce high quality potted plants or cut flowers without additional fertilization such as *Hippeastrum*, *Hyacinthus* and *Narcissus*; 2) bulbs that require either no additional fertilization or in which the application of $\text{Ca}(\text{NO}_3)_2$ can eliminate or reduce physiological disorders such as Dutch irises and tulips; 3) bulbs that require low fertilization programs, such as *Anemone*, *Freesia* and *Liatris*; and 4) bulbs that require moderate fertilization programs, such as *Dahlia*, *Gladiolus*, *Lilium* and *Ranunculus*.

Fertilization programs have been evaluated on several genera of flowering bulbs to determine their effect on flowering, flower quality, bulb growth, bulb yield, and seed yield. Flowering as well as bulb growth of *Iris*, *Tulipa* and *Lilium* were compared when plants were treated with 10.7:3.9, 12.1:5.1, 14.3:3.9, or 17.9:3.9 meq/L of N and K. (Lee et al., 2005). Results showed that flowering was slightly accelerated when *Iris* was grown with 10.7:3.9 meq/L N:K; flowering of *Tulipa* was promoted by 14.3:3.9 meq/L N:K; and neither growth or flowering of *Lilium* was significantly different between any fertilizer treatments. When 0, 30, 70, 120, 180, 250, 330, 420, and 520 kg N ha⁻¹ were applied to

Lachenalia cultivars, results demonstrated that increased rates of nitrogen had a positive influence on bulb fresh mass and circumference (Engelbrecht, 2004). Three levels of fertilizer, 50, 100, and 200 mg l⁻¹ N, were applied to *Curcuma alismatifolia* of the Zingiberaceae family and results showed that plants treated with the highest fertilizer level were taller, produced more stems per cluster, had larger diameter rhizomes, a greater number of new rhizomes and better flower quality (Ruamrungsri et al., 2005).

In onions, irrigation intervals of once a week, every 10 days and every other week were investigated in association with fertilizer levels of 90 and 180 kg N/ha to ascertain the optimum irrigation interval and fertilizer level that produced the highest yields of good quality bulbs. Results demonstrated that the 10 day irrigation interval and the 90 kg N/ha rate resulted in the highest yield per ha and the greatest average bulb weight. However, no treatment interactions were detected (Hassan, 1984). Irrigation frequencies were also investigated on *Caladium* tubers in a pot study and results showed that three times a week provided the best yield response compared to once a week and twice a week (Overman and Harbaugh, 1988).

Extremely limited information was found in the horticultural literature regarding *Habranthus* and *Zephyranthes* fertigation frequencies or fertilizer regimes. The present study was designed to address this issue and two experiments were conducted: 1) to determine optimal fertigation frequency for these two genera in order to achieve an extended flowering season with increased number of flowers per bulb, and 2) to determine optimal fertilizer rates for bulb development.

In the first experiment, different fertigation frequencies (twice a week, once a week and every other week) were applied to *Habranthus robustus* and *Zephyranthes* spp. to

determine their effect on flowering and/or on bulb development (number of leaves, number of offsets, bulb size, bulb weight and number of buds). In the second experiment, different fertilizer rates 0, 75, 150 and 300 ppm N, were applied to *Habranthus robustus* and *Zephyranthes* spp to verify their effect on flowering and bulb development.

The *Habranthus* species used in this project - *Habranthus robustus*, is the most popular species in the genus; it is native to Brazil but grows very well in Florida. The *Zephyranthes* species used in this projects were: Z. ‘Paul Niemi’, Z. JoAnn’s Trial’, and Z. ‘Fadjar Pink’ which were hybridized by Fadjar Marta in Jakarta, Indonesia.

Experiment 1: Influence of three different fertigation treatments on number of flowers and bulb development in *Habranthus robustus* and *Zephyranthes* spp.

Materials and Methods: Bulbs used in this experiment were obtained from University of Florida stock, which had been grown in ground beds for a year prior to the beginning of the experiment. On July 02, 2004, these bulbs were planted in 15 cm plastic pots, three bulbs per pot using sphagnum peat based Fafard No. 2 soiless growing medium (Agawam, MA) consisting of 70% Canadian sphagnum peat, 10% perlite and 20% vermiculite. All plants were placed in a greenhouse (Figure 4-1) under 11% shade, natural photoperiods and a temperature range of 31/24°C (day/night). These plants received 250 ml of water with N at 150 mg.L⁻¹, using Peters Professional ‘Florida Special’, a water soluble fertilizer with 20N-4.7P-16.6K (Scotts Co., Marysville, OH).

This experiment was conducted in two different years: year 1 - July 15 to December 1, 2004 (week 29 to 47), and year 2 – May 3 to December 1, 2005 (week 18 to 49). Fertigation treatments of 1) twice a week, 2) once a week, and 3) every other week were started on July 15, 2004 the first year and May 3, 2005 on the second year.

There were 16 pots (48 bulbs) per treatment. During the growing phase of the experiment, number of flowers was recorded twice a week during both years. A flower was counted when the petals opened to expose the anthers and was removed after collection of data. At completion of each year all bulbs were sectioned in order to compare bulb development and floral initiation. Number of leaves, number of offsets produced, total fresh weight (bulb with all leaves, roots and offsets attached), fresh weight (bulb only), bulb size (diameter), and number of flower buds produced were recorded, and were subjected to regression analysis.



Figure 4-1: *Habranthus* bulbs during fertigation experiment with different plastic tags in different color distinguishing the three treatments

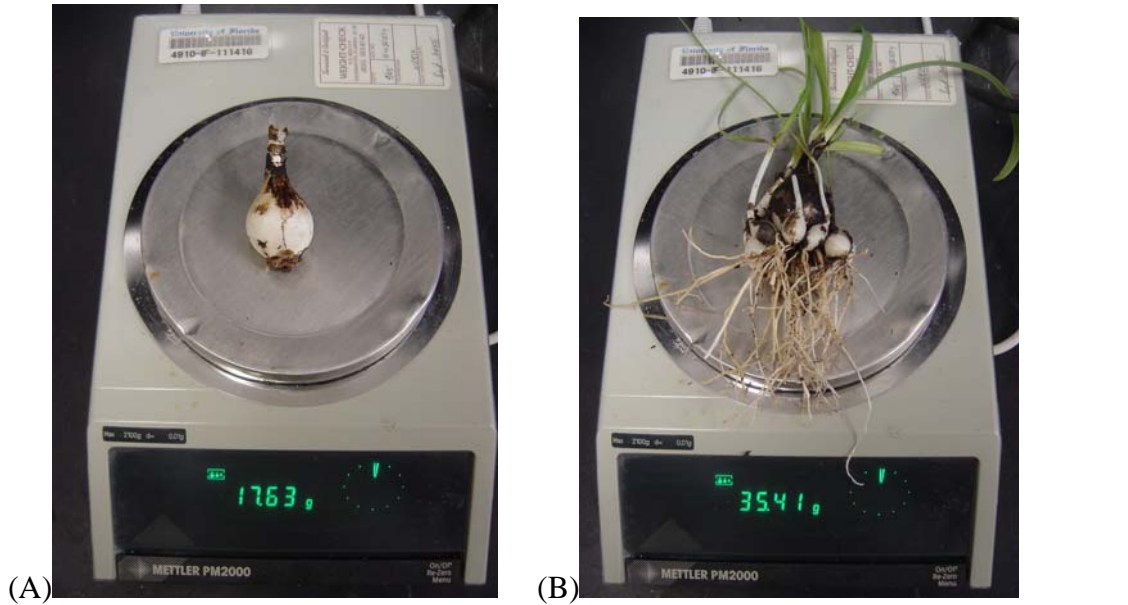


Figure 4-2: *Habranthus* bulbs being weighed after completion of experiment, only bulb (A) and bulb with leaves, roots and offsets (B)

Results and Discussion

The effects of the different fertigation treatments on number of flowers of *Habranthus robustus* could not be analyzed during the first year as the data collection started after the flowering peak for this crop.

During year 2 plants responded differently to treatments regarding the number of flowers (Figure 4-3). Plants that were fertigated every other week flowered one week earlier than plants fertigated once and twice a week. This may have occurred due to drought stress. These plants ended their flowering season two weeks earlier than plants fertigated once a week and eight weeks earlier than plants fertigated twice a week. Plants fertigated once and twice a week started flowering during week 19 but plants fertigated twice a week flowered longer, until week 37, while plants fertigated once a week stopped flowering in week 31. Peak flowering occurred much earlier in plants fertigated twice a week (week 21), than plants fertigated once a week (week 24) and every other week (week 26). Number of flowers produced during peak flowering differed dramatically

among the treatments, as plants fertigated twice a week had 41 flowers compared to 25 for plants fertigated once a week and 34 for plants fertigated every other week.

Plants fertigated once and twice a week produced flowers more consistently than plants fertigated every other week, as these plants had a flush of flowers at the beginning of the season, flowered poorly during following weeks, did not flower for a month and then had a second flush of flowers. Both regimens of fertigation – watered twice or once a week seemed to be effective on *Habranthus* under greenhouse environment, as these regimens resulted in longer flowering periods and greatest number of flowers.

Similar results were observed in onions where water deficits resulted in underdeveloped plants with reduced yields (Kadayifci et al., 2004). According to Mermoud et al. (2005) changes in the irrigation frequency significantly influences the components of the water balance. A decrease in irrigation frequency causes an increase in the water storage in the root zone and a moisture deficit in the immediate vicinity of the soil surface, which affect the crop's performance. This may have occurred in this study when plants were fertigated every other week.

The results obtained after completion of the first year demonstrated that different fertigation frequencies affected *Habranthus* bulb development. Regression analyses of all factors investigated (number of leaves, number of offsets, bulb size, total fresh bulb weight, bulb weight and number of flower buds) showed linear responses with coefficient of determination above 0.50. All factors increased as fertigation increased in year 1 (Figures 4-4 to 4-9). Number of offsets, total fresh bulb weight and bulb weight had the highest coefficient of determinations; all were above 0.90. These results can be compared to those obtained by Overman and Harbaugh (1988) who tested different irrigation

frequencies in *Caladium* tubers and observed that most frequent irrigations resulted in the best yields.

After completion of the second year the results obtained supported the conclusion that different fertigation systems affect some aspects of *Habranthus* bulb development as described bellow. There were no linear responses for number of leaves and number of flower buds (Figures 4-10 and 4-15). Number of offsets decreased as fertigation frequencies increased ($r=1$) (Figure 4-11). Bulb size, total fresh bulb weight and bulb weight increased as fertigation frequencies increased; however bulb weight (total and only bulb) had higher coefficients of determination; both were above 0.90 (Figures 4-12, 4-13 and 4-14).

During year 1 *Zephyranthes* responded differently regarding flowering to different fertigation frequencies compared to *Habranthus*. This was evident in *Zephyranthes* during the first year, but not in *Habranthus* as both species (*Habranthus* and *Zephyranthes*) have different flowering seasons and *Zephyranthes* plants begin to flower much later than *Habranthus* plants (Figure 4-16).

The results of year 1 showed that *Zephyranthes* bulbs fertigated once a week and twice a week had three gradual peaks of flower followed by an abrupt decline. This did not happen when plants were fertigated every other week. Plants fertigated once and twice a week flowered similarly which differed from plants fertigated every other week (Figure 4-17).

Plants fertigated twice a week and every other week flowered for one week more than the ones fertigated once a week. Plants fertigated twice a week had, overall, a greater

quantity of flowers during the entire season, but plants fertigated every other week had more flowers during the first peak -37 flowers in a group of 36 bulbs (Figure 4-17).

During year 2 plants fertigated once a week and twice a week demonstrated three flowering peaks followed by an abrupt decline in flower production. These two groups had similar flowering patterns, which differed from plants fertigated every other week. Plants fertigated twice a week had a greater number of flowers (Figure 4-18).

Plants fertigated once a week started flowering two weeks earlier than plants fertigated twice a week and finished their flowering season one week before both plants fertigated twice a week and every other week. Plants fertigated twice a week had, overall, a greater number of flowers during the entire season, but plants fertigated every other week had more flowers during their first peak -39 flowers in a group of 36 bulbs.

Plants that were fertigated once and twice a week produced their first flowers earlier in the season (week 19 for plants fertigated once a week and week 21 for plants fertigated twice a week), but plants under both regimens flowered poorly for more than two months, until the first flush of flowers, on week 31.

Both once and twice a week fertigation regimens seemed to be effective for flowering in *Zephyrathes* under greenhouse environments. But fertigating twice a week would be preferable since the results showed that plants under this fertigation regimen produced more flowers. Similar experiments were performed with onion and garlic (a tunicate type and a non-tunicate type of bulb), and a once to twice a week watering regimen has also been found to be preferable for these crops (Hanson et al., 2003; Kadayifci et al., 2004; Mermoud et al. 2005). Fertigating plants every other week reduced flowering of *Zephyranthes* bulbs as it resulted in a shorter flowering season with intervals

of no flowers. Similar experiments could be done in further studies using different conditions of light and temperature in order to better define the ideal fertigation frequency for these two species of tropical bulbs.

The treatments affected *Zephyranthes* bulb development in year 1. Regression analysis of all factors investigated, with the exception of number of offsets (Figure 4-20), showed linear responses with coefficient of determination above 0.50. All factors that had a linear response (number of leaves, bulb size, total fresh bulb weight, bulb weight and number of flower buds) increased as fertigation increased during the first year (Figures 4-19, 4-21, 4-22, 4-23, and 4-24), similarly to the *Habranthus* study. Number of leaves and fresh bulb weight had highest coefficient of determination, both were above 0.90.

During year 2, number of offsets and total fresh bulb weight were the only factors that had linear responses, with coefficient of determination above 0.50 (Figures 4-25 to 4-30). Number of offsets decreased as fertigation frequencies increased (Figure 4-26), while total fresh bulb weight increased as fertigation frequencies increased and was highest when bulbs were fertigated once a week (Figure 4-28).

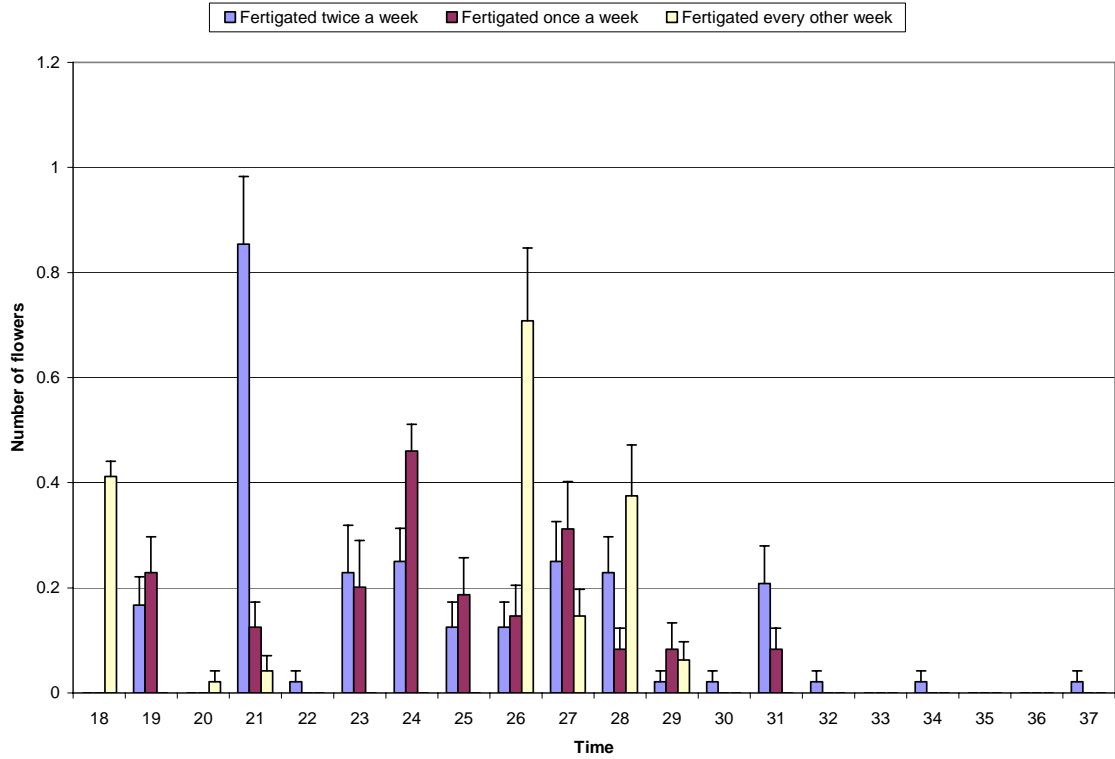


Figure 4-3: Number of flowers of *Habranthus robustus* bulbs in year 2 as affected by fertigation frequency (n=48). Bars represent standard errors.

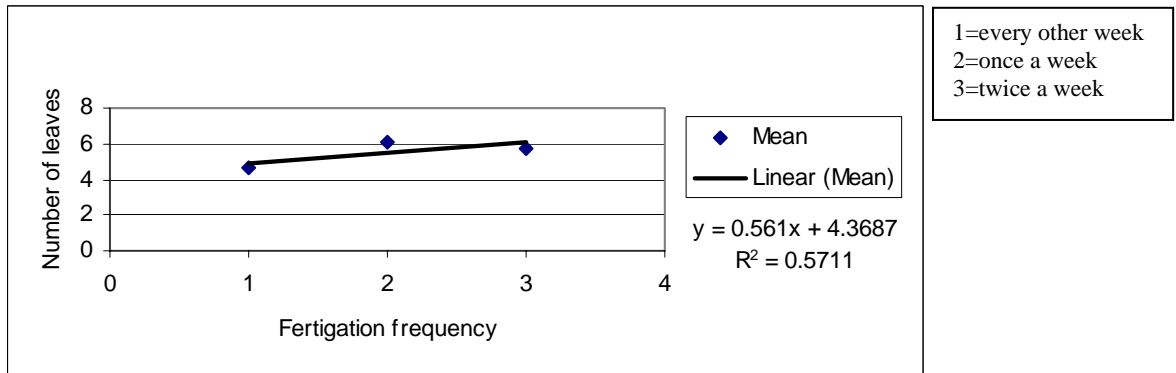


Figure 4-4: Number of leaves of *Habranthus robustus* bulbs in year 1 as affected by fertigation frequency.

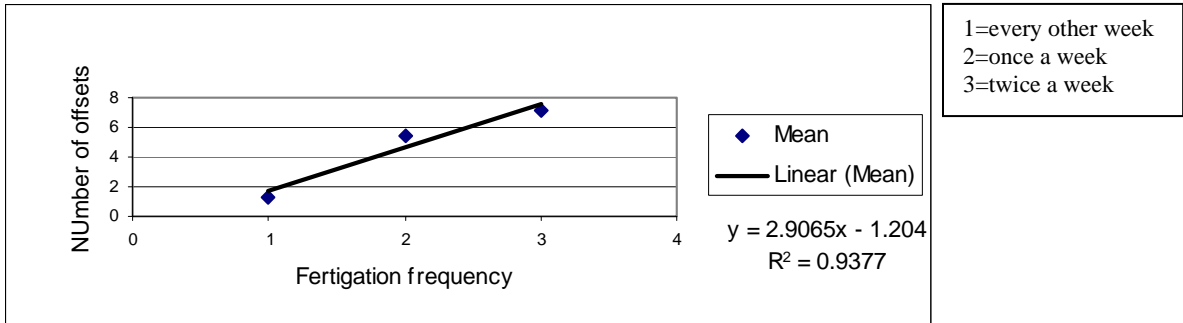


Figure 4-5: Number of offsets of *Habranthus robustus* bulbs in year 1 as affected by fertigation frequency.

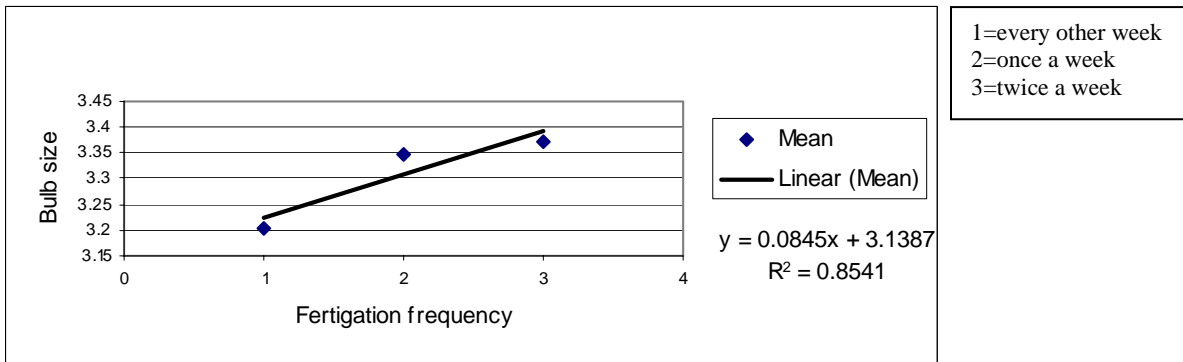


Figure 4-6: Bulb size of *Habranthus robustus* in year 1 as affected by fertigation frequency.

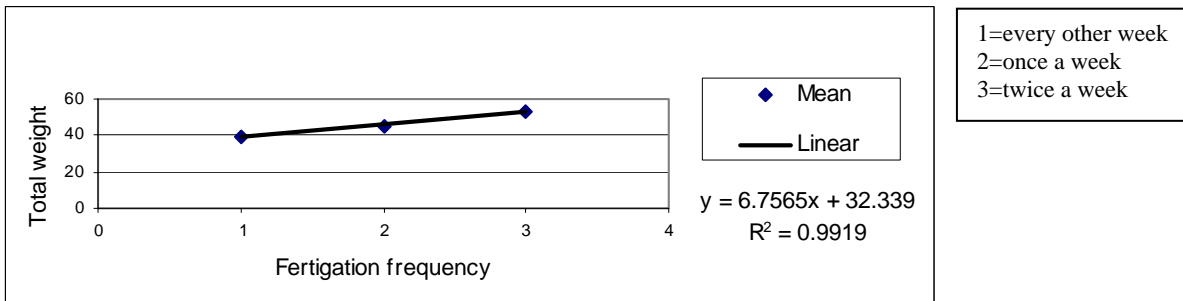


Figure 4-7: Total weight of *Habranthus robustus* bulbs in year 1 as affected by fertigation frequency.

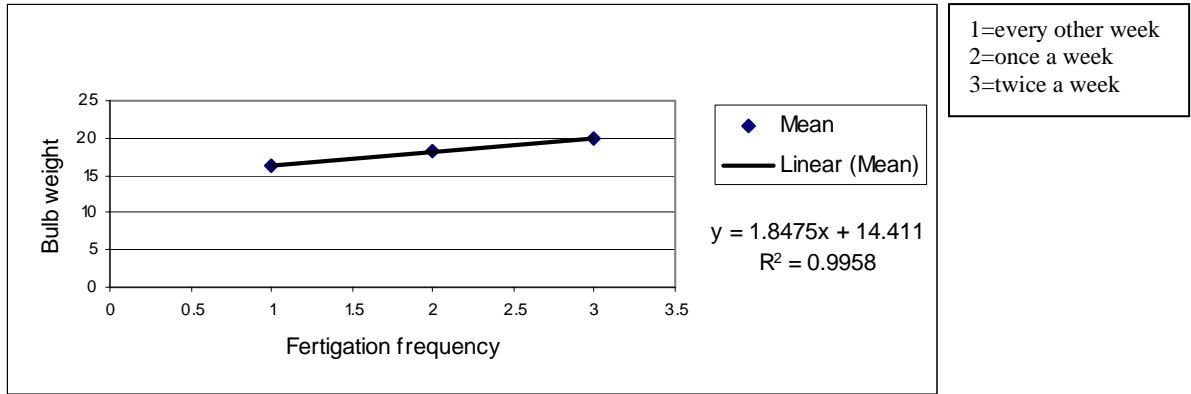


Figure 4-8: Bulb weight of *Habranthus robustus* in year 1 as affected by fertigation frequency.

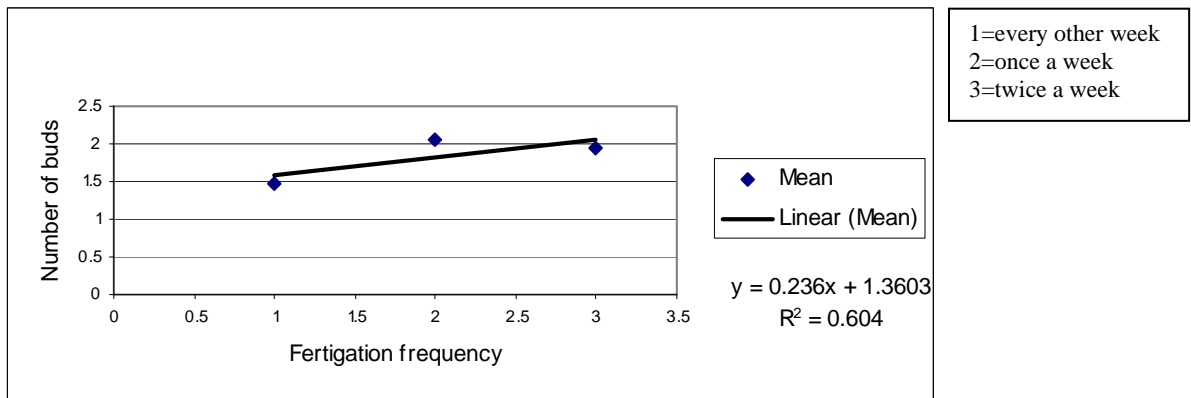


Figure 4-9: Number of flower buds of *Habranthus robustus* bulbs in year 1 as affected by fertigation frequency.

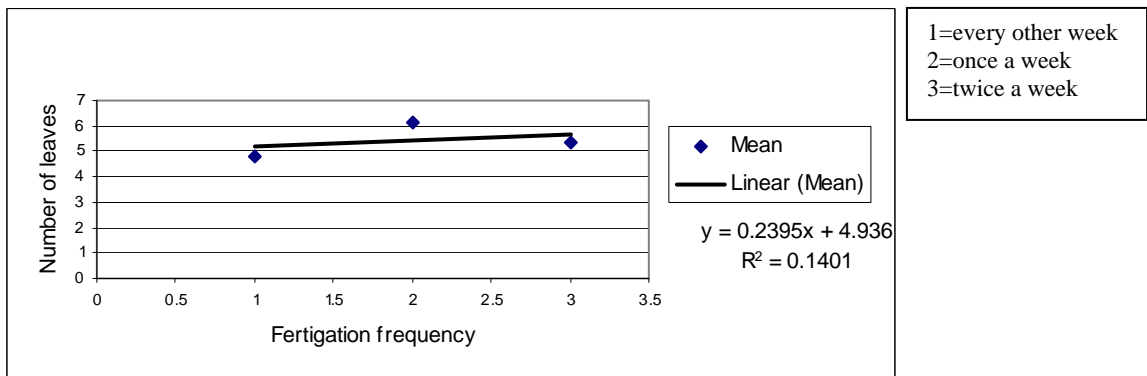


Figure 4-10: Number of leaves of *Habranthus robustus* bulbs in year 2 as affected by fertigation frequency.

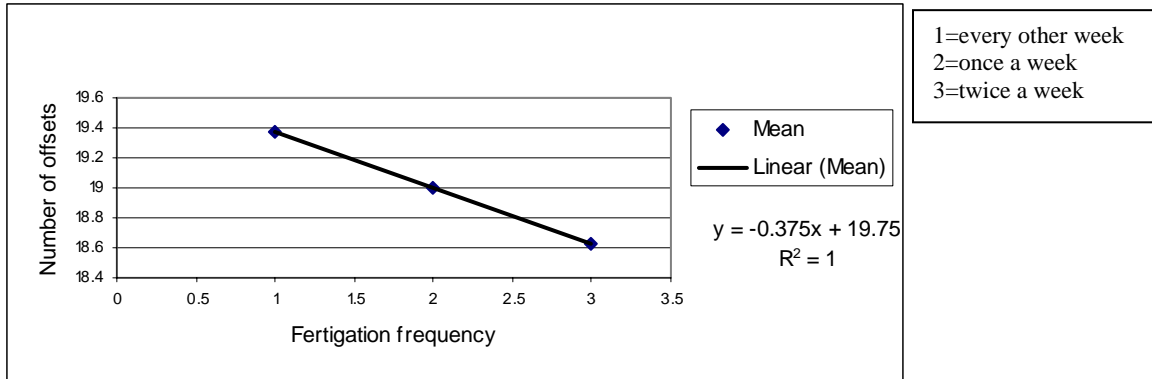


Figure 4-11: Number of offsets of *Habranthus robustus* bulbs in year 2 as affected by fertigation frequency.

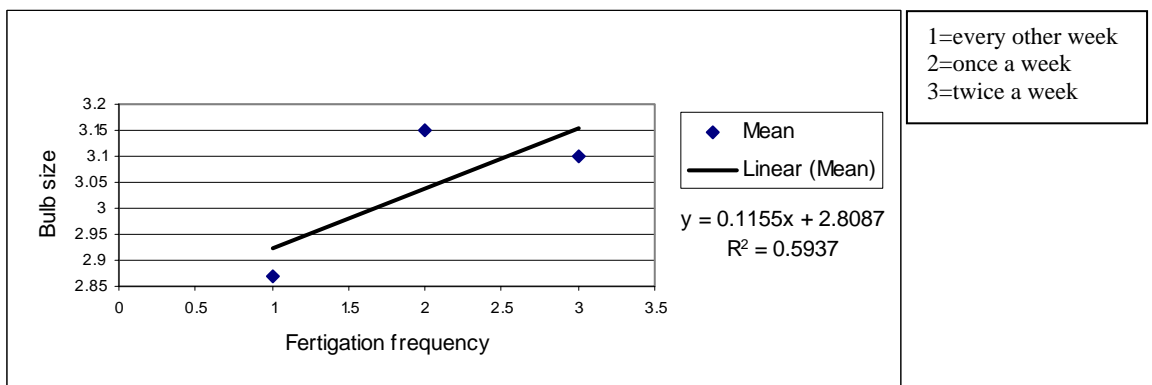


Figure 4-12: Bulb size of *Habranthus robustus* in year 2 as affected by fertigation frequency.

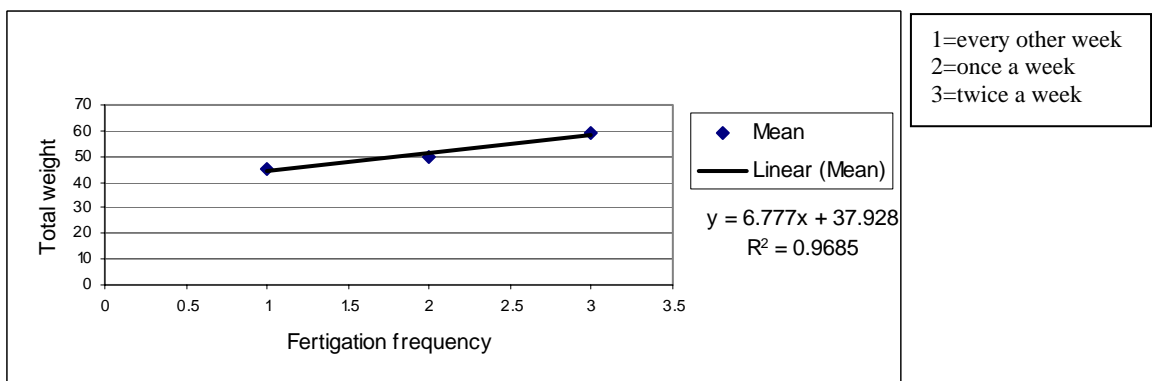


Figure 4-13: Total bulb weight of *Habranthus robustus* in year 2 as affected by fertigation frequency.

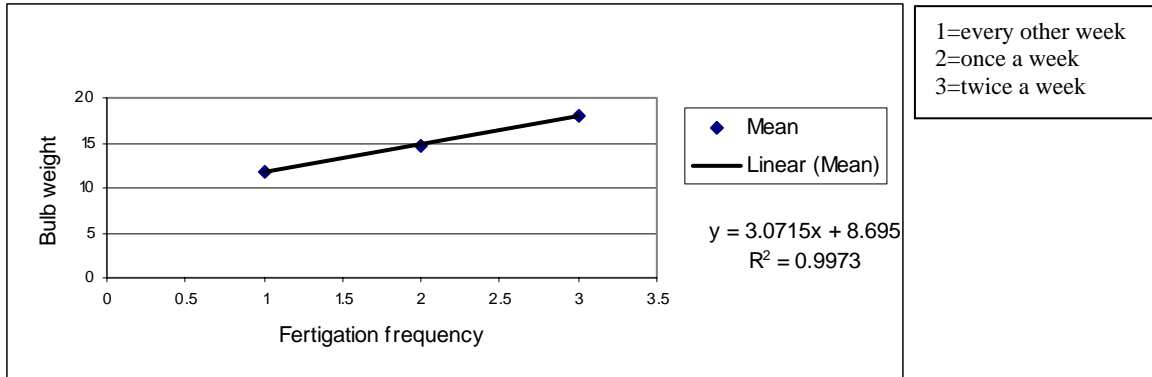


Figure 4-14: Bulb weight of *Habranthus robustus* in year 2 as affected by fertigation frequency.

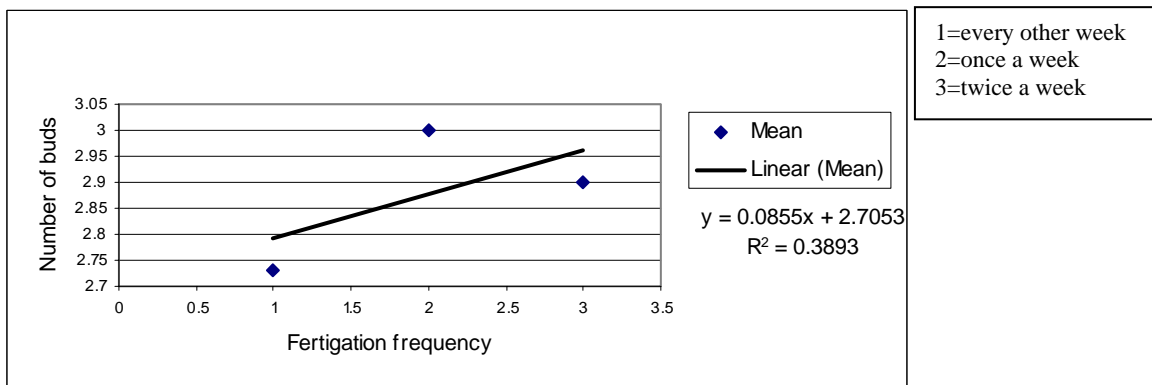


Figure 4-15: Number of flower buds of *Habranthus robustus* bulbs in year 2 as affected by fertigation frequency.

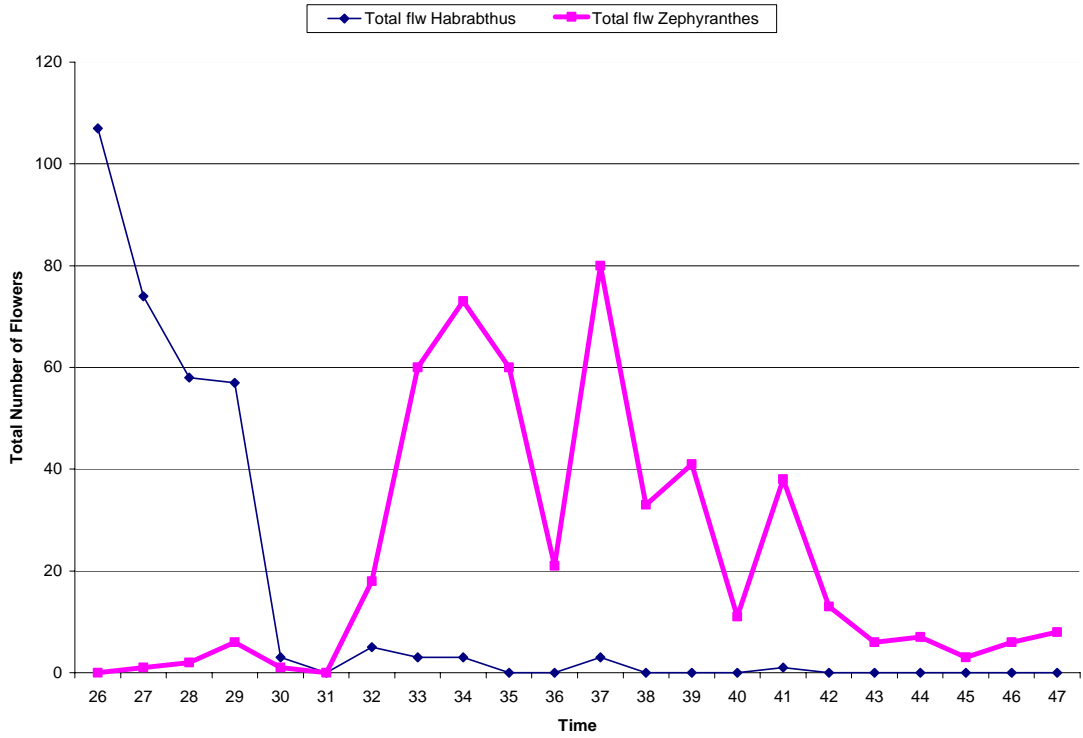


Figure 4-16: Total number of flowers on *Habranthus* and *Zephyranthes* bulbs from July to December 2004 (n=142)

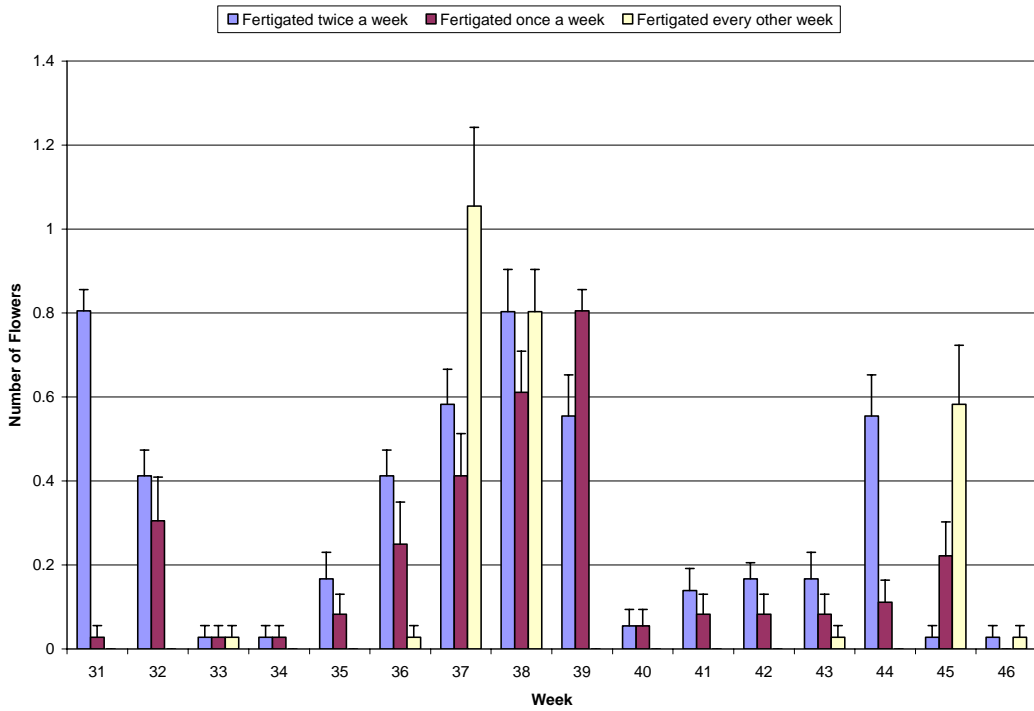


Figure 4-17: Number of flowers of *Zephyranthes* spp. bulbs in year 1 as affected by fertigation frequency (n=48). Bars represent standard errors.

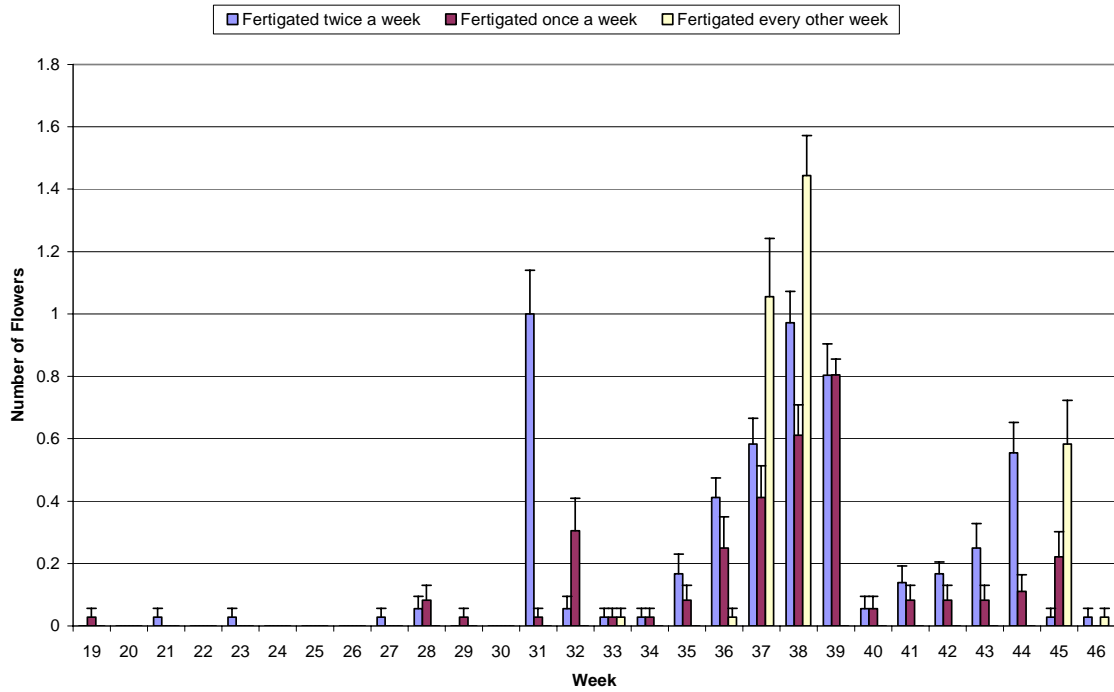


Figure 4-18: Number of flowers of *Zephyranthes* spp. bulbs in year 2 as affected by fertigation frequency (n=48). Bars represent standard errors.

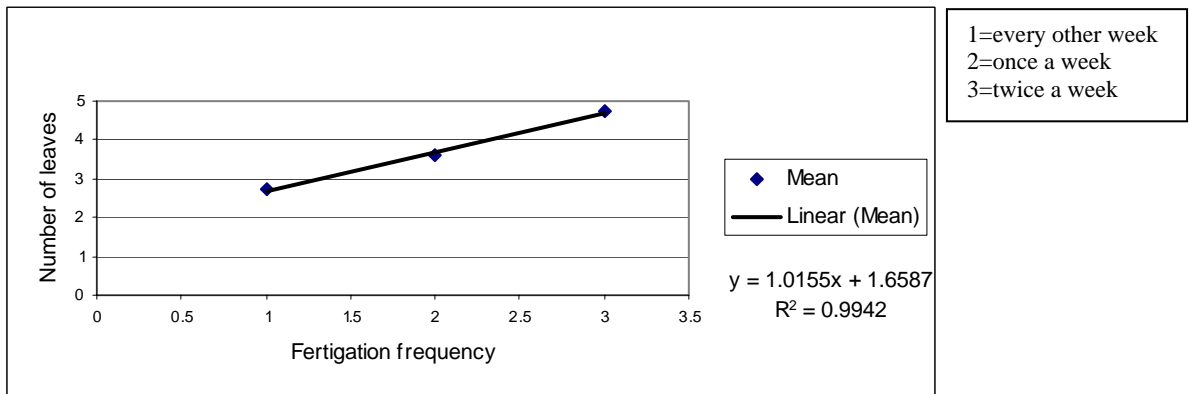


Figure 4-19: Number of leaves of *Zephyranthes* spp. bulbs in year 1 as affected by fertigation frequency.

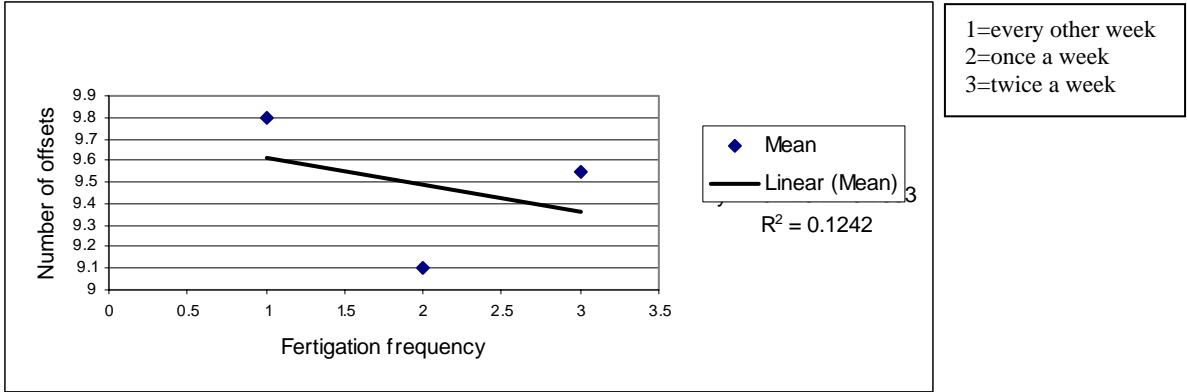


Figure 4-20: Number of offsets of *Zephyranthes* spp. bulbs in year 1 as affected by fertigation frequency.

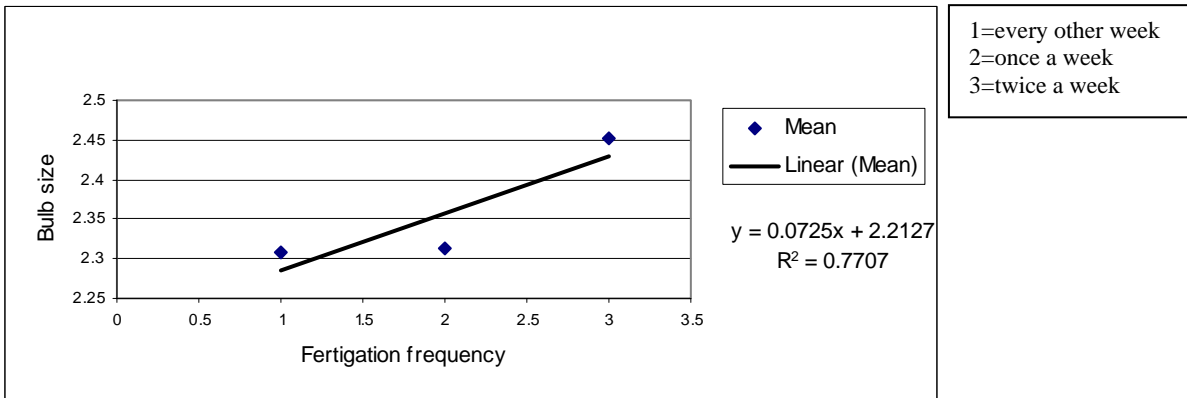


Figure 4-21: Bulb size of *Zephyranthes* spp. in year 1 as affected by fertigation frequency.

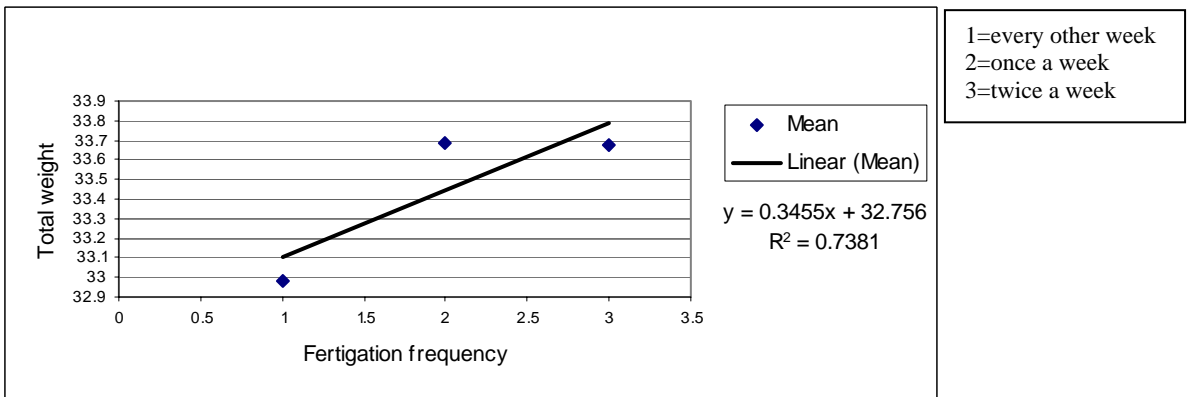


Figure 4-22: Total fresh weight of *Zephyranthes* spp. bulbs in year 1 as affected by fertigation frequency.

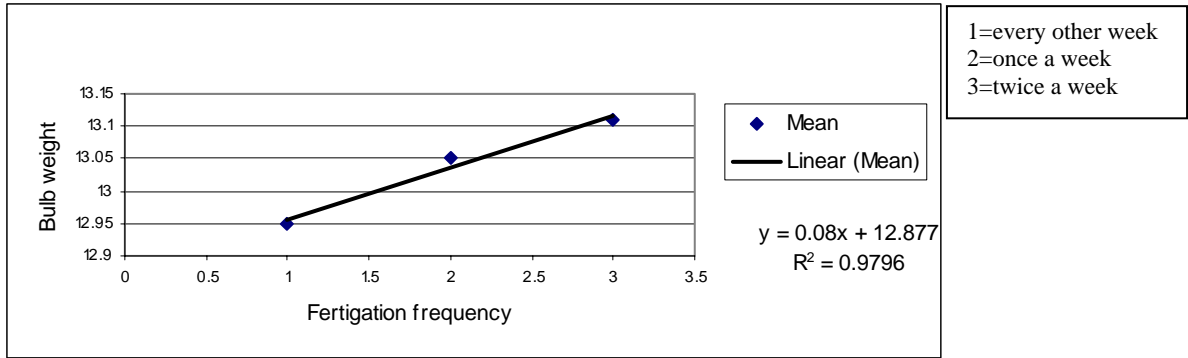


Figure 4-23: Bulb weight of *Zephyranthes* spp. in year 1 as affected by fertigation frequency.

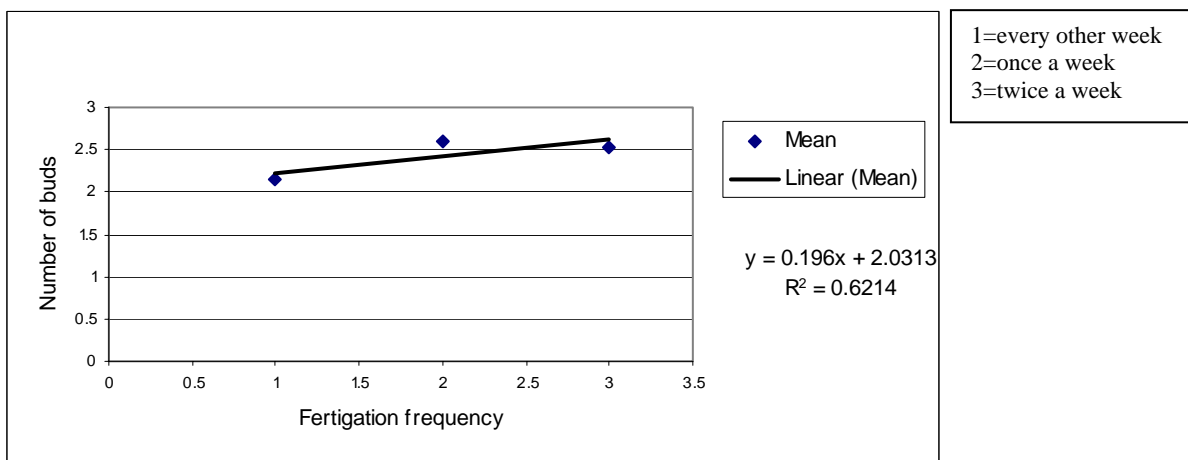


Figure 4-24: Number of flower buds of *Zephyranthes* spp. bulbs in year 1 as affected by fertigation frequency.

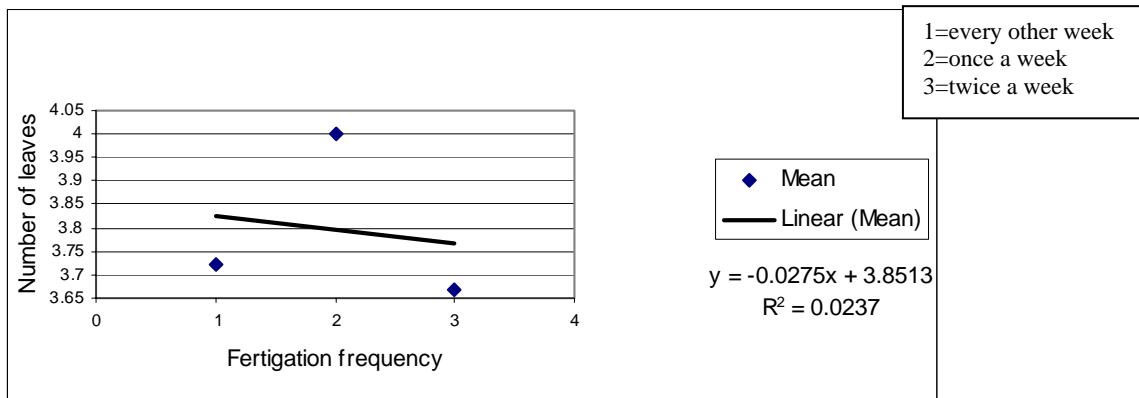


Figure 4-25: Number of leaves of *Zephyranthes* spp. bulbs in year 2 as affected by fertigation frequency.

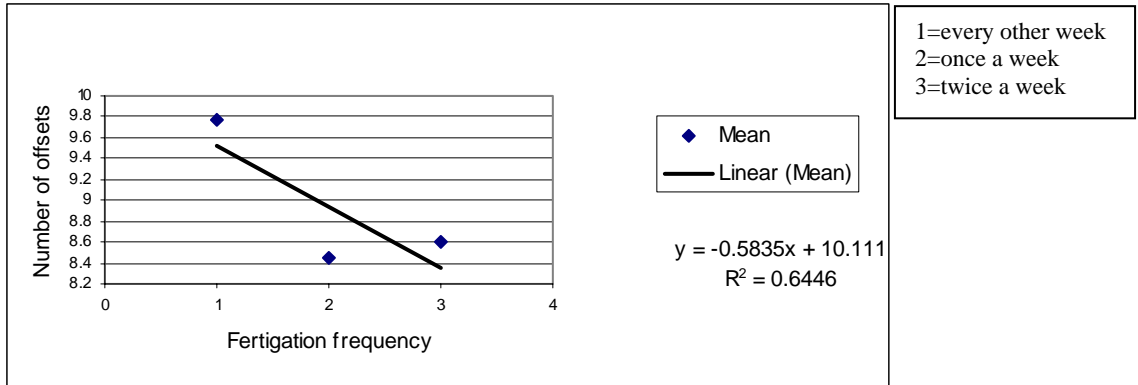


Figure 4-26: Number of offsets of *Zephyranthes* spp. bulbs in year 2 as affected by fertigation frequency.

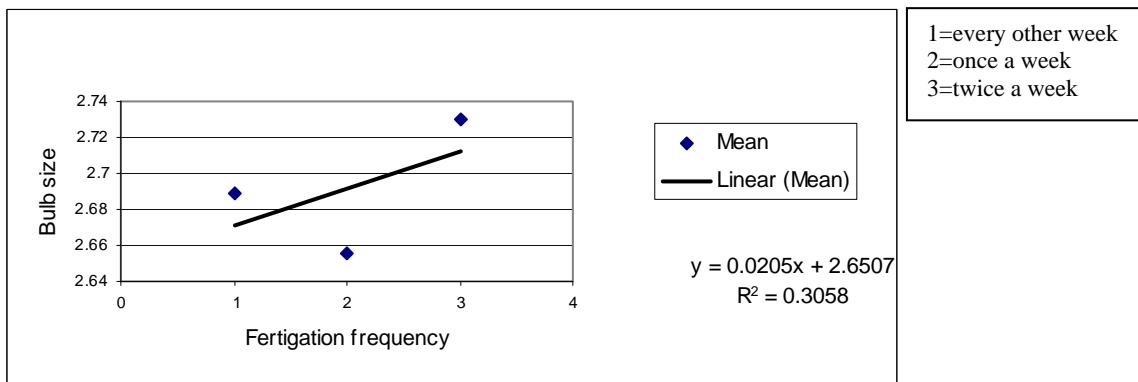


Figure 4-27: Bulb size of *Zephyranthes* spp. in year 2 as affected by fertigation frequency.

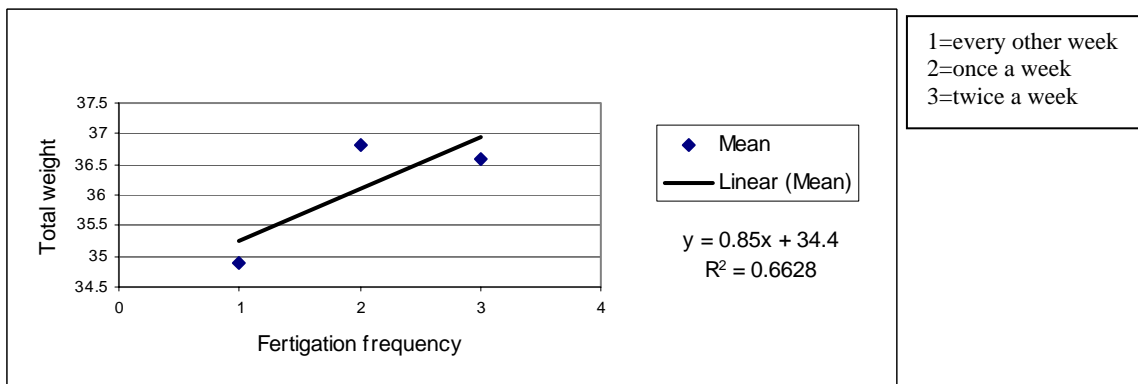


Figure 4-28: Total fresh weight of *Zephyranthes* spp. bulbs in year 2 as affected by fertigation frequency.

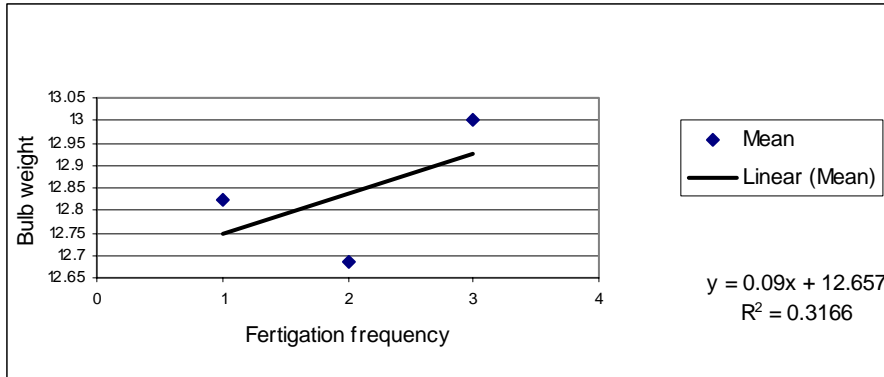


Figure 4-29: Bulb weight of *Zephyranthes* spp. in year 2 as affected by fertigation frequency.

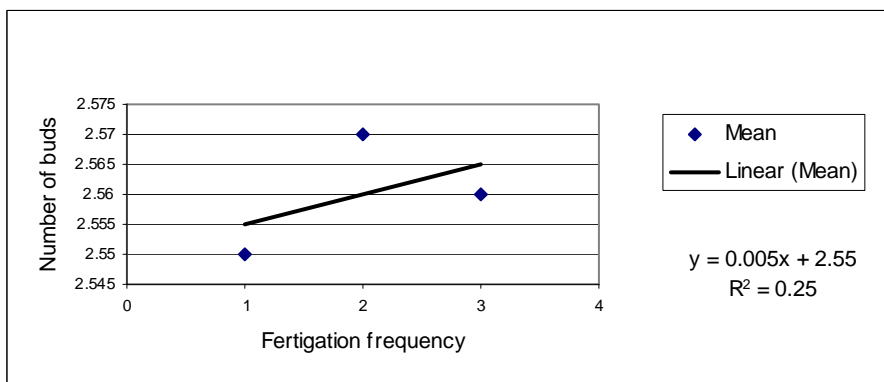


Figure 4-30: Number of flower buds of *Zephyranthes* spp. bulbs in year 2 as affected by fertigation frequency.

Experiment 2: Effect of different fertilizer rates on leaf production and bulb development in *Habranthus robustus* and *Zephyranthes* spp.

Materials and Methods: On November 6, 2005, 36 *Habranthus robustus* and *Zephyranthes* spp. bulbs were selected from University of Florida stock, which had been grown in ground beds for two years prior to the beginning of this study. Each bulb had existing bulblets (offsets) removed, two leaves per *Zephyranthes* bulb and four leaves per *Habranthus* (extra leaves were also removed). All bulbs were weighed and the diameter measured prior to planting (Table 4-1).

All bulbs were planted 15 cm plastic pots, one bulb per pot. The media used was a sphagnum peat based Fafard No. 2 soilless growing medium (Agawam, MA) consisting of 70% Canadian sphagnum peat, 10% perlite and 20% vermiculite.

Four groups with nine pots each were placed in the same greenhouse, under 11% shade, spaced pot to pot on the bench and were manually watered and fertilized twice a week with 250 ml of water containing 300 ppm N (0.2 oz of fertilizer per gallon of water); 150 ppm N (0.1 oz of fertilizer per gallon of water), 75 ppm N (0.05 oz of fertilizer per gallon of water) and no fertilizer (control group) of the water soluble 20-10-20 Peter's Excel. A control group was included in this study to verify the performance of *Habranthus* and *Zephyranthes* bulbs under regular irrigation regimens with no fertilizer, which can occur in commercial production and/or in low maintenance landscapes.

During the growing phase of the experiment data was collected twice a month on number of leaves per bulb. Data collected after completion of the experiment included number of leaves, number of offsets produced, total fresh weight (bulb with all leaves, roots and offsets attached), fresh bulb weight (only bulb), bulb size (diameter), and number of flower buds produced. Regressions were made to compare and contrast responses of *Habranthus* and *Zephyranthes* bulb development to the standard crop response to fertilizer rates demonstrated by Janick et al. (1976).

Table 4-1 - Mean bulb size and weight prior to experiment

	<i>Habranthus</i>	<i>Zephyranthes</i>
Mean bulb diameter (cm)	2.6	2.5
Mean bulb weight (g)	16.56	15.85

Results and Discussion

Different fertilizer rates affected *Habranthus* bulb development. This contrasted with results obtained by Lee et al. (2005) in *Lilium* since neither flowering nor bulb growth was affected by different concentrations of fertilizer.

Regression analysis of all factors investigated (number of leaves, number of offsets, bulb size, total fresh bulb weight, bulb weight and number of flower buds) showed a quadratic response with coefficients of determination above 0.90. With the exception of number of offsets, all factors followed the standard crop response curve to fertilizer rates, with a gradual increase in growth followed by a luxury consumption period and a gradual decrease in growth.

Bulbs fertilized with 75 and 150 ppm N had greater number of leaves and plants that did not receive any fertilizer had the least number of leaves (Figure 4-31). Number of offsets increased as fertilizer rates increased and was highest when bulbs were treated with 300ppm N (Figure 4-32). Bulb size and bulb weight (both total fresh weight and bulb weight) were higher when bulbs were fertilized with 75 and 150 ppm N (Figures 4-33 to 4-35). These results slightly differ from those obtained by Engelbrecht (2004) in *Lachenalia* since largest and heaviest bulbs were obtained with higher concentrations of fertilizer.

Bulbs that were fertilized with 150 ppm N produced the greatest number of flower buds, followed by those that received 75 and 300 ppm N (Figure 4-35). Different concentrations of fertilizer were tested in *Iris* and only the least concentrated fertilizer accelerated flowering (Lee et al., 2005).

This study demonstrated that to propagate *Habranthus* bulbs using the separation method (removing and transplanting bulblets or offsets) the optimal fertilizer rate for

mother plants would be 300 ppm of Peter's Excel 20-10-20, since bulbs produced more offsets under this treatment. However, to grow bulbs for the market optimal fertilizer rates would be 75 or 150 ppm of Peter's Excel 20-10-20, which produced largest bulbs. Additionally, for flowering, fertilizing plans with 150 ppm would be optimal since this treatment produced the greatest amount of flower buds.

Zephyranthes bulb development was affected by the treatments. Regression analysis of all factors investigated (number of leaves, number of offsets, bulb size, total fresh bulb weight, bulb weight and number of flower buds) showed a quadratic response with coefficients of determination above 0.90, and all factors followed the standard crop response curve to fertilizer rates.

Plants fertilized with 150 ppm N demonstrated best results for number of leaves (Figure 4-37), number of offsets (Figure 4-38) and number of flower buds produced (Figure 4-42), while those that did not receive any fertilizer demonstrated the least favorable results. Bulb size increased as fertilizer rates increased and was largest when plants were fertilized with 300 ppm N (Figure 4-39). This is comparable to onions that produced highest yields when fertilized with high concentrations of nitrogen (90 kg N/ha) (Hassan, 1984). Different concentrations of fertilizer were also tested in *Curcuma alismatifolia* and largest rhizomes were obtained with highest fertilizer concentrations (Ruamrungsri et al., 2005).

For bulb weight (both total fresh weight and bulb weight) fertilizer concentrations of 75, 150, and 300 ppm N demonstrated similar results producing the heaviest bulbs (Figures 4-40 and 4-41). These results differ from those obtained by Hassan (1984) in onion since heaviest bulbs were generated by highest concentrations of nitrogen.

Plants fertilized with 150 ppm N produced the highest number of flower buds (Figure 4-42). This study demonstrated that the best fertilizer level for propagation and flowering of *Zephyranthes* bulbs was 150 ppm of Peter's Excel 20-10-20, since this treatment led to the highest numbers of offsets and flower buds produced. However, 300 ppm of Peter's Excel 20-10-20 was the optimal concentration for growing *Zephyranthes* bulbs for the market, since it produced the largest bulbs.

Both *Habranthus* and *Zephyranthes* can be classified as either: bulbs that require low or moderate fertilization programs, type 3 or 4 in the nutrient requirement categories defined by De Hertogh and Le Nard (1993).

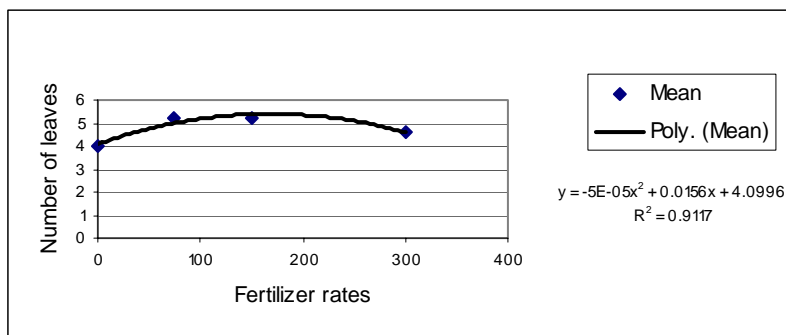


Figure 4-31: Data points, regression lines, equations and coefficient of determination of number of leaves of *Habranthus*.

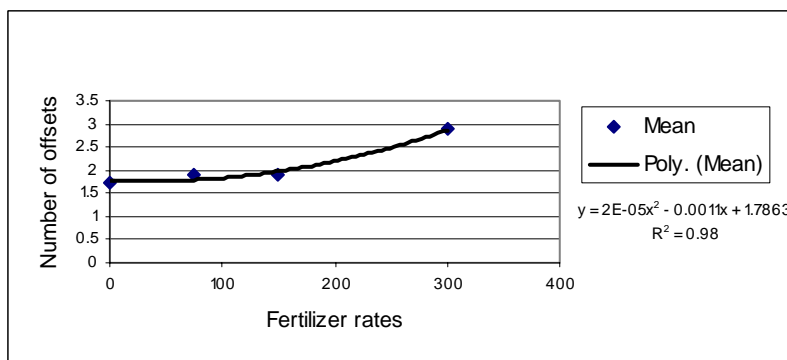


Figure 4-32: Data points, regression lines, equations and coefficient of determination of number of offsets of *Habranthus*.

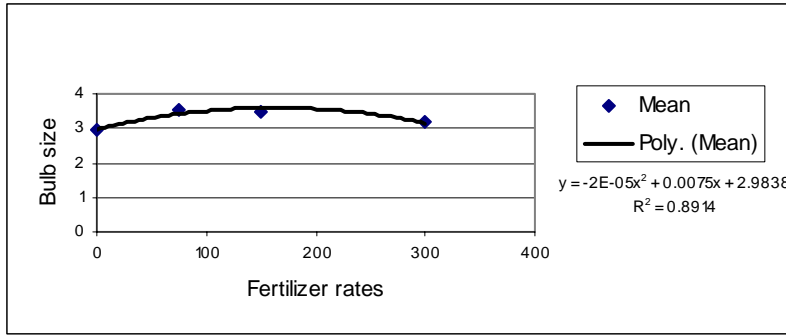


Figure 4-33: Data points, regression lines, equations and coefficient of determination of bulb size of *Habranthus*.

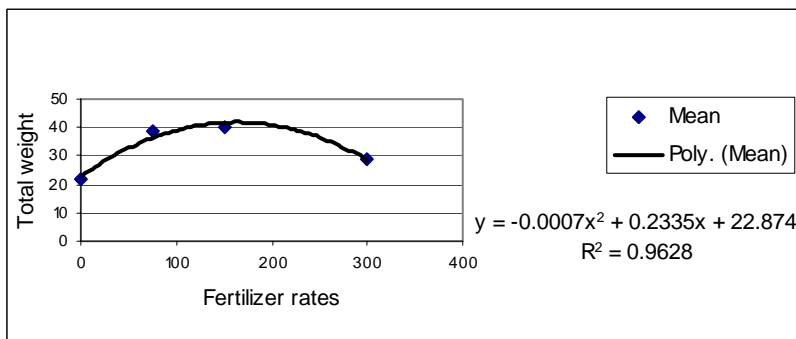


Figure 4-34: Data points, regression lines, equations and coefficient of determination of total fresh bulb weight of *Habranthus*.

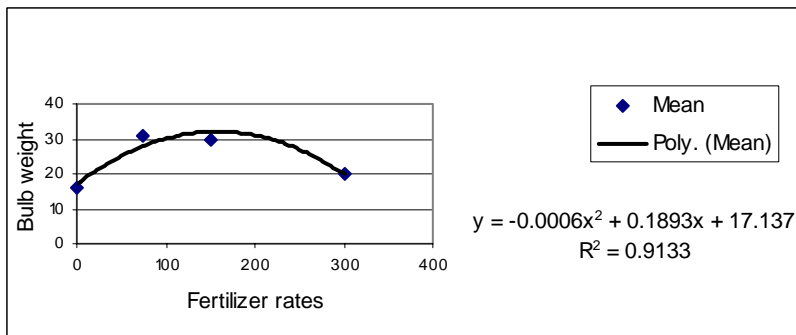


Figure 4-35: Data points, regression lines, equations and coefficient of determination of fresh bulb weight of *Habranthus*.

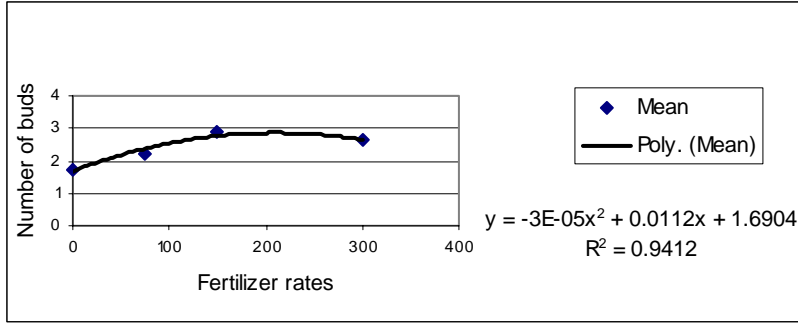


Figure 4-36: Data points, regression lines, equations and coefficient of determination of number of flower buds of *Habranthus*.

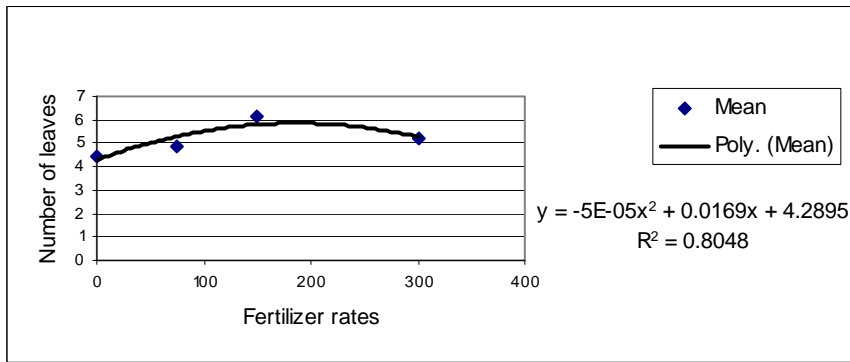


Figure 4-37: Data points, regression lines, equations and coefficient of determination of number of leaves of *Zephyranthes*.

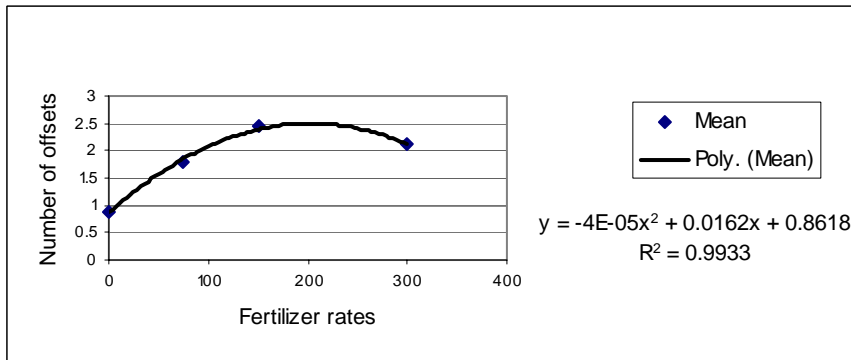


Figure 4-38: Data points, regression lines, equations and coefficient of determination of number of offsets of *Zephyranthes*.

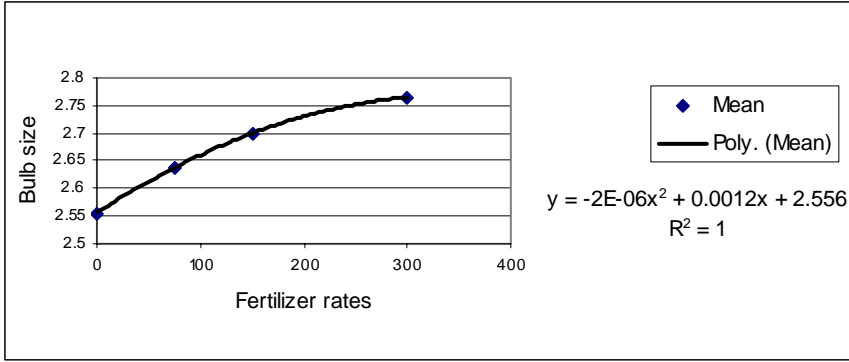


Figure 4-39: Data points, regression lines, equations and coefficient of determination of bulb size of *Zephyranthes*.

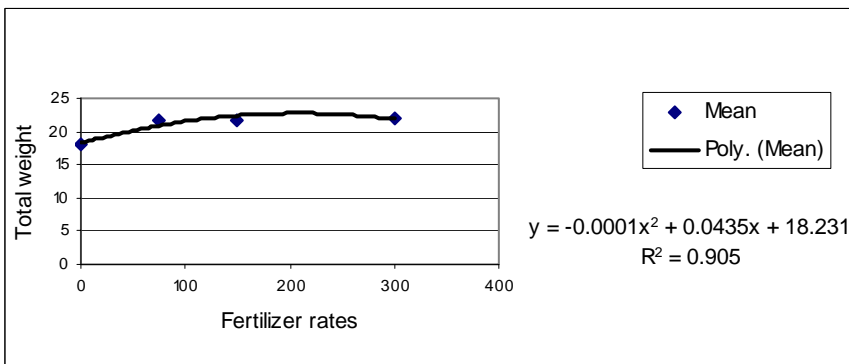


Figure 4-40: Data points, regression lines, equations and coefficient of determination of total fresh bulb weight of *Zephyranthes*.

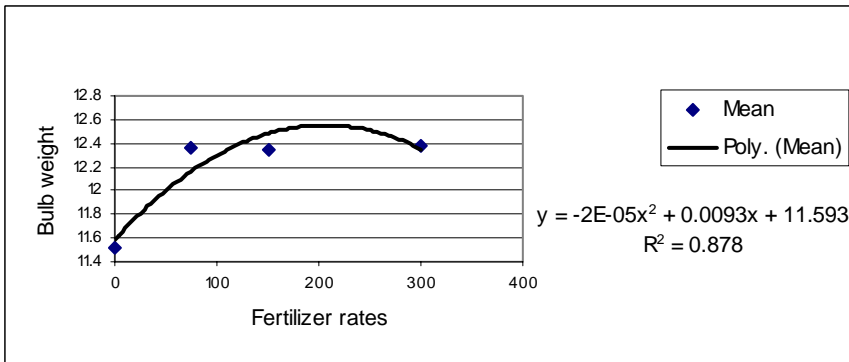


Figure 4-41: Data points, regression lines, equations and coefficient of determination of fresh bulb weight of *Zephyranthes*.

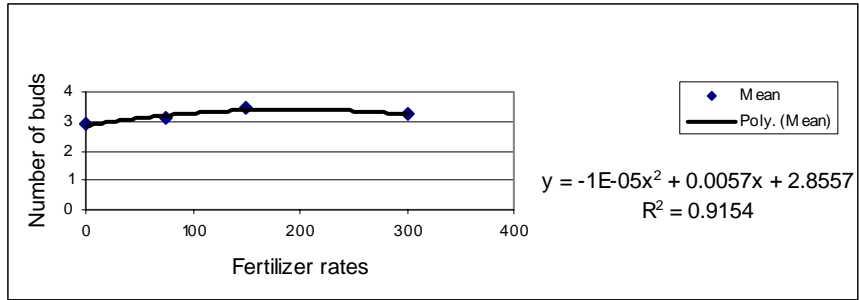


Figure 4-42: Data points, regression lines, equations and coefficient of determination of fresh bulb weight of *Zephyranthes*.

CHAPTER 5
ENVIRONMENTAL EFFECTS – LIGHT LEVELS ON FLOWERING AND BULB
DEVELOPMENT IN *Habranthus robustus* AND *Zephyranthes* SPP.

Light intensity and photoperiod influence several physiological processes of flowering bulbs, including photosynthesis, flower quality, flower abortion and abscission (De Hertogh and Le Nard, 1993). Photosynthesis is a vital process in which plants utilize sun light and carbon dioxide in the air to produce sugars by converting light energy into chemical energy. Light intensity and quality also directly affects several important plant quality characteristics, such as number of flowers produced, foliage color and overall plant appearance. In many cases, effects can be enhanced by selecting optimal temperature, nutrient and soil moisture levels (Gest, 2002).

Photoperiodism was first described by Garner and Allard (1920, 1923) in a study that classified plants as either long day or short day plants for flowering. Plants that required more than 12 hours of light per 24-hour cycle were considered long day (LD)/short night plants, and plants that required more than 12 hours of dark per 24-hour cycle were considered short day (SD)/long night plants. Onions (*Allium cepa*) are considered LD plants (Lercari, 1982). Their bulb formation and subsequent growth are influenced by photoperiod (Scully et al., 1945) and temperature (Brewster, 1977), with inflorescence initiation accelerated under long photoperiods (Brewster, 1992). Bulb growth and development in garlic is also largely dependent on photoperiod and temperature prevailing during the growth period (Ledesma et al., 1980).

Habranthus and *Zephyranthes* do not require a critical amount of light or dark period in order to flower. These plants are not qualitative since they do not flower in response to short or long days. Basic light requirements for flower bulbs in the landscape have been broadly defined as full sun, partial shade or full shade, and according to Haynes et al. (2001), both *Habranthus* and *Zephyranthes* are considered full sun plants.

Alstroemeria rhizomes were grown under shade levels of 0, 50%, and 70% and shading increased flower stem length but had no effect on the number of flowers per plant (Zizzo et al. 1992). However, when *Oxalis braziliensis* was grown under the shade levels of 35%, 55%, and 75%, number of flowers increased as shade increased (Suh et al. 2003). Similar experiment conducted using banana rhizomes grown under 0, 30%, 60% and 80% shade revealed that only 80% shade affected rhizome development (Israeli et al., 1995).

This investigation was conducted to determine if *Habranthus* and *Zephyranthes* were full sun plants and identify optimum light levels for flowering and bulb development of these two species during commercial production. The *Habranthus* species used in this study was *Habranthus robustus*, and three *Zephyranthes* cultivars evaluated were 'Paul Niemi', 'JoAnn's Trial', and 'Fadjar Pink'.

Materials and Methods

Experiment 1: Effect of light levels on flowering and bulb development of *Habranthus robustus*. To determine optimal light levels and verify their effect on flowering and bulb development (size, weight, number of buds), plants were grown in full sun, 30% shade and 60% shade. Bulbs used in this experiment were obtained from the University of Florida stock, where they had been grown in ground beds for a year prior to the beginning of the experiment. On July 4, 2004, bulbs were planted in 30 cm

plastic pots, three bulbs per pot using sphagnum peat based Fafard No. 2 soilless growing medium (Agawam, MA) consisting of 70% Canadian sphagnum peat, 10% perlite and 20% vermiculite. Plants were placed in three different locations under different amounts of light: ambient outdoor – full sun, and two different shadehouses (covered by black shade cloth) with 30% and 60% shade. There were 16 pots (48 bulbs) per treatment. Photometric readings and temperatures of these three locations are listed in table 5-1. Plants were fertigated with 500ml of water containing N at 150 mg.L^{-1} using Peters Professional ‘Florida Special’ water soluble fertilizer 20N-4.7P-16.6K, from Scotts Co., Marysville, OH twice a week. However, since plants were located in open environments rainfall was also monitored. A summary of monthly rainfall totals in the Gainesville area for 2004 and 2005 is listed in table 5-2.

This experiment was conducted in two different years: year 1: July 15 to December 12 2004, from week 29 to 47, and year 2: May 3 to December 13 2005, from week 18 to 49. Light level treatments in both years were 1) full sun, 2) 30% shade, and 3) 60% shade.

At completion of each yearly study all bulbs were sectioned in order to compare bulb development and floral initiation between treatments. Data collected after completion of the experiment included number of leaves, number of offsets produced, total fresh weight (bulb with all leaves, roots and offsets attached), fresh bulb weight (only bulb), bulb size (diameter), and number of flower buds produced, and regression analysis were made to compare *Habranthus* and *Zephyranthes* growth to the standard plant growth curve demonstrated by Janick et al. (1976).

Experiment 2. Effect of light levels on flowering and bulb development of *Zephyranthes* spp. To determine optimal light levels and verify their effect on flowering and bulb development (size, weight, number of buds), plants were grown under full sun, 30% shade and 60% shade. Three types of bulbs were used in this present experiment: *Zephyranthes*. ‘Paul Niemi’, *Z.* ‘JoAnn’s Trial’, and *Z.* ‘Fadjar Pink’. Bulbs were obtained from the University of Florida stock, were they had been grown in ground beds for a year prior to the beginning of the experiment.

This experiment was conducted in the same manner as experiment 1, using the same type of pots, media, fertilizer and placing plants in the same shadehouses. The experiment was initiated and terminated on same dates; data were collected and analyzed as experiment 1.

Table 5-1 - Photometric readings and temperatures at three locations / treatments

Treat.	Location	Light Level ($\mu\text{Mols.m}^2.\text{sec}$) Average - sunny day at noon (in September)	Temperature - $^{\circ}\text{C}$ Average- between three readings	Temperature - $^{\circ}\text{C}$ Average- between three readings
1	Full sun	1500	31.67	28.33
2	30% Shade	1050	30.82	27.94
3	60% Shade	600	30.02	27.01



Figure 5-1: Plants under three different treatments: full sun (A), 30% shade (B) and 60% shade (C)

Table 5-2 - Rainfall monthly summary in inches for Gainesville area in 2004 and 2005 according to the Florida Automated Weather Network

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2004	1.33	5.65	1	1.58	0.64	6.86	10.03	5.94	12.94	1.3	2.65	1.87
2005	1.98	2.16	5.62	4.14	4.52	7.9	5.43	4.66	0*	6.54	4.02	22.3*

*these values may reflect data inaccuracies by FAWN.

Results and Discussion

Experiment 1: The effects of the different light level treatments on number of flowers of *Habranthus robustus* could not be analyzed during the first year as the data collection started after the flowering peak for this crop.

During year 2, data collected showed that treatments did affect flower number. Plants in 30% shade had more open flowers during the entire flowering season than in the other light levels. These results differ from those obtained by Zizzo et al. (1992) who observed that shading increased flower stem length but had no effect on the number of flowers per plant in *Alstroemeria* bulbs. Results also differ from those observed by Suh et al. (2003), who reported that number of *Oxalis braziliensis* flowers increased as shade levels increased.

The three groups of plants started flowering during week 21, however, plants in full sun and in 30% shade ceased flowering after week 32, while the ones in 60% shade ceased flowering after week 27. These results also differ from those obtained by Zizzo et al. (1992) with *Alstroemeria*, since they demonstrated that plants under higher level of shading had an extended flowering season.

Flowering of plants in full sun peaked during week 23, the same week that plants in 30% shade produced their first of two peaks; however, plants in full sun had less than

50% of the flowers produced by plants in 30% shade. Furthermore, plants in 30% shade had a second flowering peak during week 27 with a great number of flowers (20% higher than the first peak of the full sun group). Plants in 60% shade also had two peaks of flowering; however, their flowering season was much shorter than plants in the other shade levels (Figure 5-2).

The results obtained after completion of the first year demonstrated that different light levels affected *Habranthus* bulb development. Regression analysis of all factors investigated (number of leaves, number of offsets, bulb size, total fresh bulb weight, bulb weight and number of flower buds) showed linear responses with coefficient of determination above 0.89. All factors, with the exception of number of leaves, increased as light levels increased during year 1 (Figures 5-3 to 5-8).

Number of leaves decreased as light levels increased (Figure 5-3). This may have occurred because plants in full sun received more solar radiation and fewer leaves were needed to produce sufficient energy via photosynthesis; while plants in 60% shade received less solar radiation and responded by producing more leaves for photosynthetic production. These results differ from those obtained by Sush et al. (2003) who tested different shade levels (35-55-75%) in *Oxalis braziliensis* and observed that number of leaves was increased by shade levels as compared to natural light. However, our results can be compared to those obtained by Israeli et al. (1994) who tested the effect of different shade levels (0-30-60-80%) on growth of banana and observed that shading reduced the rate of leaf emergence.

Results obtained on bulb development during the first year contrasted with those obtained by Rahim and Fordham (1990) who tested the effect of shade on the

development of garlic bulbs and observed that bulbs grown under 50% shade were more developed (regarding number of cloves formed) than those grown under 60 and 75% shade. Our results also contrasted with those obtained by Barkham (1980) who observed that *Narcissus* bulbs were heavier under the highest levels of canopy shade.

After completion of the first year it was observed that the root system of plants grown under the different light levels differed. Plants grown under full sun had shorter roots with no ramifications; plants grown under 30% shade had medium roots with few ramifications, and plants grown under 60% shade had very long roots with several ramifications (Figure 5-9). This could have been due to higher soil temperature in full sun pots.

The results obtained after completion of the second year emphasized results obtained during the first year that different light levels affect *Habranthus* bulb development. Regression analysis of all factors investigated (number of leaves, number of offsets, bulb size, total fresh bulb weight, bulb weight and number of flower buds) showed linear responses with coefficient of determination above 0.80. All factors increased as light levels increased during year 1 (Figures 5-10 to 5-15). Number of leaves increased as light levels increased during the second year, which did not happen during year 1 (Figure 5-10).

Comparing the slopes of the linear responses it could be observed that the increase in number of offsets and number of flower buds was more accentuated in the second year; total fresh bulb weight increase was more accentuated during the first year; and bulb size and fresh bulb weight increase were similar during both years.

Experiment 2: Effect of light levels on flowering and bulb development of *Zephyranthes* spp. Light levels affected the number of *Zephyranthes* flowers for this species during the first year. This result differed from *Habranthus* as *Zephyranthes* plants begin to flower much later than *Habranthus* plants (Figure 4-16) and in this case, data collection started prior to the flowering peak for this crop.

Plants grown under all three treatments demonstrated gradual peaks of flowering followed by an abrupt decline during week 33 (Figures 5-16 and 5-17).

In the first year plants grown under 30% shade demonstrated a more uniform flowering season compared to plants in the other two light levels, with a more gradual increase in flowers leading to a peak and only one week with no flowers. Additionally, these plants had the highest number of flowers in almost all weeks. Plants grown under shade (both 30% and 60%) flowered until week 42, while plants grown under full sun flowered until week 44, two weeks more than the other two groups. Plants grown under full sun and 60% shade also demonstrated gradual peaks of flowering (similar to the ones under 30% shade), however here, these peaks were followed by gaps of one or two weeks with no flowers, whereas plants under 30% shade produced flowers continually (Figure 5-16).

In the second year, plants grown under 30% shade again had a more uniform flowering season compared to the other two groups. However, during year 2 the number of flowers during the first two peaks (week 32 and 37) were very similar among all treatments, differing from the previous season. During the third peak of flowering (week 41) plants under full sun had the highest number of flowers. Plants grown under full sun and 30% shade started flowering during week 24; both demonstrated a gap of two weeks

without flowers, and flowered again on week 27, when 60% shade plants began to flower. Plants grown under full sun flowered until week 44, two weeks more than plants under any shade level. Plants grown under the three treatments presented gaps without flowering between peaks and the beginning of the next gradual increase in number of flowers, but it was more accentuated on plants under full sun and under 60% shade (Figure 5-17).

Results obtained during year 1 were very similar to year 2. These results differ from those obtained by Cavins and Dole (2002) who tested different shade levels (0-30-60%) in *Narcissus* and *Tulipa* and observed that increasing shade increased stem length but did not influenced flowering percentage.

Regarding bulb development, treatments affected *Zephyranthes* bulb development during both years. Regression analysis of all factors investigated (number of leaves, number of offsets, bulb size, total fresh bulb weight, bulb weight and number of flower buds) showed linear responses with coefficient of determination above 0.89. All factors increased as light levels increased during both year 1 and year 2 (Figures 5-18 to 5-23).

Number of leaves increased during both year 1 and 2; however, it was more accentuated during the first year when comparing the slope of the linear responses. These results differ from those obtained by Sush et al. (2003) who tested different shade levels (35-55-75%) in *Oxalis braziliensis* and observed that number of leaves was increased by shade levels as compared to full sun.

Number of offsets, bulb size and total fresh bulb weight increased similarly during year 1 and 2. Bulb weight increase was more accentuated during the first year, while

number of flower buds increase was more accentuated during the second year, when comparing the slopes of the linear responses.

After completion of the experiment it could be observed that the root system of these plants were distinct under the different treatments and was very similar to observations of *Habranthus* bulbs. Plants grown under full sun had shorter roots with no ramifications, plants grown under 30% shade had medium roots with few ramifications, while plants grown under 60% shade had very long roots with several ramifications.

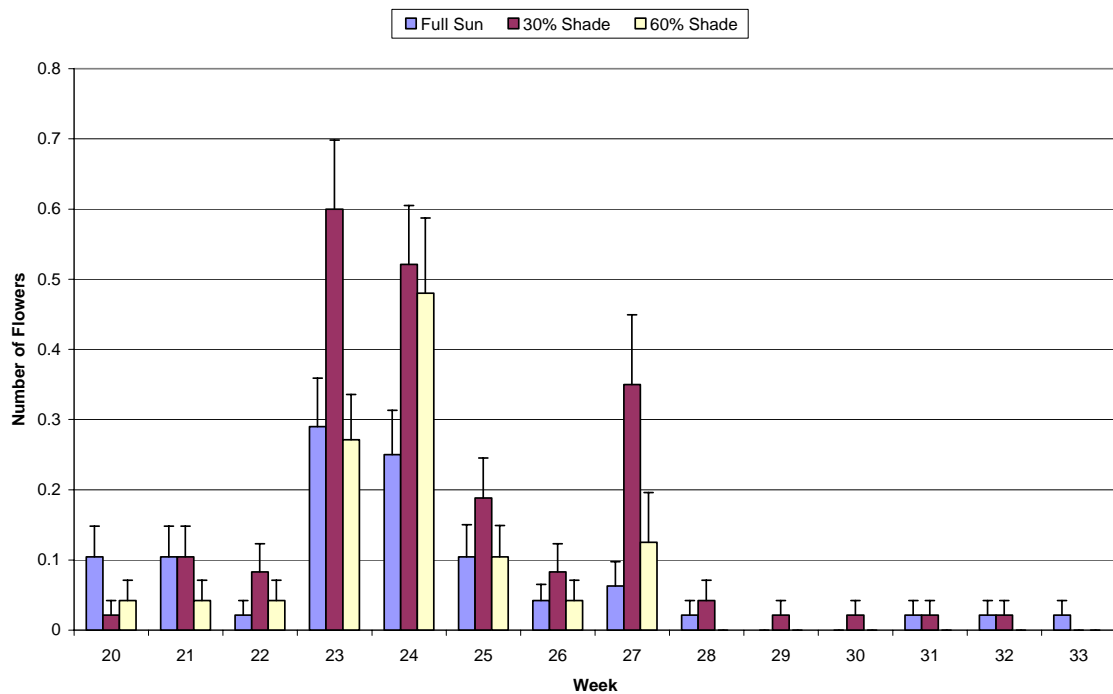


Figure 5-2: Number of flowers of *Habranthus robustus* bulbs in year 2 as affected by light levels (n=48). Bars represent standard errors.

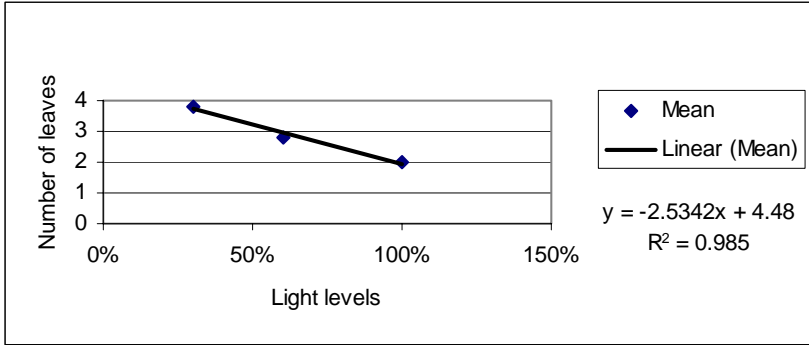


Figure 5-3: Number of leaves of *Habranthus robustus* bulbs in year 1 as affected by light levels.

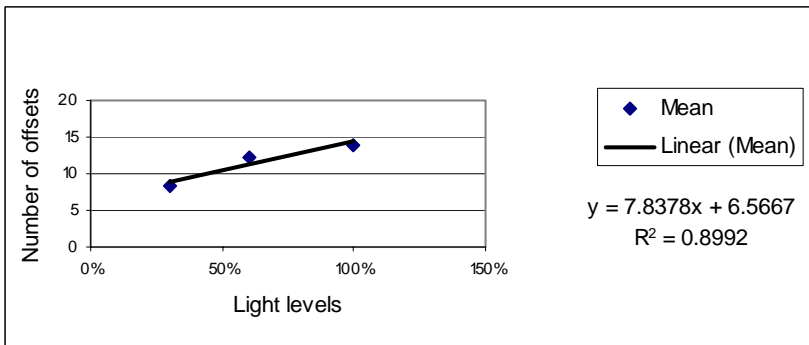


Figure 5-4: Number of offsets of *Habranthus robustus* bulbs in year 1 as affected by light levels.

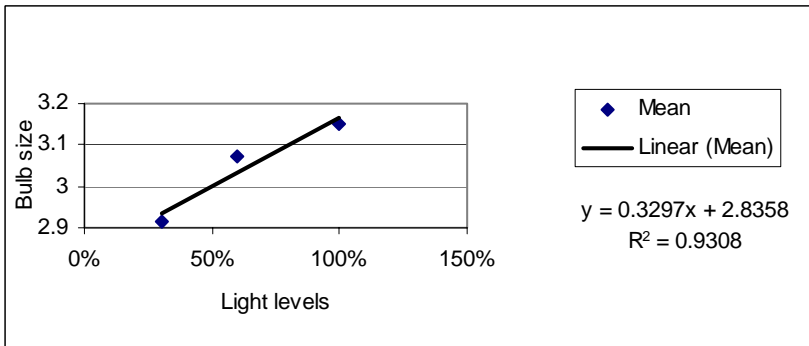


Figure 5-5: Bulb size of *Habranthus robustus* in year 1 as affected by light levels.

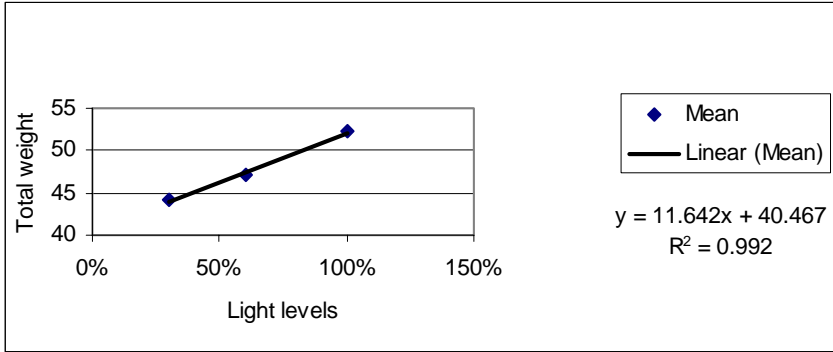


Figure 5-6: Total weight of leaves of *Habranthus robustus* bulbs in year 1 as affected by light levels.

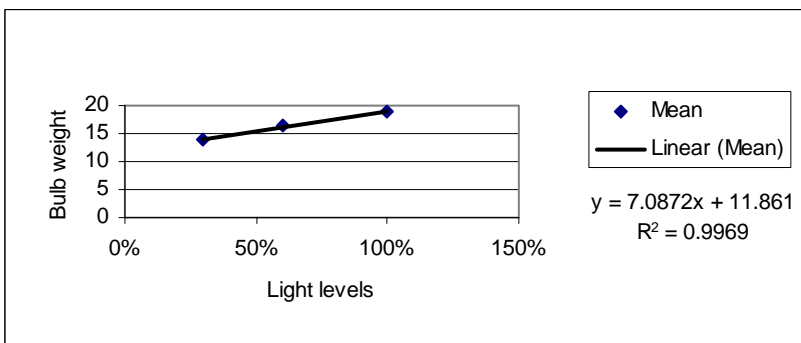


Figure 5-7: Bulb weight of *Habranthus robustus* in year 1 as affected by light levels.

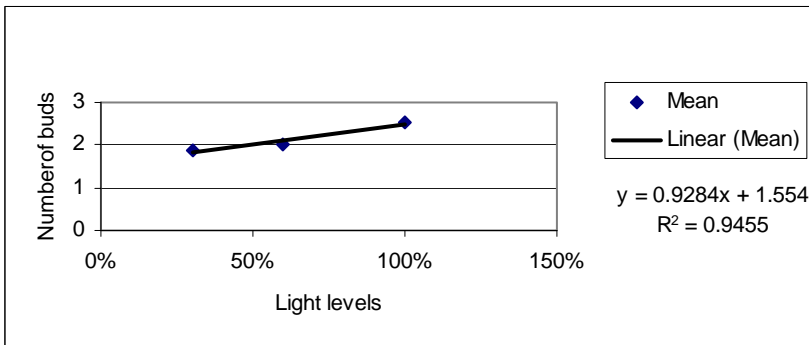


Figure 5-8: Number of flower buds of *Habranthus robustus* bulbs in year 1 as affected by light levels.



Figure 5-9: Root condition of *Habranthus* bulbs, under different treatments, after completion of experiment 1. From left to right full sun, 30% shade and 60% shade

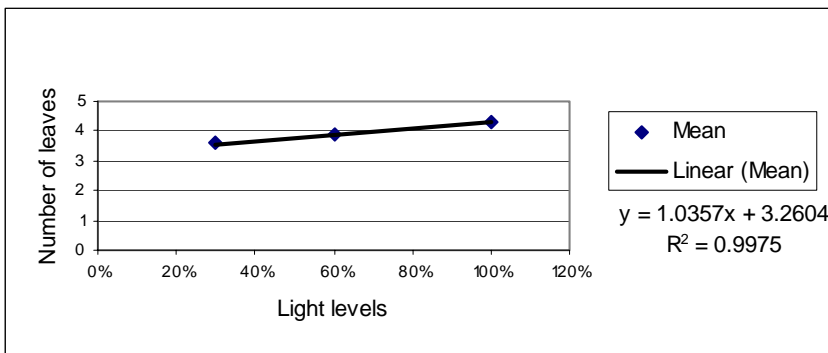


Figure 5-10: Number of leaves of *Habranthus robustus* bulbs in year 2 as affected by light levels.

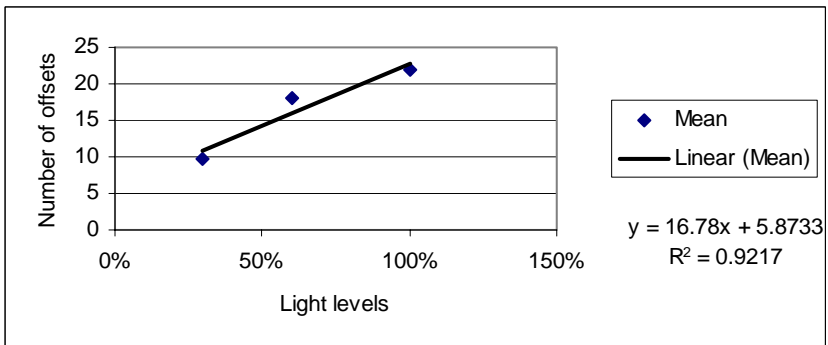


Figure 5-11: Number of offsets of *Habranthus robustus* bulbs in year 2 as affected by light levels.

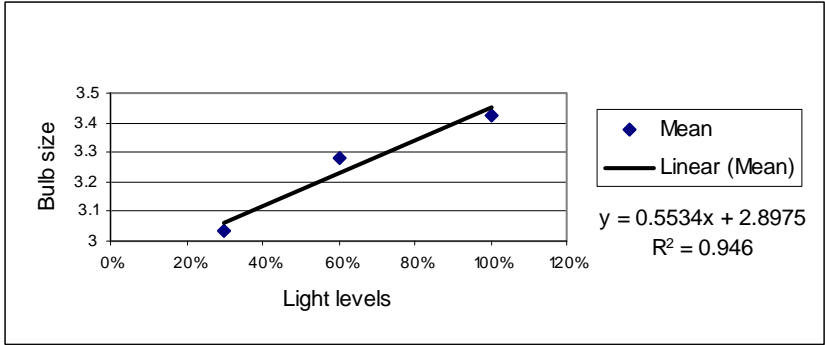


Figure 5-12: Bulb size of *Habranthus robustus* in year 2 as affected by light levels.

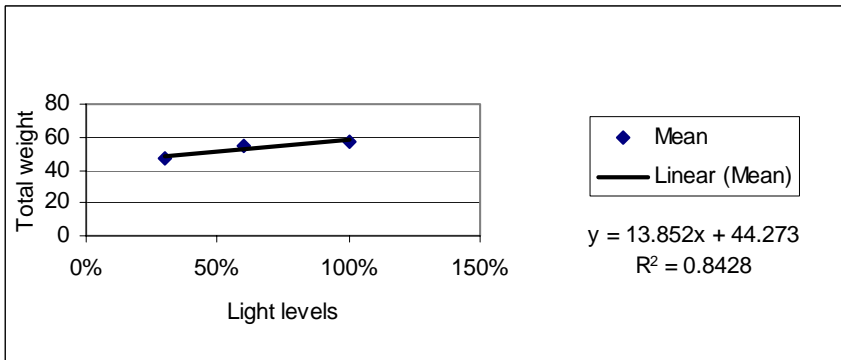


Figure 5-13: Total weight of *Habranthus robustus* bulbs in year 2 as affected by light levels.

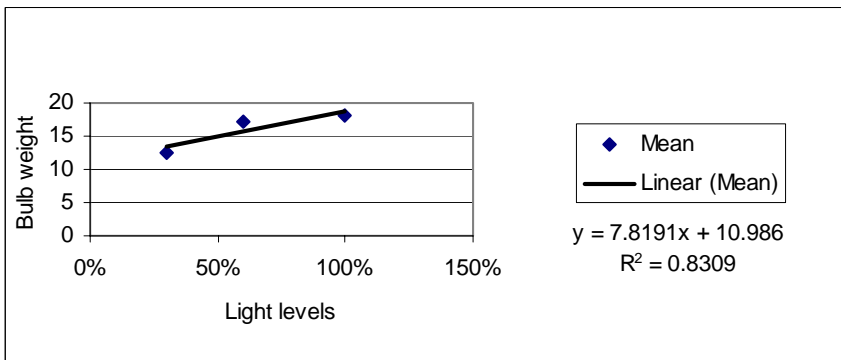


Figure 5-14: Bulb weight of *Habranthus robustus* in year 2 as affected by light levels.

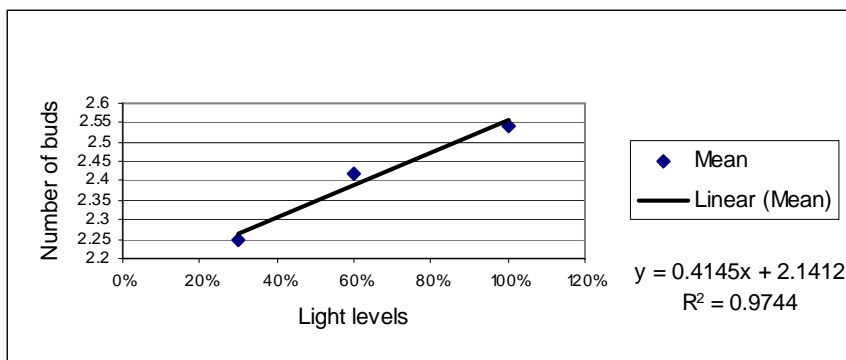


Figure 5-15: Number of flower buds of *Habranthus robustus* bulbs in year 2 as affected by light levels.

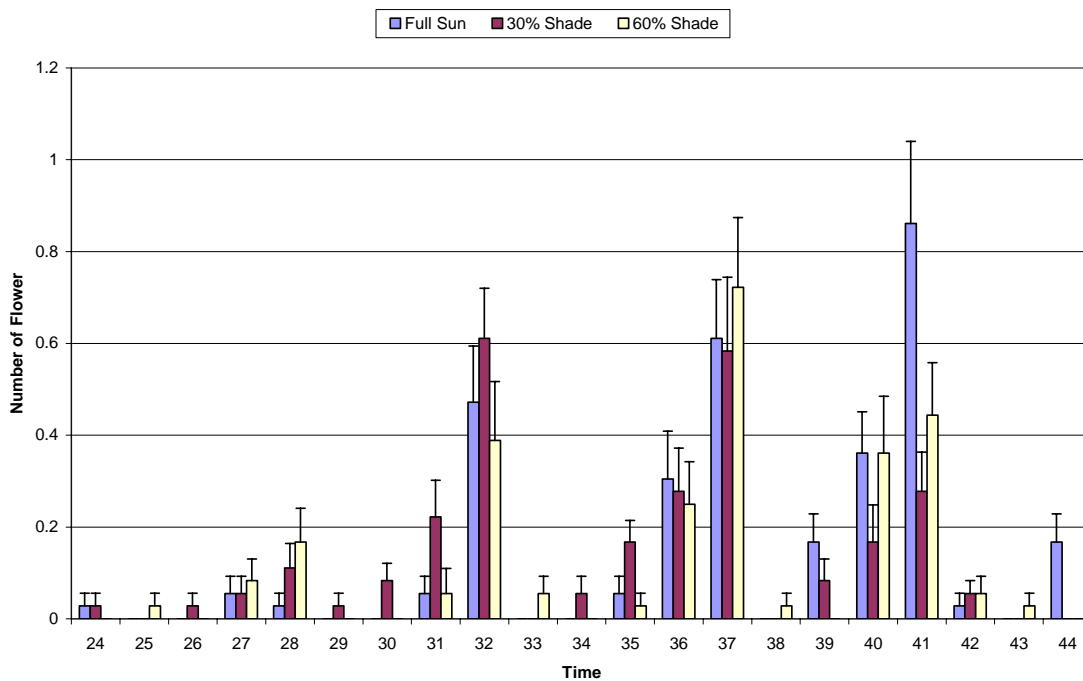


Figure 5-16: Number of flowers of *Zephyranthes* spp. bulbs in year 1 as affected by light levels (n=48). Bars represent standard errors.

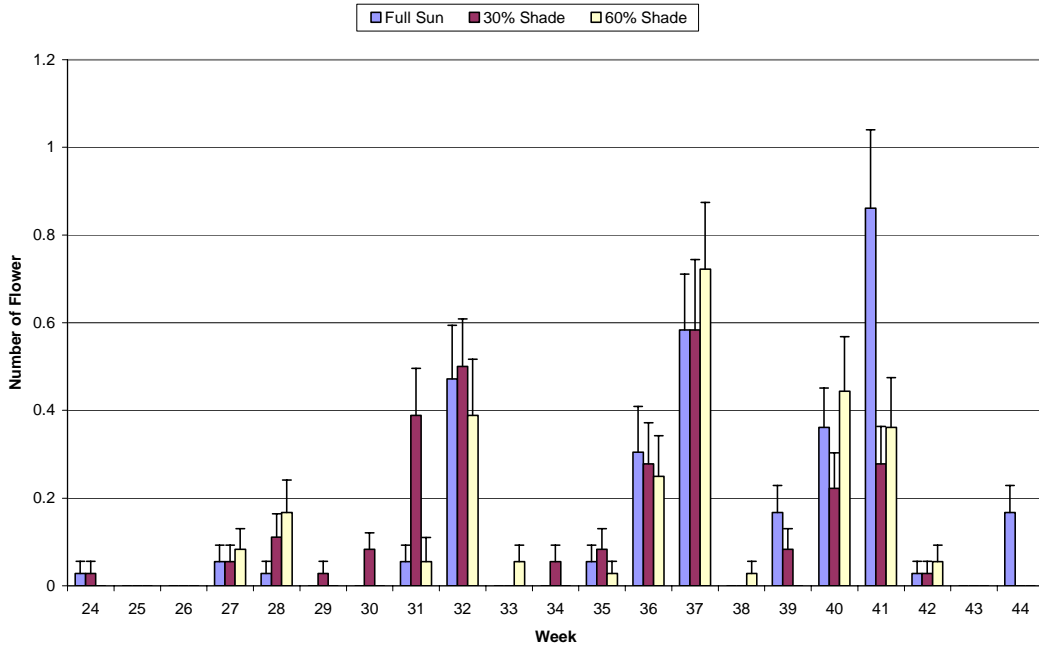


Figure 5-17: Number of flowers of *Zephyranthes* spp. bulbs in year 2 as affected by light levels (n=48). Bars represent standard errors.

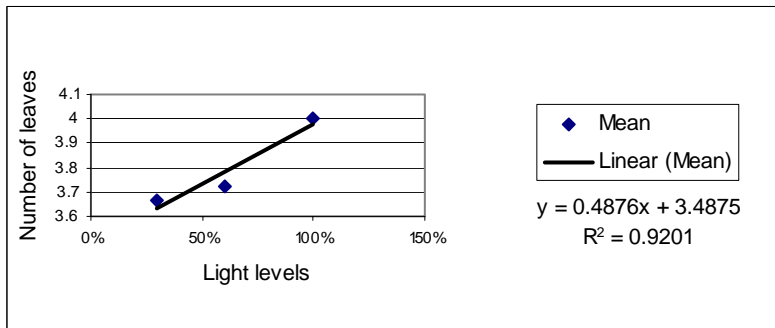


Figure 5-18: Number of leaves of *Zephyranthes* spp. bulbs in year 1 as affected by light levels.

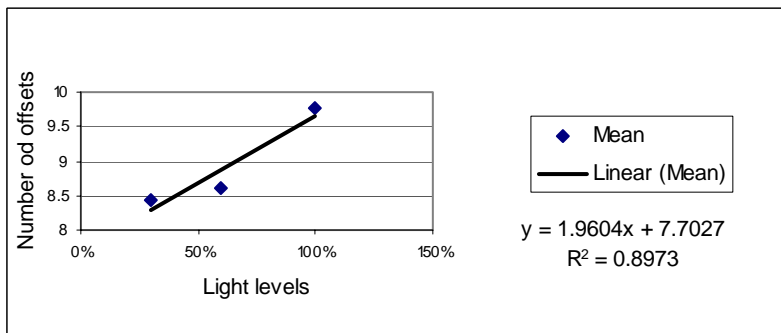


Figure 5-19: Number of offsets of *Zephyranthes* spp. bulbs in year 1 as affected by light levels.

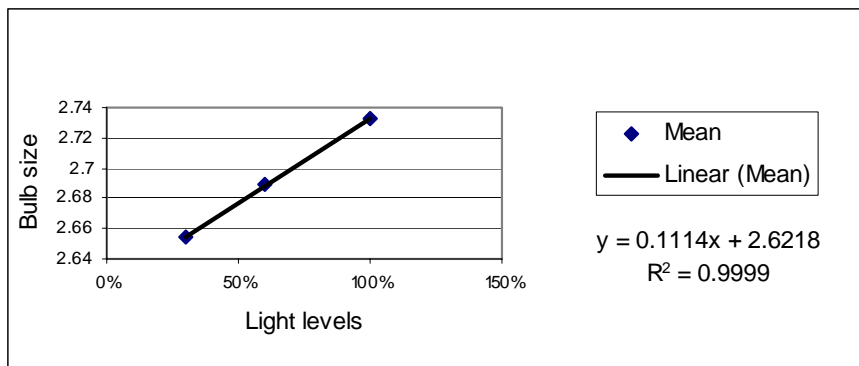


Figure 5-20: Bulb size of *Zephyranthes* spp. in year 1 as affected by light levels.

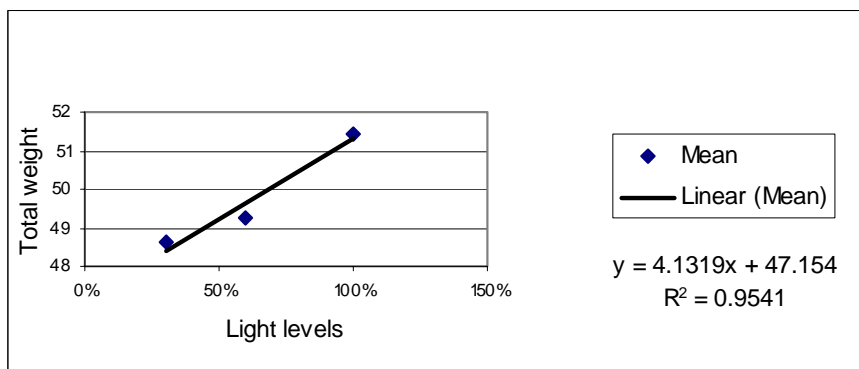


Figure 5-21: Total weight of *Zephyranthes* spp. bulbs in year 1 as affected by light levels.

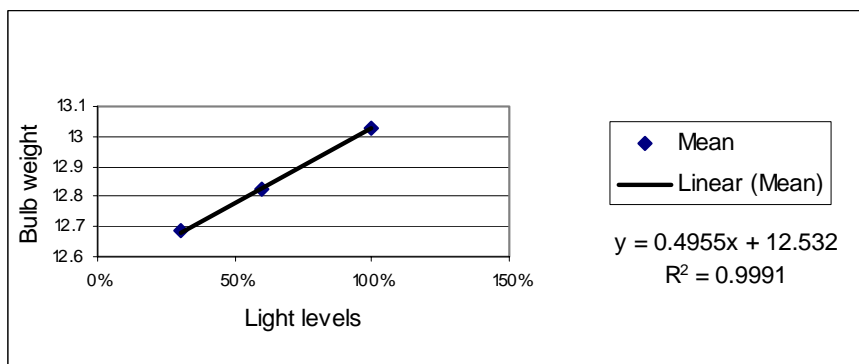


Figure 5-22: Bulb weight of *Zephyranthes* spp. in year 1 as affected by light levels.

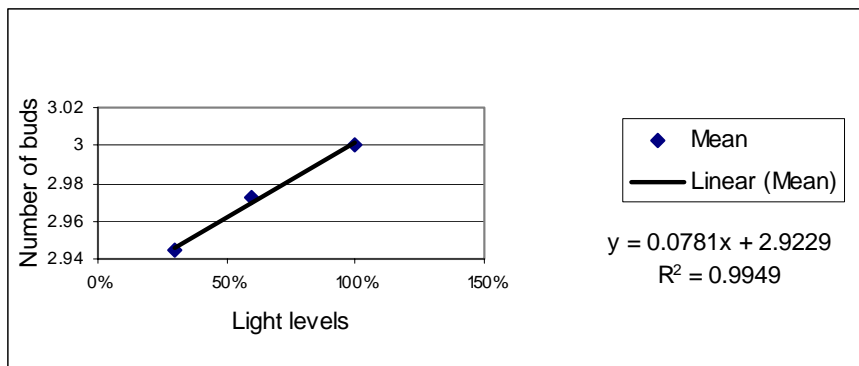


Figure 5-23: Number of flower buds of *Zephyranthes* spp. bulbs in year 1 as affected by light levels.

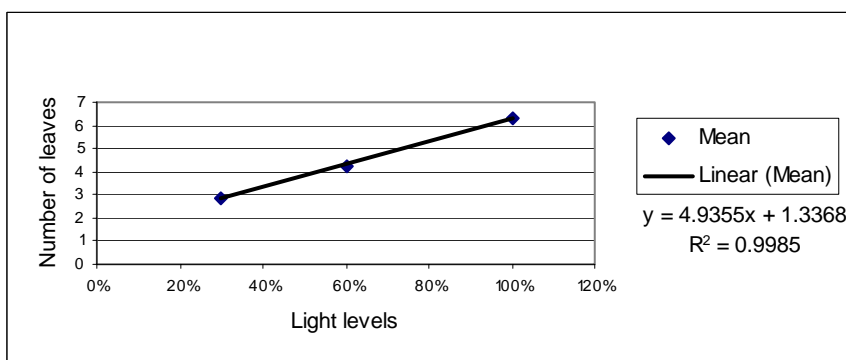


Figure 5-24: Number of leaves of *Zephyranthes* spp. bulbs in year 2 as affected by light levels.

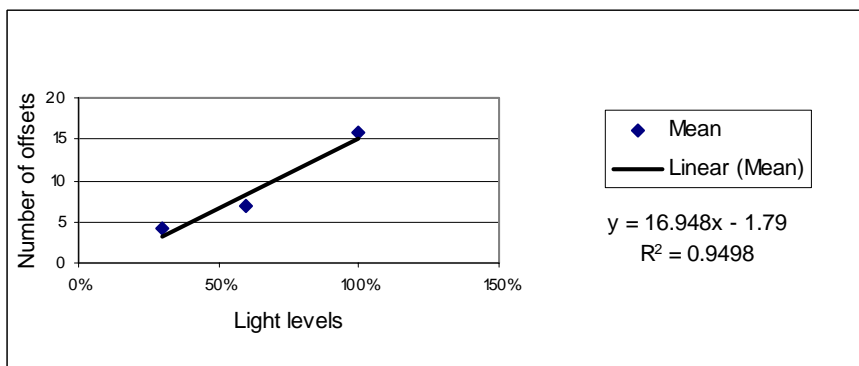


Figure 5-25: Number of offsets of *Zephyranthes* spp. bulbs in year 2 as affected by light levels.

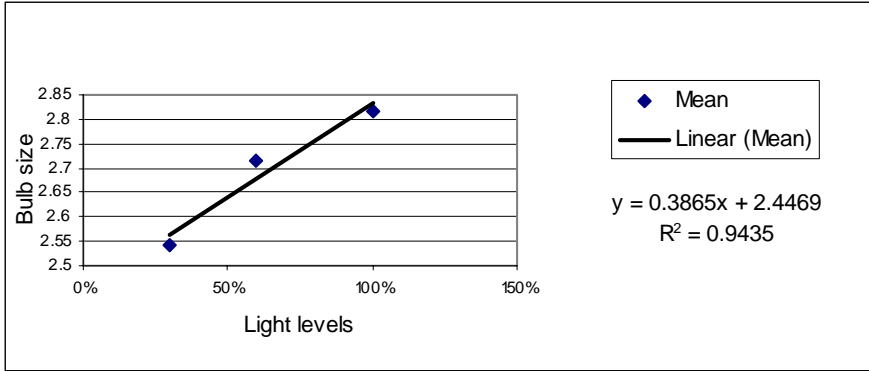


Figure 5-26: Bulb size of *Zephyranthes* spp. in year 2 as affected by light levels.

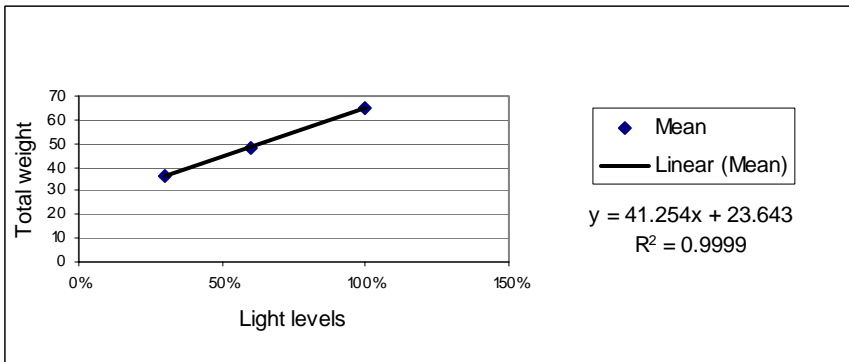


Figure 5-27: Total weight of *Zephyranthes* spp. bulbs in year 2 as affected by light levels.

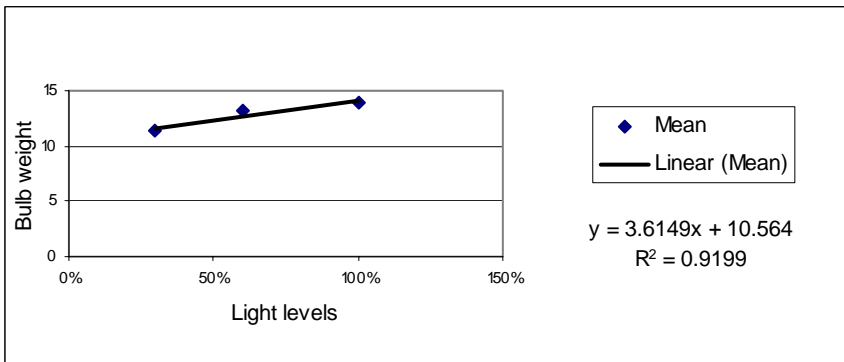


Figure 5-28: Bulb weight of *Zephyranthes* spp. in year 2 as affected by light levels.

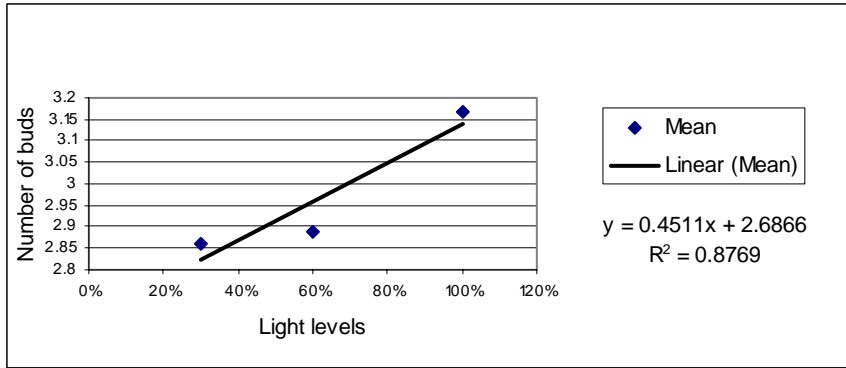


Figure 5-29: Number of flower buds of *Zephyranthes* spp. bulbs in year 2 as affected by light levels.

CHAPTER 6 CONCLUSIONS

When talking about bulbs, the first ones that come to our minds are members of the genera *Tulipa*, *Hyacinthus*, *Narcissus* and other temperate zone favorites. However, there is a large selection of tropical and subtropical bulbous plants that produce great spring and summer color, are easy to grow, and are suitable for Florida's climate; some examples include genera used in this study: *Hippeastrum*, *Habranthus*, *Zephyranthes*, *Scadoxus* and *Agapanthus*.

The cultivation of ornamental bulbous crops is no longer limited to countries with a moderate climate. The production of high-quality flower bulbs in warm regions has become important during the last decades. However, the tropical and subtropical bulb market is practically non-existent in Florida, because most species are very slow to produce, some have viral problems, many consumers are not sure how to grow them, and research is needed for this branch of the ornamental industry. This study was designed to address some of these issues, raise both homeowners and industry awareness of this group of plants; provide growers with improved methodology and guidelines to facilitate the production and commercialization of two genera of tropical bulbs: *Habranthus* and *Zephyranthes*.

The morphology of five species of tropical geophytes - *Hippeastrum* hybridum, *Scadoxus multiflorus*, *Agapanthus africanus*, *Habranthus robustus* and *Zephyranthes* spp were compared and contrasted in chapter 3. *Hippeastrum*, *Habranthus* and *Zephyranthes* were true tunicate bulbs with similar scales thickness, similar shapes and a brown papery

tunica covering the bulb. *Hippeastrum* bulbs had the largest diameter and height, and *Habranthus* were slightly larger than *Zephyranthes* bulbs. Their leaves were simple, linear, with entire margins and parallel venation, and emerged alternately (leaves originated on either side of the meristem) from the center of the bulb. Flower buds were formed alternately on each side of the apical meristem (forming a cross line in cross section), and four leaves were formed between each inflorescence/flower initiation.

Scadoxus was a true tunicate bulb covered by a brown papery tunica with a thick rhizomatous structure at its base. Its size was comparable to *Hippeastrum* bulbs; however, the scales were thicker than those from *Hippeastrum*, *Habranthus* and *Zephyranthes*. Leaves had distinct oblong shapes compared to *Hippeastrum*, *Habranthus* and *Zephyranthes* and arose in a cluster from the center forming a pseudostem (a false stem formed by the sheathing and overlapping of the leaf basis). Flower buds were formed centrally in the apical meristem, and an inflorescence stalk emerged first followed by the leaf pseudo-stem.

Agapanthus was a rhizome with simple, linear leaves with entire margins and parallel venation, similar to those of *Hippeastrum*, *Habranthus* and *Zephyranthes*, that arose alternatively from lateral meristems (leaves form on either side of the meristem). Flower buds were formed centrally in the apical meristem. *Hippeastrum*, *Scadoxus*, *Habranthus* and *Zephyranthes* had similar meristematic arrangements and apical meristems were responsible for both leaf and flower initiation; in *Agapanthus africanus* flowers were formed at apical meristems and leaves arose from lateral meristems.

Of the five species examined in the morphological study, *Habranthus* and *Zephyranthes* were the least investigated by other researchers, and since they were used

in the subsequent phases of this study an experiment was designed to understand their leaf and flower production. It was observed that these two species had distinct patterns of leaf production. *Habranthus* bulbs had fewer leaves emerge when flowering, while leaves of *Zephyranthes* bulbs continue to emerge during flowering. Overall, *Zephyranthes* bulbs had a greater number of leaves during the entire year but with oscillations, while *Habranthus* bulbs demonstrated a more uniform progress with a gradual decrease and increase in leaf production correlated with flowering periods.

In chapter 4 two experiments compared the responses of *Habranthus robustus* and *Zephyranthes* spp. to fertigation frequencies and fertilizer rates. Experiment 1 tested fertigation frequencies of twice a week, once a week and every other week on both species. Fertigation regimens of once or twice a week seemed to be effective for flowering of *Habranthus robustus*, however, when fertigated every other week they had a shorter flowering period which begun and finished earlier. Plants fertigated twice a week had a flowering peak sooner and 40% more flowers compared to the other two groups.

Regarding *Habranthus* bulb development, regression analysis of all factors investigated (number of leaves, number of offsets, bulb size, total fresh bulb weight, bulb weight and number of flower buds) showed linear responses and all factors increased as fertigation frequencies increased during year 1. During year 2, similar responses were obtained for number of leaves, bulb size, total fresh bulb weight and bulb weight; however, there were no linear responses for number of offsets and flower buds.

Fertigation regimens of once and twice a week were also effective for flowering of *Zephyranthes* during both year 1 and 2 under greenhouse environments. However,

fertigating twice a week would be preferable since the results showed that plants under this fertigation regimen produced more flowers.

Regarding *Zephyranthes* bulb development, regression analysis of all factors investigated, with the exception of number of offsets, showed linear responses and increased as fertigation frequencies increased during the first year, similarly to the *Habranthus* study. During year 2, number of offsets and total fresh bulb weight were the only factors that had linear responses.

Experiment 2 tested bulb development responses of *Habranthus* and *Zephyranthes* when plants were fertilized with 20-10-20 at rates of 0, 75, 150, 300 ppm N. With the exception of number of offsets, all factors investigated in *Habranthus* bulbs had a gradual increase in growth followed by a luxury consumption period and a gradual decrease in growth; following the standard crop response curve to fertilizer rates demonstrated by Janick et al. (1976). Bulbs fertilized with 75 and 150 ppm N had greater number of leaves; number of offsets increased as fertilizer rates increased and was highest when bulbs were treated with 300ppm N; bulb size and bulb weight (both total fresh weight and bulb weight) were higher when bulbs were fertilized with 75 and 150 ppm N. These results demonstrated that optimum fertilizer rates for *Habranthus* bulb propagation by separation was 300 ppm of N using Peter's Excel 20-10-20, since bulbs produced more offsets under this treatment. However, the optimum fertilizer rates for growing bulbs to the market were 75 or 150ppm of Peter's Excel 20-10-20, which produced largest bulbs. Additionally, optimal fertilizer rates for flowering would be 150ppm since this treatment produced the greatest amount of flower buds.

In chapter 5 an experiment compared the responses of *Habranthus robustus* and *Zephyranthes* hybrids to light levels of full sun, 30% and 60% shade. Results demonstrated that both *Habranthus* and *Zephyranthes* flowered for a longer period under full sun and 30% shade but both species had more flowers when grown under 30% shade. These results contrasted to the responses of *Alstroemeria* bulbs as their flower stem length increased when shading was increased but the number of flowers per plant did not (Zizzo et al., 1992).

Regarding *Habranthus* bulb development, all factors investigated (number of leaves, number of offsets, bulb size, total fresh bulb weight, bulb weight and number of flower buds) showed linear responses and increased as light levels increased during both year 1 and year 2. The only exception was number of leaves which decreased as light levels increased during the first year. *Zephyranthes* bulb development was also affected by the treatments. All factors investigated showed linear responses and increased as light levels increased during both year 1 and year 2.

The root system of both *Habranthus* and *Zephyranthes* were affected by the treatments. Plants grown under full sun had shorter roots with no ramifications, plants grown under 30% shade had medium roots with few ramifications, while plants grown under 60% shade had very long roots with several ramifications.

From this study it was concluded that preferred conditions for both species were fertigation twice a week with a fertilizer rate of 150 ppm N. and grown in full sun. However, further research with *Habranthus* and *Zephyranthes* should be considered. Fertigation frequency treatments could be applied to these plants under different conditions of light and temperature from those used in this study. Furthermore, fertilizer

with different concentrations of nitrogen, phosphorus and potassium could be used. The current research on these two species is somewhat limited and would benefit from additional investigations.

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BIOGRAPHICAL SKETCH

Camila do Amaral Brito was born on November 26, 1974, in São Paulo, Brazil, to José Fernando and Sônia Brito. Camila graduated from Colégio Objetivo (High School) in 1992 and two years later started her undergraduate degree in architecture and urbanism at the University of São Paulo, Brazil. While pursuing her degree, she has spent eight months in Vancouver, Canada, and visited several countries around the world. On her last year at the University, Camila worked as an intern in a landscape design company and became fascinated by the plasticity of plants. Her experience on this company, under the supervision of the company's owner, changed her life and the focus of her career. After earning her bachelor's degree from the University of São Paulo, she specialized in landscape architecture and worked for three years on this field. Camila was married to Luiz Augusto de Castro e Paula in January 2003 and changed her name to Camila do Amaral Brito de Castro e Paula. She and her husband moved to Gainesville, Florida, in May of the same year and both became graduate students at the University of Florida. Camila was interested in environmental horticulture and pursued her graduate degree under the guidance of Dr. Rick Schoellhorn; a year later Dr. Dennis McConnell became her major professor, while her husband pursued his graduate degree in animal sciences under Dr. Peter Hansen. Camila then earned her Master of Science in May of 2006.