

## **INFORMATION TO USERS**

While the most advanced technology has been used to photograph and reproduce this manuscript, the quality of the reproduction is heavily dependent upon the quality of the material submitted. For example:

- Manuscript pages may have indistinct print. In such cases, the best available copy has been filmed.
- Manuscripts may not always be complete. In such cases, a note will indicate that it is not possible to obtain missing pages.
- Copyrighted material may have been removed from the manuscript. In such cases, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, and charts) are photographed by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each oversize page is also filmed as one exposure and is available, for an additional charge, as a standard 35mm slide or as a 17"x 23" black and white photographic print.

Most photographs reproduce acceptably on positive microfilm or microfiche but lack the clarity on xerographic copies made from the microfilm. For an additional charge, 35mm slides of 6"x 9" black and white photographic prints are available for any photographs or illustrations that cannot be reproduced satisfactorily by xerography.

8708291

Hunter, Dale M.

AN ECOLOGICAL STUDY OF THREE SPECIES OF EPIPHYTIC BROMELIADS  
IN JAMAICA

*City University of New York*

PH.D. 1987

University  
Microfilms  
International 300 N. Zeeb Road, Ann Arbor, MI 48106

**PLEASE NOTE:**

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark .

- 1. Glossy photographs or pages \_\_\_\_\_
- 2. Colored illustrations, paper or print \_\_\_\_\_
- 3. Photographs with dark background
- 4. Illustrations are poor copy \_\_\_\_\_
- 5. Pages with black marks, not original copy \_\_\_\_\_
- 6. Print shows through as there is text on both sides of page \_\_\_\_\_
- 7. Indistinct, broken or small print on several pages
- 8. Print exceeds margin requirements \_\_\_\_\_
- 9. Tightly bound copy with print lost in spine \_\_\_\_\_
- 10. Computer printout pages with indistinct print \_\_\_\_\_
- 11. Page(s) \_\_\_\_\_ lacking when material received, and not available from school or author.
- 12. Page(s) \_\_\_\_\_ seem to be missing in numbering only as text follows.
- 13. Two pages numbered \_\_\_\_\_. Text follows.
- 14. Curling and wrinkled pages \_\_\_\_\_
- 15. Dissertation contains pages with print at a slant, filmed as received
- 16. Other \_\_\_\_\_  
\_\_\_\_\_  
\_\_\_\_\_

University  
Microfilms  
International

AN ECOLOGICAL STUDY OF THREE SPECIES OF EPIPHYTIC BROMELIADS  
IN JAMAICA

by


DALE M. HUNTER

A dissertation submitted to the Graduate Faculty in  
Biology in partial fulfillment of the requirements  
for the degree of Doctor of Philosophy, The City  
University of New York.


1987


This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirements for the degree of Doctor of Philosophy.

1/16/1987  
Date

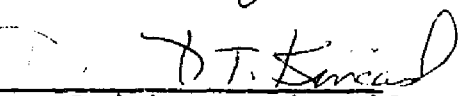
  
Chair of Examining Committee  
Dr. G. T. Prance  
The New York Botanical Garden

2/5/87  
Date

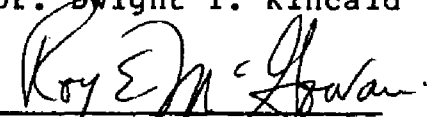
  
Executive Officer  
Dr. P. C. Chabora  
The Graduate Center, CUNY

  
Dr. Durland Fish

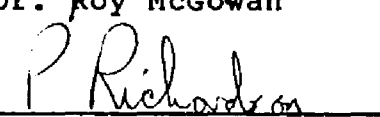
Fordham University

  
Dr. Dwight T. Kincaid

Lehman College, CUNY

  
Dr. Roy McGowan

Brooklyn College, CUNY

  
Dr. P. M. Richardson

The New York Botanical Garden

The City University of New York

ABSTRACT

AN ECOLOGICAL STUDY OF THREE SPECIES OF EPIPHYTIC BROMELIADS  
IN JAMAICA

by

Dale M. Hunter

Adviser: Dr. Ghilleen T. Prance

Three bromeliad species, Tillandsia complanata, Vriesia incurva and V. sintenisii, were found to partition vertical space in their Mor Ridge Forest habitats in the Blue Mountains of Jamaica. The 750 m<sup>2</sup> study area had 7454 bromeliads supported by 648 trees of 15 families and 22 species. Mean heights above ground were significantly different for each species (1.6, 2.7, 1.8 m respectively). The three bromeliads showed definite support tree preferences which were independent of tree frequency and were not greatly influenced by the texture, pH or capillarity of bark. I designed a new instrument (based on water displacement) for measuring bark texture and capillarity.

The leaves of all three species are long lived. The calculated mean leaf life of Vriesia incurva is 1,279 days, that of Tillandsia complanata is 724 days and that of V. sintenisii is 450 days. There were no significant differences in the relative growth

rates of leaves among the species and among the size classes. The absolute growth of Vriesia sintenisii was greater than that of Tillandsia complanata and V. incurva. There were more individuals of V. sintenisii (N = 4804) than T. complanata (N = 1880) and V. incurva (N = 769) combined. The larger number of V. sintenisii plants may be due to the greater measured fecundity of this species.

Only Vriesia sintenisii occurs naturally on the forest floor and individuals of each size class of all three species were transplanted to the ground. All transplants had significantly higher relative growth rates of leaves than non-transplanted ones. It is proposed that since all size classes of the three species grow well on the forest floor, Tillandsia complanata and Vriesia incurva are excluded at the seed stage or earliest germination stage of the life cycle. The very low pH of the forest floor (2.8 - 3.5) may also inhibit the germination of the seeds of Tillandsia complanata and Vriesia incurva. Since the rates of growth for all species within each group (transplanted and non-transplanted) are not different, the general climate of the area may have the greatest influence on the growth of these species.

The three bromeliads, rather than directly competing, may have partitioned the vertical space as well as the support trees in their habitat.

## ACKNOWLEDGEMENTS

I wish to thank my parents Beryl and Frank Hunter for their constant encouragement and moral and financial support throughout my academic career. Thanks also go to my sisters Marcia Lewis and Ingrid Hunter who provided support and helped with data entry.

I wish to thank my adviser Dr. Ghilleen T. Prance and the other members of my committee, Dr. Durland Fish, Dr. P. Mick Richardson, Dr. Roy McGowan, Dr. Scott Mori and Dr. Peter Nelson, for their continued interest, encouragement and guidance. Special thanks go to Dr. Dwight T. Kincaid for introducing me to plant population biology and computers, advice throughout the research and for help with and advise on data analysis.

I thank Dr. Edmund V. J. Tanner of Cambridge University, who introduced me to the forests of the Blue Mountains, for helping me find my first field site, for plant identification, helpful suggestions, support and encouragement throughout and for the loan of his Land Rover for the first year of the study. Thanks also to Dr. Valerie Kapos for helpful suggestions.

The field work was facilitated by Sherol Dixon, Marcia Thames, Lou Henslee, and John Healey. I thank John Dono of the Academic Computer Center of Lehman College for help with SAS.

Special thanks go to my late aunt Novlet C. Jones, former Director of the Southern Region of the Ministry of Agriculture of Jamaica, for her good offices and moral and material support. Thanks also to Aston Duffus of the Ministry of Agriculture of Jamaica.

I wish to thank Joy Klein, Russel Bickler, Jeff Canfield, Rosie Crabtree, Erica Schwarz, June Bellew, Carl Norman and Cleveland Robinson for providing moral support and a congenial atmosphere at the Cinchona greathouse.

I am grateful for the helpful suggestions and support of my fellow graduate students especially, Drs. Susan Yost, Cecile Lumer, Ricardo Callejas, Lucia Atehortua, Magdon Jayasuriya and Edmond Badham. I also thank Ann Soll, Martin Supnick, Barbara Junker, Dawn Frame and Abigail Miller.

I wish to thank my friends Niki Whitehead, Claire Laurenson, John Laurenson, Dalton Thames, Stephanie Thames and Pauline Karrfalt for their help and support.

I thank Mr. Roy Jones, Director of the Forest Department of Jamaica, for permitting me to carry out field work in the Blue Mountains. Thanks also to Mr. A. C. Allen, Director of Public Gardens, for permission to live in the greathouse at the Cinchona Botanical Garden.

I appreciate the help of the employees of the Cinchona Botanical Garden and the residents of the nearby districts especially Raff Menardes, Lloyd Stamp,

Sybil Francis, Glen Parks, Alexander Tyrell, Delphene McPherson, Euklyn Hibbert, Roxy, Esmeline, Roy, Edgar Edwards, Lorraine Lowe, Carol Hall, Joseph Wolfe and Orville Campbell.

Thanks also go to the employees of the Coffee Industry Development Corporation especially, Romeo Thompson, Elleston Feron, Gracey Brown, Roy Landley, Ainsley Taylor, Paul Gregory, Allan Campbell, Eastburn Grant, Desmond Sterling, Vassel Willis and Eula Lindo.

I am grateful to the staff of the Biology Department of Lehman College especially the former secretary Barbara Smith. I thank the staff of the Ph.D program in Biology especially Elsie Grant. I appreciate the help of Frances Maroncelli, Linda Marschner and Don Black of the New York Botanical Garden (NYBG). Thanks also to the staff of the library of the NYBG especially Lothian Lynas.

I wish to thank the Research Foundation of the City University of New York for a \$5000 grant and the NYBG for a \$2275 grant. I appreciate the teaching positions provided by the Biology Department of Lehman College.

Finally, I wish to thank my husband Eric Karrfalt for moral and financial support, helpful suggestions throughout, assistance in the field, designing and making equipment and maintenance (routine and otherwise) of my field vehicles. Without his total support, this project would have been impossible.

## TABLE OF CONTENTS

1. Title page .....	i
2. Approval page.....	ii
3. Abstract.....	iii
4. Acknowledgements.....	v
5. Table of contents.....	viii
6. List of tables.....	ix
7. List of figures.....	xi
8. Introduction.....	1
9. Description of bromeliad species.....	9
10. Description of study site.....	12
11. Population census.....	16
12. Leaf demography and phenology.....	32
13. Transplant experiment.....	41
14. Colonization experiment.....	45
15. Bark studies.....	50
16. Stem flow.....	57
17. General discussion.....	59
18. Tables.....	66
19. Figures.....	102
20. Literature cited.....	202

## LIST OF TABLES

1.	Frequency table of support species. Site 1.....	66
2.	Frequency table of support species. Site 2.....	67
3.	Frequency table of support species. Site 3.....	68
4.	Frequency table of support species Combined sites.....	69
5.	Frequency table of bromeliads on support species. Site 1.....	70
6.	Frequency table of bromeliads on support species. Site 2.....	71
7.	Frequency table of bromeliads on support species. Site 3.....	72
8.	Frequency table of bromeliads on support species. Combined sites.....	73
9.	Frequency table of bromeliad species by Size class. Site 1.....	74
10.	Frequency table of bromeliad species by Size class. Site 2.....	75
11.	Frequency table of bromeliad species by Size class. Site 3.....	76
12.	Frequency table of bromeliad species by Size class. Combined sites.....	77
13.	Frequency table of bromeliad species by site.....	78
14.	Frequency table for plot by bromeliad species Site 1.....	79
15.	Frequency table for plot by bromeliad species Site 2.....	80
16.	Frequency table for plot by bromeliad species Site 3.....	81
17.	Frequency table for plot by bromeliad species Combined sites.....	82
18.	Two-way ANOVA (no replication) height above ground.....	83

19.	Statistics for height of <u>Tillandsia complanata</u> by size class. Combined sites.....	84
20.	Statistics for height of <u>Vriesia incurva</u> by size class. Combined sites.....	84
21.	Statistics for height of <u>Vriesia sintenisii</u> by size class. Combined sites.....	85
22.	Spearman correlation height vs size class Combined sites.....	85
23.	Spearman correlation height vs size class by site.....	86
24.	Plot analysis of bromeliad species on support trees..	87
25.	Ranked support tree preferences.....	88
26.	Mean number of leaves produced and mean standing crop of leaves.....	89
27.	Calculated mean leaf life in days.....	90
28.	Paired comparisons of slopes of relative growth curves for epiphytically growing bromeliads.....	91
29.	Mean number of leaves produced and mean standing crop of leaves for transplanted bromeliads.....	92
30.	Mean leaf life (days) for transplanted bromeliads....	93
31.	Paired comparisons of slopes of relative growth curves for transplanted bromeliads.....	94
32.	Paired comparisons of slopes of relative growth curves for epiphytic x transplanted bromeliads.....	95
33.	Colonization - experimental plot.....	96
34.	Colonization - control plot.....	96
35.	Bark texture and capillarity.....	97
36.	Bark texture gradient.....	98
37.	Bark capillarity gradient.....	99
38.	Bark pH gradient and type.....	100
39.	Stem flow data.....	101

## LIST OF FIGURES

1.	Maps.....	102
2.	Mean height above ground.....	104
3.	Frequency distribution <u>T. complanata</u> heights Site 1.....	106
4.	Frequency distribution <u>V. incurva</u> heights Site 1.....	108
5.	Frequency distribution <u>V. sintenisii</u> heights Site 1.....	110
6.	Frequency distribution <u>T. complanata</u> heights Site 2.....	112
7.	Frequency distribution <u>V. incurva</u> heights Site 2.....	114
8.	Frequency distribution <u>V. sintenisii</u> heights Site 2.....	116
9.	Frequency distribution <u>T. complanata</u> heights Site 3.....	118
10.	Frequency distribution <u>V. incurva</u> heights Site 3.....	120
11.	Frequency distribution <u>V. sintenisii</u> heights Site 3.....	122
12.	Frequency distribution <u>T. complanata</u> heights Combined sites.....	124
13.	Frequency distribution <u>V. incurva</u> heights Combined sites.....	126
14.	Frequency distribution <u>V. sintenisii</u> heights Combined sites.....	128
15.	Absolute growth of <u>T. complanata</u> , <u>V. incurva</u> and <u>V. sintenisii</u> .....	130
16.	Relative growth of <u>T. complanata</u> .....	132
17.	Relative growth of <u>T. complanata</u> adults.....	134
18.	Relative growth of <u>T. complanata</u> small adults.....	136
19.	Relative growth of <u>T. complanata</u> seedlings.....	138

20.	Relative growth of <u>T. complanata</u> small seedlings.....	140
21.	Relative growth of <u>T. complanata</u> tiny seedlings.....	142
22.	Relative growth of <u>V. incurva</u> .....	144
23.	Relative growth of <u>V. incurva</u> adults.....	146
24.	Relative growth of <u>V. incurva</u> seedlings.....	148
25.	Relative growth of <u>V. incurva</u> small seedlings.....	150
26.	Relative growth of <u>V. incurva</u> tiny seedlings.....	152
27.	Relative growth of <u>V. sintenisii</u> .....	154
28.	Relative growth of <u>V. sintenisii</u> adults.....	156
29.	Relative growth of <u>V. sintenisii</u> small adults.....	158
30.	Relative growth of <u>V. sintenisii</u> seedlings.....	160
31.	Relative growth of <u>V. sintenisii</u> small seedlings....	162
32.	Relative growth of <u>V. sintenisii</u> tiny seedlings.....	164
33.	Relative growth of <u>T. complanata</u> transplants.....	166
34.	Relative growth of <u>T. complanata</u> adults transplants.....	168
35.	Relative growth of <u>T. complanata</u> small adults transplants.....	170
36.	Relative growth of <u>T. complanata</u> seedlings transplants.....	172
37.	Relative growth of <u>T. complanata</u> small seedlings transplants.....	174
38.	Relative growth of <u>T. complanata</u> tiny seedlings transplants.....	176
39.	Relative growth of <u>V. incurva</u> transplants.....	178
40.	Relative growth of <u>V. incurva</u> adults transplants....	180
41.	Relative growth of <u>V. incurva</u> small adults transplants.....	182
42.	Relative growth of <u>V. incurva</u> seedlings transplants.....	184

43.	Relative growth of <u>V. incurva</u> small seedlings transplants.....	186
44.	Relative growth of <u>V. incurva</u> tiny seedlings transplants.....	188
45.	Relative growth of <u>V. sintenisii</u> transplants.....	190
46.	Relative growth of <u>V. sintenisii</u> adults transplants.....	192
47.	Relative growth of <u>V. sintenisii</u> small adults transplants.....	194
48.	Relative growth of <u>V. sintenisii</u> seedlings transplants.....	196
49.	Relative growth of <u>V. sintenisii</u> small seedlings transplants.....	198
50.	Relative growth of <u>V. sintenisii</u> tiny seedlings transplants.....	200

## INTRODUCTION

The neotropics support the greatest diversity of vascular epiphytes (Richards 1952). Madison (1977) estimated the total number of species in the neotropics as 15,000, compared to 12,560 in the entire paleotropics. Madison (1977) suggested two reasons for the large number of neotropical epiphytes. First there are extensive middle-elevation cloud forests in the Andes, Central American ranges and coastal mountains of the Caribbean where most of the neotropical epiphytes occur. Second there are families such as the Bromeliaceae, Cactaceae, Marcgraviaceae, Cyclanthaceae and Gesneriaceae subfamily Gesnerioideae, largely confined to the neotropics, which contribute large numbers of species to the epiphyte flora.

Research on epiphytic plants was pioneered by Schimper. In his 1888 study "Die Epiphytische Vegetation Amerikas", attention was focused on the anatomy, morphology and ecology of epiphytes. Studies were performed in Java by Van Oye (1921, 1924) and Went (1931, 1940), in Micronesia by Hosokawa (1943, 1952), and in Africa by Sanford (1968, 1969). These studies addressed the distribution of epiphytes and the factors such as climate, which control these distributions. Johansson (1974) in a study of the ecology of vascular

epiphytes in a West African rain forest, recorded and characterized the growing sites of these epiphytes which were mostly orchids and pteridophytes. He recognized and characterized the development of ten different epiphyte communities. In addition he studied the colonization of host trees and found that light intensity and substrate composition were important factors. In the neotropics Richards (1952) suggested that montane habitats were more favorable for epiphytes than were the lowland forests. Grubb et al. (1963) found the density of epiphytes in the montane regions of Ecuador to be nearly ten times higher than that in the lowland forest. Sugden and Robbins (1979) reported similar results in Colombia. These findings support Grubb and Whitmore (1966), who concluded that cloud cover was of primary importance for epiphytes because it maintained their water supply during periods of very low rainfall. Sugden and Robbins (1979) suggest that high density and diversity of epiphytes in montane regions is mainly due to the frequency and duration of cloud cover.

Pantropically, the Orchidaceae dominate the vascular epiphyte flora (Madison 1977). In the neotropics, this family also contributes the largest number of species, but the Bromeliaceae constitute the most conspicuous component of the epiphyte vegetation (Madison 1977). About 919 species of epiphytic

bromeliads grow in the neotropics. Their systematics is well known (Smith and Downs 1974, 1977, 1979); and their ecology has received more attention than that of any other group of epiphytes.

Much of the work done on the Bromeliaceae has been concerned with the fauna which inhabit those which impound water and debris ("tank species"). The macrofauna of large tank species was described by Picado (1913), Pittendrigh (1948) and Fish (1976). These workers discovered that the micro-community may make important contributions to nutrition of the epiphytes. Laessle (1961), in an in situ study of the microlimnology of Jamaican tank bromeliads reported that there were important differences in gas content of axillary fluids which depended not only on the position of the plant with respect to light intensity but also on the related microfauna. Studies of host plant specificity and distribution of malaria mosquitoes which inhabit bromeliads were done in Trinidad (Downs and Pittendrigh, 1946; Pittendrigh, 1948). Frank and Curtis (1977a, 1977b,) did similar studies with the mosquito genus Wyeomyia in Florida.

In recent years a considerable amount of work has been done on the morphology, physiology, ecology and distribution of the Bromeliaceae. The members of this family absorb minerals, organic nutrients and water through foliar trichomes (Benzing and Burt 1970;

Benzing 1973; Benzing et al., 1976; Vrizo de Santo et al. 1976). Sugden (1981) studied habitat preferences of Bromeliaceae in the Serrania de Macuira in Colombia. He found that different species had different microclimate preferences ranging from dry to very moist sites. Many studies have been done on Tillandsia circinnata in Florida. The life history profile, germination, early establishment and population dynamics of this species have been studied (Benzing 1978a, 1978b, 1981, Benzing and Renfrow 1971). The mineral allocation patterns and nutritional dynamics of the species have also been investigated (Benzing and Davidson 1979, Benzing and Renfrow 1980).

While it is true that a considerable body of knowledge has been accumulated for this family, no detailed studies have been done on the population dynamics and ecology of local populations of sympatric species in the neotropics. Such a study was done on the vascular epiphytes (mainly orchids and pteridophytes) in a West African rain forest by Johansson (1974). A study similar to Johansson's needed to be done in the neotropics. The Bromeliaceae was an appropriate choice for such a study since they are a dominant part of the epiphytic flora in the neotropics. Epiphytic bromeliads are regarded as accurate indicators of climatic conditions because they are independent of the substrate for water and mineral

nutrition (Gilmartin 1973). Benzing (1970) studied absorption of organic nitrogen and minerals by bromeliad leaves. He reported that Aechmea nudicaulis, Aechmea bracteata, Billbergia pyramidalis and a Neoregelia hybrid absorbed phosphorus-32. Aechmea bracteata absorbed protein, amino acids and ammonium nitrogen. He further reported that the bromeliads tested appeared to be "well equipped to utilize minerals and organic nitrogen originating from tank-impounded plant and animal debris as nutrients."

A study of the factors controlling local distribution of sympatric species could be important to the understanding of the ecosystem. Since there are so many members of the Bromeliaceae in the neotropics, the factors controlling their local distribution may be fundamental to the workings of the ecosystem they inhabit and may ultimately provide a deeper understanding of ecosystem structure and function in tropical rain forests. The research identified and characterized some of the factors controlling the local distribution of three species of bromeliad - Tillandsia complanata, Vriesia incurva and V. sintenisii- in an upper montane rain forest in Jamaica.

Tillandsia complanata, Vriesia incurva, and V. sintenisii are three water and debris impounding members of the subfamily Tillandsioideae. Members of this subfamily are regarded as the most advanced in

terms of indumentum (Smith and Downs, 1974). The members of this taxon are either obligate or facultative epiphytes.

Many ecological classifications describing the numerous life strategies in the Bromeliaceae have been formulated (Schimper, 1888; Tietze, 1906; Pittendrigh, 1948; Benzing and Renfrow, 1974). Schimper (1888) used the methods by which water and minerals were obtained by the plants and their relationships to morphological characters to classify bromeliads. In that and all subsequent ecological classifications, special emphasis was placed on trichomes.

Pittendrigh (1948) recognized three classes of bromeliads. The "exposure group" occurred at the highest level of the forest, on the crowns of emergent and semi-emergent trees. The members of the "sun group" were found in the upper levels of the canopy. This group contained only tank species, many with the "nest habit" (i.e. the tanks also impound debris). The "shade tolerant group" dominated the lowermost levels of the forest canopy and heavily shaded areas near the ground.

Benzing (1976) recognized four ecological types of bromeliads: Type 1, "soil rooting species without tanks or absorbing trichomes;" Type 2, "soil rooting species with rudimentary to modestly developed tanks;" Type 3, "tank species with holdfast roots that can be

absorptive and trichomes that exhibit moderate to high uptake capacity;" and Type 4, "tankless xeromorphic species with dense investments of absorbing trichomes and nonabsorbptive holdfast roots (atmospherics)."

Tillandsia complanata and Vriesia sintenisii can be classified in Benzing's system as a Type 3. Vriesia incurva falls somewhere between Type 3 and Type 4. This species impounds water and debris but also has dense trichome cover on the leaves. This dense cover of trichomes gives the leaves a highly reflective, silvery surface. Tillandsia complanata, Vriesia incurva and V. sintenisii grow on the boles of trees as well as in the canopy.

In this study I tested three hypotheses.

1. Distribution is controlled by events at the seedling stage.
2. Distribution is the result of interspecific interactions.
3. Distribution is determined by the species of support trees.

For the purpose of this study, distribution means the local distribution within 5 X 5 m plots.

I addressed these questions by choosing six approaches: population census; leaf demography and phenology; transplant experiment; colonization experiment; bark texture and stem flow.

The population census provided data on the actual distribution of the three bromeliads, the size and age structure of the populations as well as information on support tree preferences and interspecific interactions. The transplant and colonization experiments provided information on barriers to germination of seeds, establishment of seedlings and the fate of transplanted adults. The leaf demography and phenology studies, provided data on plant growth rates, standing crop, mean leaf life and fecundity. Bark studies and stem flow observations provided data on the physical and physiological characteristics of the support trees which are important in seed germination and seedling establishment.

## DESCRIPTION OF BROMELIAD SPECIES

The family Bromeliaceae is divided into three subfamilies: the Pitcairnioideae, the Tillandsioideae and the Bromelioideae. Nine genera and 62 species of bromeliads occur in Jamaica (Adams 1972). Bromeliads are herbs or rarely shrubby perennials. They are mostly epiphytic. Roots are usually present but often serve merely as holdfasts in the epiphytic species. The leaves are spirally arranged, usually basal with dilated-sheathing bases. Leaves are simple entire or spinose-serrate, bearing peltate scales at least when young. The inflorescence is simple or paniculate, of spikes or racemes usually bearing brightly colored conspicuous bracts. The flowers are bisexual or functionally dioecious. The perianth is biseriate and 6-merous. The sepals and petals are dissimilar, free or connate. There are six stamens in two series; filaments are free or joined to the petals or to each other. The anthers are two-locular, opening lengthwise; pollen is smooth porous or grooved. The ovary is superior to inferior, three-locular with numerous ovules, anatropous on axile placentas. The stigmas are three and the style short or slender. The fruit is a capsule or berry or (in Ananas) fleshy and compound. Seeds are often plumose with a small embryo located at the base of a copious, mealy endosperm (Adams 1972).

The three species I studied are in the subfamily Tillandsioideae. Members of this taxon are herbs, largely epiphytic, caulescent or acaulescent. Their roots often function only as holdfasts and are sometimes completely lacking. Leaves are rosulate or fasciculate or distributed along a stem and are entire. There is an indument of radially symmetrical scales. The ovary is superior or nearly so except in Glomeropitcairnia. The fruit is capsular and septicidal, and the seeds have a plumose appendage at the base or apex or both (Smith and Downs, 1977).

Tillandsia complanata Benth, Bot. Sulph. 173. 1846.

Overall Distribution: Epiphytic in forests 800-3500 m alt. Greater Antilles, Costa Rica to Bolivia and Northern Brazil. (Smith and Downs, 1977).

Distribution in Jamaica: Local St. Andrew, Portland and St. Thomas. Epiphytic in montane forest and mossy woodlands 1230-1785 m alt (Adams, 1972).

Vriesia incurva (Grisebach) R. W. Read, Phytologia 16: 458. 1968.

Overall Distribution: Epiphytic in cloud forest, 1000-3000 m alt, Costa Rica to Venezuela and Bolivia, Greater Antilles.

Distribution in Jamaica: Local St. Andrew, St. Ann, Portland, St. Thomas. Epiphytic in wet Montane forests

and higher elevations than any other bromeliad in Jamaica; 769-2154 m alt.

Vriesia sintenisii (Baker) L. B. Smith & Pittendrigh, Jour. Wash. Acad. 43: 403. 1953.

Overall Distribution: Epiphytic in forest, 725-3000 m alt, Greater Antilles (Smith and Downs, 1977).

Distribution in Jamaica: Frequent epiphyte in montane forest, 923-1692 m alt (Adams, 1972).

## DESCRIPTION OF STUDY SITE

I chose three sites in the Blue Mountains of Jamaica, West Indies. The Blue Mountain Range, which reaches a height of 2,265 meters, runs east to west in the eastern part of the island. The forests of the Blue Mountains have been studied in detail by Shreve (1914) who characterized the vegetation, soils and climate. Asprey and Robbins (1953) defined the vegetation types of the entire island. More recently, the forests have received intensive study by Grubb and Tanner (1976) reassessed the forests and soils of the montane region. Tanner continues his intensive studies of various aspects of the ecology of the area. He has studied mineral cycling (Tanner 1977a), the floristics, the soils and foliar mineral levels (Tanner 1977b), biomass, productivity, litterfall and decomposition of leaf litter (Tanner 1980a, 1980b, 1981), species diversity and reproductive mechanisms in trees and leaf structure of the montane forest trees (Tanner 1982, Tanner and Kapos 1982). The flora of Jamaica is also well known. A recent angiosperm flora (Adams 1972) and a guide to pteridophytes (Proctor 1985) are available.

All three sites are located in Mor Ridge forests. Grubb and Tanner (1976) found this forest type occurring only between Morce's Gap and Silver Hill Peak at elevations between 1,500 and 1,699 m in the Blue

Mountain Range. I discovered three new Mor Ridge Forests. Each site is located in one of these. Site three is at Morce's Gap, while Sites 1 and 2 are located between Morce's Gap and St. Helen's Gap (figure 1). The area in which Mor Ridge Forests are found has therefore been extended by me.

The Mor Ridge forest is "characteristic of knolls and ridges" and has an open canopy with trees four to seven meters tall and usually less than 0.3 m DBH (Grubb and Tanner, 1976). Sixteen dicotyledonous and one coniferous tree species have been recorded by Grubb and Tanner from this type of forest. Of these, six are "core species" which occur in other forest types in the Blue Mountains, Port Royal Mountains and John Crow Mountains. The core species are Alchornea latifolia, Clethra occidentalis, Clusia havetioides, Cyrilla racemiflora, Ilex macfadyenii and Podocarpus urbanii. The remaining ten tree species are also found on Mull Ridges as well as on Wet Slopes. These species are: Chaetocarpus globosus, Ilex obcordata, Lyonia jamaicensis, L. octandra, Mecranium purpurascens, Persea alpigena, Schefflera sciadophyllum, Vaccinium meridionale, Myrica cerifera, Myrsine coriacea and Rhamnus sphaerospermus. In addition the study sites contained Dendropanax pendulus, Calyptranthes rigida, Eugenia virgultosa and Hedyosmum arborescens. These tree species were found in Mull Ridge Forests by Grubb

and Tanner. The tall, woody Mull Ridge herbs Psychotria corymbosa and Wallenia subverticillata were also present in the study sites. The shrub layer is poorly developed, containing only two species, Blakea trinervia and Miconia rigida, both in the Melastomataceae. The "herb layer" in this forest type is dominated by tree seedlings, Elaphoglossum latifolium and Peperomia c.f. clusifolia. In addition several primarily epiphytic species such as Columnnea hirsuta (Gesneriaceae) and several orchids are common on the forest floor. Vascular epiphytes are common in this area. Bromeliads, particularly Tillandsia complanata, Vriesia sintenisii, V. incurva and to a lesser extent Guzmania fawcettii are the most prominent. Several species of orchids are also common in the Mor Ridge Forest (Grubb and Tanner, 1976). There are also large numbers of nonvascular plants present. There are several mosses including Sphagnum and large numbers of lichens, the most common being in the genus Usnea.

The three sites, identified as Site 1, Site 2 and Site 3, were used for portions of the research. Sites 2 and 3 were only used for collecting data for the population censuses. Site 1 was used for population census as well as for the transplant and colonization experiments. Site 1, which measures 80 m X 5 m is located on a narrow, somewhat exposed and windy ridge

on the north side of the hiking trail from St. Helen's Gap to Morce's Gap. The site is approximately two miles east of St. Helen's Gap. Site 1 is frequently covered by mist throughout the day. Site 2 is located at Morce's Gap. The forest is sheltered and there is very little wind and almost no mist. The site measures 15 m X 25 m. Site 3 (10 m X 25 m) is located on the east side of Bellevue Peak, approximately 250 m west of Morce's Gap (figure 1). Site 3 is partially sheltered and partially exposed. Like Site 1 there is frequent mist cover in parts of the site throughout the day.

## POPULATION CENSUS

### INTRODUCTION

Schimper (1903) noted that epiphytes on trees in virgin forests were not the same at the base of the trees as on the topmost branches. They exhibited well marked differentiations in habitat. This partitioning of space on host trees by epiphytes has also been observed by other investigators (Moreau and Moreau 1943, Pittendrigh 1948, Richards 1952, Holtum 1960, Morris 1970). I performed a detailed population census to determine the spatial distribution of my three bromeliad taxa.

### MATERIALS AND METHODS

Ten 5 m X 5 m contiguous plots were laid out in each of three sites. All trees with diameters at breast height (DBH) greater than 0.2 m were numbered, identified and had their DBH measured. Each tree was given a plot number and a tree number. The numbers were painted on the bark using Berger Everglow exterior house paint. The DBH was measured at 1.3 m on the uphill side of the tree. A band was painted around the circumference of each tree at the DBH line. The height above ground was determined for each individual bromeliad plant using a Leitz SK digital reading telescoping measuring pole graduated in feet, tenths,

and hundredths. The height of plants which grew below the first graduation on the measuring pole was determined using a ruler graduated in the same way as the measuring pole. The species identity was recorded for each individual.

Each bromeliad was classified into one of five size categories. These classes were: tiny seedling (longest leaf < 5% of the maximum adult leaf length for the species in question), small seedling (longest leaf = 5-24% of the species maximum), seedling (longest leaf = 25-49% of the species maximum), small adult (longest leaf = 50-74% of the species maximum), and adult (longest leaf = 75-100% of the species maximum). Clumps of Vriesia incurva (the only one of the three species which reproduces vegetatively) were scored as one individual (as in Sugden and Robins 1979).

The census of the bromeliads would have been more accurate if the trees had been felled but this was undesirable from a conservation point of view. All observations were made with the unaided eye.

All the data were analyzed using SAS (Statistical Analysis System) on the CUNY mainframe computers and with programs written in Basic and implemented on Apple II series computers. The programs were adapted from Sokal and Rohlf (1981).

## RESULTS

### Support Trees

In Site 1, I found 275 individual support trees belonging to 18 species representing 14 families (table 1). The most common trees were Clusia havetioides (N=40; 14.55%), Lyonia octandra (N=37; 13.5%) and Cyrilla racemiflora (N=29; 10.55%). Ten families were represented by a single species each while four families, Ericaceae, Aquifoliaceae, Myrtaceae and Euphorbiaceae, were represented by two species each. Twenty (7.3%) of the trees in the site were dead.

Site 2 had 16 species of support trees representing 13 families and 167 individuals (table 2). The most common trees were again Clusia havetioides (N=28; 16.8%) and Cyrilla racemiflora (N=26; 15.6%). Ten families were represented by one species each and three families, Ericaceae, Aquifoliaceae, and Euphorbiaceae, were represented by two species each. Only four (2.4%) of the trees in this site were dead.

Site 3 had 14 species of support trees representing 11 families and 206 individuals (table 3). The three most common trees were Lyonia octandra (N=41; 19.9%), Cyrilla racemiflora (N=27; 13.1%) and Clusia havetioides (N=24; 11.7%). Eight families were represented by one species each while three families had two species each.

The three study sites, with a combined area of 750 m<sup>2</sup>, supported 648 trees representing 15 families and 22 species (table 4). None of the sites contained all 15 families. The family Chloranthaceae was represented by one individual in Site 2 only. Site 2 was also lacking in Myrsinaceae and Rubiaceae. Myrsinaceae was represented by one species, Wallenia subverticillata, all nine individual of which were found in Site 1. Site 3 was lacking in four families, Myrtaceae, Myrsinaceae, Araliaceae and Chloranthaceae. The 10 most abundant tree species, Lyonia octandra, Clusia havetioides, Cyrilla racemiflora, Clethra occidentalis, Vaccinium meridionale, Chaetocarpus globus, Ilex macfadyenii, Alchornea latifolia, Ilex obcordata and Podocarpus urbanii, were found in all three sites.

The most common family was the Ericaceae with two species Lyonia octandra (N=106, 16.4%) and Vaccinium meridionale (N=39; 6.0%). Lyonia octandra was the most abundant tree species overall. The family Melastomataceae was represented by three species, Blakea trinervia (N=15; 2.3%) Mecranium purpurascens (N=10;1.5%) and Miconia rigida (N=2; 0.3%). The most abundant species in each site were the same: Lyonia octandra, Clusia havetioides and Cyrilla racemiflora.

Bromeliad Frequency on Support Trees.

Site 1 contained 2872 bromeliads supported by 255 living trees (in 18 species), 20 dead trees and the forest floor. There were 9.7 bromeliads per tree. Clusia havetioides supported 620 (21.6%) bromeliads, Cyrilla racemiflora supported 464 (16.2%) and Lyonia octandra supported 422 (14.7%). Dead trees supported 115 (4.0%) bromeliad plants and the forest floor 193 (6.7%). None of the remaining supports had more than 10% of the bromeliads (table 5).

Site 2 contained 2012 bromeliads supported by 163 living trees (in 16 species), 19 dead trees and the forest floor. There were 11.5 bromeliads per tree. Lyonia octandra supported 535 (26.5%) bromeliads, while Cyrilla racemiflora supported 418 (20.8%) and Clusia havetioides 227 (11.3%). There were 19 (1.0%) bromeliads found on dead trees and 136 (6.8%) observed on the forest floor. As in Site 1 no individual of the remaining trees supported more than 7% of the bromeliads (table 6).

Site 3 contained 2570 bromeliads supported by 190 living trees, 16 dead trees and the forest floor. Six hundred and fifty four (654) (25.5%) bromeliads were observed on Lyonia octandra, while Cyrilla racemiflora supported 485 (18.9%) and Clusia havetioides 353 (13.7%). Ninety six (96) (3.7%) bromeliads were

observed on dead trees and 58 (2.3%) were found on the forest floor (table 7).

The entire study area supported 7454 bromeliads. Of these 1611 (21.6%) were found on Lyonia octandra, 1367 (18.3) were found on Cyrilla racemiflora and 1200 (16.1%) were observed on Clusia havetioides. Three hundred and eighty seven (387) (5.2%) bromeliads were observed growing on the forest floor and 232 (3.1%) were found on dead trees. Of the bromeliads growing on the forest floor, 342 were Vriesia sintenisii, 28 were Tillandsia complanata and 17 were V. incurva.

The three most common tree species Lyonia octandra, Clusia havetioides and Cyrilla racemiflora supported the bulk of the bromeliads. In Site 1, 1506 (52.4%) bromeliads were supported by these three species combined. In Site 2 it was 1180 (58.7%) and in Site 3, 1492 (58.1%). Overall, 4178 (56.1%) bromeliads were found on the three most common support trees (table 8).

#### Bromeliad Frequency By Size Class

Site 1 had a total of 1150 individuals of Tillandsia complanata. This comprised 40.0% of the bromeliads in the site. Of the 1150 individuals, 94 were adults, 44 were small adults, 248 were seedlings, 292 were small seedlings and 472 were tiny seedlings. Vriesia incurva had 601 individuals comprising 20.9% of

the bromeliads. There were 99 adults, 31 small adults, 165 seedlings, 187 small seedlings and 119 tiny seedlings. The total number of V. sintenisii in Site 1 was 1121. Of these 296 were adults, 51 were small adults 185 were seedlings, 233 were small seedlings and 356 were tiny seedlings (table 9). The total number of bromeliads in the site was 2872.

Table 10 is the frequency distribution of bromeliad species by size class in Site 2. The total number of bromeliads was 2011. Of these 447 were Tillandsia complanata (38 adults, 9 small adults, 48 seedlings, 76 small seedlings and 276 tiny seedlings). There were 84 individuals of Vriesia incurva (28 adults, 4 small adults, 170 seedlings, 19 small seedlings, and 16 tiny seedlings). Vriesia sintenisii had 1480 individuals in Site 2. There were 339 adults, 85 small adults, 119 seedlings, 323 small seedlings and 614 tiny seedlings.

The frequency distribution of bromeliad species by size class, for Site 3 is shown in table 11. There were 2570 bromeliads, 283 Tillandsia complanata (8 adults, 4 small adults, 9 seedlings 34 small seedlings and 228 tiny seedlings), 84 Vriesia incurva (8 adults, 2 small adults, 16 seedlings, 35 small seedlings and 23 tiny seedlings) and 2203 V. sintenisii (260 adults, 49

small adults, 135 seedlings, 308 small seedlings and 1451 tiny seedlings.

Overall, 7453 bromeliads were observed (table 12). These were 1170 adults, 279 small adults, 942 seedlings, 1507 small seedlings and 3555 tiny seedlings.

The frequency table of bromeliad species by site is shown in (table 13).

Tables 14 - 17 show the frequency table for plot by species for each site as well as the data for all sites combined.

#### Height Distribution

The mean height above ground of Tillandsia complanata was 1.6 m (N = 1860, SD = 1.0). Vriesia incurva had a mean height above ground of 2.67 m (N = 769, SD = 1.6), while V. sintenisii had a mean height above ground of 1.8 m (N = 4804, SD = 1.3) (table 18, figure 2). Single ANOVA shows that the means for bromeliad height among species and study sites are significantly different (table 18).

In each of the three sites there are statistically significant differences ( $p < .001$ ) among the mean heights above ground for all the species. Single ANOVA shows statistically significant differences in mean height for almost all comparisons. There were highly significant differences in the heights of Vriesia

incurva X V. sintenisii and V. incurva X Tillandsia complanata for all sites and overall. For the comparison of the mean heights of Tillandsia complanata X Vriesia sintenisii, there was no significant differences in mean height for Site 1. In Sites 2 and 3 and for the overall data for these two species there were statistically significant differences in mean height ( $p < .01$ ,  $< .05$  and  $< .001$ , respectively).

Tables 19 - 21 show the statistics for the height of the three bromeliad species by size class. For both Tillandsia complanata and Vriesia incurva the height above ground increased with plant size (tables 22, 23). For Vriesia sintenisii there was no general trend toward increase in height above ground with increasing plant size (table 22). The continuum from lowest to highest occurring was adult - small seedling - tiny seedling - small adult - seedling.

The data for the combined sites show that height is positively correlated with size class for Tillandsia complanata and Vriesia incurva (table 22). The Spearman correlation coefficients ( $r$ ) are so low (0.37, 0.02) however, that there is probably no biological significance. For Vriesia sintenisii there is no correlation between height and size class (table 22). For individual sites there was positive correlation between height and size class for all species except

for Vriesia sintenisii in Site 1. In this site (Site 1) there was no positive correlation between height above ground and size class (table 23). The correlation coefficients (r) for T. complanata and V. incurva in Site 2 (0.45, 0.68) and V. incurva in Site 3 (0.61) are large enough to indicate that height above ground has a meaningful positive influence on size of epiphyte. Figures 3 - 14 show the frequency distribution for height for all three species.

#### Support Tree Preferences

Table 24 shows the plot analysis of bromeliad species on support trees. An R x C G-test for independence showed that the frequency of bromeliads was dependent on the frequency of the tree species, therefore the mean number of each bromeliad species per tree was used instead of the total number per tree.

Two-way ANOVA (table 24) shows that there are no significant differences between the mean number of epiphytes found on each support taxon, while there are highly significant differences in the average density of bromeliads on support taxa. Table 25 shows support tree preferences for the three bromeliad species. While there is some overlap of bromeliads on support trees, the epiphytes do have different preferred support species.

The preferred support of Tillandsia complanata is Clusia havetioides. Clusia havetioides, with 92 individuals was the second most common support species (table 4).

Vriesia incurva preferred Cyrilla racemiflora, but was also found nearly as often on Chaetocarpus globosus and Clusia havetioides (tables 24, 25). The mean number of V. incurva per tree was small but this is not unexpected since there were relatively few individuals of this species in the study area. Cyrilla and Clusia are fairly common trees but Chaetocarpus is not. There were only 34 (5.3%) individuals in the entire study area.

The preferred support trees of Vriesia sintenisii are Chaetocarpus globosus and Cyrilla racemiflora (tables 24, 25) There was a mean of 11.1 V. sintenisii per Chaetocarpus tree. The mean for Cyrilla was 11.2. The fairly uncommon Chaetocarpus is well colonized by V. sintenisii whenever it is present. The mean number of epiphytes per Chaetocarpus and Cyrilla were 5.0 and 5.5 respectively, while the mean number of V. sintenisii on those trees was 11.2 (table 24).

#### DISCUSSION

In the montane rain forests of the Blue mountains there are two floristic groups for the dicotyledonous

species of trees. There are the core species which are found in a variety of forest types, and there are those trees confined to specific forest types (Grubb and Tanner, 1976). No trees were found by Grubb and Tanner to be exclusive to Mor Ridge forests.

The core species were Alchornea latifolia, Clethra occidentalis, Clusia havetioides, Cyrilla racemiflora, Ilex macfadyenii and Podocarpus urbanii. These six species were among the 10 most common in the study area. Clusia havetioides (N = 920) was in fact the second most common support species, Cyrilla racemiflora (N = 82) the third most common and Clethra occidentalis (N = 42) the fourth next common.

The typical Mor Ridge species (which are also common in Mull Ridge and Wet Slope forests) were Chaetocarpus globosus, Ilex obcordata, Lyonia octandra, Mecranium purpurascens, Persea alpigena, Schefflera sciadophyllum and Vaccinium meridionale. One member of this group, Lyonia octandra (N = 106) was the most common species observed. In my study area I found six species not found by Grubb and Tanner in the Mor Ridge forests. These were Calyptranthes rigida, Dendropanax pendulus, Eugenia virgultosa, Hedyosmum arborescens (Mull Ridge and Wet Slope species), and the shrubs Psychotria corymbosa and Wallenia subverticillata.

In all three sites, Lyonia octandra, Cyrilla racemiflora and Clusia havetioides supported more than 50% of bromeliads studied.

These three species accounted for 43% of the trees in my study area. These species along with Clethra occidentalis and Vaccinium meridionale are the largest and presumably the oldest in the area studied. Their larger surface areas, contributed to by their size and abundance, would provide more micro sites on which bromeliad seeds could land and germinate. Since these trees are presumably also the oldest in the study area they would have been "presenting" sites for colonization by bromeliads over a long period. It is logical to assume that a larger number of seeds would come in contact with the surfaces of these trees over time than would be expected for smaller younger, trees. The larger the number which landed on the tree trunks the more germinations and establishments one could expect. Of the bromeliads observed, there were more individuals of Vriesia sintenisii than the other two species combined. There were 4804 individuals of V. sintenisii. This was 64.4% of the bromeliads studied. Tillandsia complanata (N = 1880) comprised 25.2% and Vriesia incurva (N = 769) contributed 10.3% (table 13).

Throughout the study area, more plants of Vriesia sintenisii were observed flowering than were members of

the other two species. In fact, V. incurva was never observed flowering. In ten years of study and observation, Tanner, (personal communication) has never seen this species flowering. This species does reproduce sexually as the dead remains of inflorescences have been observed attached to the largest plants in clumps. Tillandsia complanata plants were observed flowering. This species produced several flower spikes per plant while Vriesia sintenisii produced only one. Tillandsia complanata however, made fewer and smaller fruits per plant than did V. sintenisii. The seeds of the two species are indistinguishable so one can therefore assume that V. sintenisii fruits produce more seeds than those of T. complanata. The larger number of V. sintenisii plants observed may be due to the greater fecundity of this species.

Only Vriesia incurva reproduces asexually. It sometimes formed large clumps (genets) with over seventeen individuals (ramets). In many cases the largest individual in these clump would have dead spikes still attached. Of the 7454 bromeliads studied, only 769 (10.3%) were V. incurva. As was mentioned this species flowers infrequently.

From studies done on well established herbaceous vegetation in the temperate zone, it has been shown that there is relatively infrequent recruitment among

species which are capable of vegetative reproduction (Harberd, 1961; Putwain et al., 1968; Tamm, 1972; Thomas and Dale, 1975). Vriesia incurva may fit this pattern.

Because mean height differs among the three species it can be assumed that they have partitioned the space in their environment. All three species occur on boles as well as in crowns. In addition Vriesia sintenisii grows vigorously on the forest floor. The other two species (V. incurva and Tillandsia complanata) are only occasionally found growing on the forest floor. Although a large number of Vriesia sintenisii grow on or close to the ground this species did not have the smallest value for mean height above ground (table 18, figures 4, 7, 10, 13). Small seedlings and tiny seedlings of Vriesia sintenisii have greater mean heights than do the small adult and seedlings of the same species (table 21). These heights are not, however, abnormal since the mean height for the total V. sintenisii population is 1.82 m (table 18).

Tillandsia complanata has a smaller mean height above ground than does V. sintenisii and many individuals can be found growing (on the boles of trees) close to the ground (figures 2, 5, 8, 11). The distributions of T. complanata and V. sintenisii

(figures 11, 13) show the bulk of these bromeliads occurring at lower altitudes.

Vriesia incurva occurs across the widest range of heights (figures 6, 9, 12) and has the highest mean height above ground. V. incurva grows in the most exposed areas. This species has some morphological features for its hotter, dryer habitat. The leaves are narrower and more tapered than those of the other two species, and have full trichome cover on their surface. Leaves like those of V. incurva are expected to be better convective coolers (Vogel 1970) than those of the other two species.

Individuals of V. sintenisii, increase their heights as they grow older by producing a stem held tightly to the substrate by numerous roots. The stem grows continually from the apical meristem and dies below the rosette of leaves. I have observed old stems with lengths greater than 0.5 m.

The three bromeliad species have preferred support trees. There is some preference overlap with all three sharing a liking for Clusia havetioides and Cyrilla racemiflora while the two species of Vriesia have Cyrilla and Chaetocarpus globosus in common.

## LEAF DEMOGRAPHY AND PHENOLOGY

### INTRODUCTION

Demographic studies were done on the leaves of the three species of bromeliad. From these studies estimates of the length of life of the leaves of each species were derived. Flowering phenology data were collected for Tillandsia complanata and Vriesia sintenisii. These data were few as only a small number of individuals flowered during the study.

### MATERIALS AND METHODS

One hundred randomly chosen individuals of Vriesia sintenisii, 98 randomly chosen individuals of Tillandsia complanata and 46 randomly chosen individuals of V. incurva were measured in detail. For each species, five trees in each plot were randomly selected (by a random number generator in Applesoft BASIC) by tree number. Two bromeliads were selected on each of these 50 trees by a series of three computer generated, random coordinates of height above ground (0-2 m, the practical limit at which accurate observations can be made), radial distance from a vertical axis passing through the center of the trunk at the DBH line (0-1 m, the approximate maximum radius of the accessible portion of the crown in any of the trees in the site), and a compass direction (0-360°

from north). The bromeliad nearest each of the randomly determined coordinates was marked and observed for 12 months. Plants of Tillandsia complanata were given a number from 1 - 100. Plants of Vriesia sintenisii were numbered 101 - 200 and plants of V. incurva were numbered 201 - 300.

Individual leaves of each plant were numbered consecutively as they emerged. The leaves were numbered with a Pentel Pen bullet point marker. The length of each leaf was measured once per month. A modified Stanley 6 mm steel tape was inserted between the overlapping leaf axils on the adaxial side of each leaf. The standing crop of leaves on each plant was recorded each month. A small spot of yellow paint was put on each leaf of each plant at the start of the study. At the time of measuring each month, each plant was checked for newly senesced leaves which would be marked with yellow paint. The number of dead leaves was recorded and then the paint was removed from these leaves to prevent their being counted again the next month. The total number of dead leaves was subtracted from the previous month's standing crop and to the resulting number was added the total number of newly emerged leaves giving the new standing crop of leaves. A leaf was scored as dead when no trace of green remained. The leaves of tiny seedlings were measured with a specially made ruler.

The mean leaf life was calculated by the equation, mean leaf life = mean standing crop of leaves / mean rate of leaf production (Tanner, 1983). The leaves were measured each month with the exception of December, over the one year period from June 14, 1984 to May 20, 1985.

No data were collected for the small adults of Vriesia incurva because no small adults of this species fell within the random co-ordinates.

Pollination bags were placed over 5 newly emerged inflorescences of Tillandsia complanata, and over 10 new inflorescences of Vriesia sintenisii in order to determine if these species were self compatible.

During the study, 36 plants of T. complanata, 24 plants of V. sintenisii and 4 plants of V. incurva died.

## RESULTS

### Leaf Production

The range of standing crop of living leaves for Tillandsia complanata was from 38 for adults to 13 for small seedlings. Interestingly the tiny seedlings of this species had a larger standing crop of leaves than did the older, small seedlings (table 26).

Vriesia incurva had standing crops ranging from 39 (adult) to 19 (tiny seedlings), and in V. sintenisii there were 35 for adults and 11 for small seedlings.

Like T. complanata, the tiny seedlings of V. sintenisii were often observed to have larger numbers of leaves than did older juvenile plants (table 26).

Tillandsia complanata adults produced a mean number of 16 leaves per year. Small adults produced 10, seedlings 9, small seedlings 7 and tiny seedlings 6. Vriesia incurva produced a mean of 9 leaves per adult per year. Seedlings and small seedlings produced 7 and tiny seedlings produced a mean of 6 leaves per year. V. sintenisii produced more leaves per year than did the other two species. The mean numbers of leaves produced by this species per year were 23 for adults, 21 for small adults, 15 for seedlings, 10 for small seedlings and 8 for tiny seedlings (table 26).

#### Leaf Life

Vriesia incurva leaves had a mean leaf life of 1274 days. The leaves of Tillandsia complanata had a mean life of 724 days, and those of V. sintenisii, 450 days (table 27). In V. incurva the leaves of the adults lived longest, and those of the seedlings had the shortest life. In both T. complanata and V. sintenisii, however, the tiny seedlings had the longest mean leaf life (table 27).

The shortest lived leaves of V. incurva (tiny seedlings, 1086 days) lived 1.5 times as long as those of T. complanata and 2.4 times longer than than those

of V. sintenisii. In general leaves of V. incurva live 1.8 times as long as those of T. complanata and 2.8 times as long as those of V. sintenisii.

#### Growth Rates

The relative growth was computed for each species by regressing the relative summed leaf lengths against time. The slopes of the resulting lines were tested for heterogeneity (Sokal and Rohlf 1981, Box 14.8). Table 28 and figures 16-32 gives the results. There were no significant differences in slope for the entire populations of each species, adults, small adults, seedlings, small seedlings or tiny seedlings (table 28, figures 21, 32).

#### Flowering

None of the three species flowered abundantly during the study. In Site 1, 20 (21.2%) of the adult Tillandsia complanata flowered while 49 (16.6%) of the Vriesia sintenisii were observed flowering. V. incurva was never observed flowering. Tillandsia complanata displayed inflorescences from August to January. The flowers opened (1 - 2 at a time per inflorescence) from November to January. By June there were mature fruits on all spikes. The flowers of T. complanata, which are red, were visited by hummingbirds. It is not known if this species is self compatible since all

inflorescences which were covered with pollination bags died. Individual plants produced 2 - 5 inflorescences per year. Inflorescences were only produced in the axils of leaves of the second oldest living gyre of leaves.

There were 49 (4.4% of adults) Vriesia sintenisii flowering in Site 1. The single inflorescence per plant develops from the apical meristem. This species starts flowering in late October or early November. By February all the flowers have opened, and fruit development starts. The fruits are very well developed by June and the seeds are dispersed in October.

The flowers of Vriesia sintenisii are inconspicuous and greenish white, and they open singly. The flowers last only one day. On the day after first opening the interior of the flower becomes discolored and the flower starts to wilt. The only visitors I observed to the flowers were hummingbirds. I found that V. sintenisii is self-compatible. Ten inflorescences were covered with pollination bags, and all produced mature fruits. Unbagged flower spikes did not fare as well as bagged ones. There was heavy predation on the flower buds and as a result, those inflorescences produced few to no fruits.

Individuals of Vriesia sintenisii do not die after flowering. A lateral bud becomes the new apical meristem. The new growth from this meristem, which is

located in the axil of a leaf in the penultimate gyre, does not become visible until approximately four months after the flower bud was first observable. Between this time and the emergence of the new adult growth, no new leaves are produced.

## DISCUSSION

Tillandsia complanata, Vriesia incurva and V. sintenisii showed no seasonality or periodicity of leaf production. It is interesting that they do not seem to be responding to wet or dry seasons as do other plant species in the same forest area. Tanner (1983) studied leaf production in the tree fern, Cyathea, in the Blue Mountains of Jamaica, within several hundred meters of my field site. He found that leaf production increased in Cyathea pubescens following periods of increased rainfall.

The three species of bromeliads studied are all water impounding, tank species. It is not surprising that they do not change their rates of leaf production with increasing or decreasing rainfall. By impounding water they become fairly independent of the frequency of rain.

It is not surprising that tiny seedlings of Tillandsia complanata and Vriesia sintenisii have larger standing crops of leaves than do the older small seedlings since some seedlings of tank forming tillandsioides produce large numbers of juvenile leaves (Adams and Martin, 1986). The tiny seedlings of these two tank forming species are atmospheric (no water impounding rosette). They have the dense cover of trichomes characteristic of atmospherics.

Adams and Martin (1986) in their study on Tillandsia deppeana found that some of the atmospheric seedlings of this tank species had over 70 juvenile leaves. Mez (1904) noted the presence of heterophylly (of juvenile versus adult) in Tillandsia heterophylla. Lieske (1914) observed that tank forming species of Tillandsia, Vriesia and Guzmania had atmospheric juveniles.

## TRANSPLANT EXPERIMENT

### INTRODUCTION

Vriesia sintenisii grows on the forest floor as well as on trunks and branches. Tillandsia complanata and V. incurva, are only rarely found growing on the forest floor and those that are, seem to have been dislodged from support trees. It is not known if the latter two species could survive indefinitely on the forest floor. The transplant experiment was set up to address this questions.

### MATERIALS AND METHODS

One 2 m X 5 m plot was cleared of all vegetation. Five (5) individuals from each size class for each of the three species were planted in the cleared area. All plants were numbered. The lives of individual leaves, mean leaf life and standing leaf crops were determined by the procedures described above in the section on Leaf Demography and Phenology. The leaves were measured over from August 18, 1984 to May 26, 1985.

### RESULTS

#### Leaf production

The mean standing crop of living leaves and mean number of leaves produced per year for the transplanted

bromeliads was very similar to those for nontransplanted individuals. Indeed, for Tillandsia complanata some numbers were identical (table 29).

All aspects of leaf production (the general differences between species as well as lack of periodicity) reported above in the section on Leaf Demography and Phenology are the same for the transplanted bromeliads.

#### Leaf life

As with their nontransplanted counterparts, the transplanted Vriesia incurva had a longer mean life than Tillandsia complanata and Vriesia sintenisii. T. complanata transplants also had longer lived leaves than V. sintenisii.

The mean length of life for all three species was, however, lower than that for nontransplanted individuals. The length of life of leaves of V. incurva was the most depressed of the three (table 30).

#### Growth Rates

Relative growth rates were computed as in Leaf Demography and Phenology above. There were no significant differences in slope for all comparisons (table 31, figures 33-50). The null hypothesis (the slopes are the same) was therefore accepted.

Table 32 gives the results for all comparisons between transplanted and nontransplanted individuals. There were significant differences between all comparisons. In addition, the slopes for transplanted individuals were larger than those for nontransplanted ones in every case.

#### DISCUSSION

The lack of differences in leaf production between transplanted and nontransplanted individuals may be the result of all the new leaves having been initiated before transplantation. This lack of difference may also be because leaf production is not inhibited by transplantation to the forest floor. The relative growth rates of transplanted individuals do not differ from each other in pairwise comparisons as was true for the nontransplanted individuals. Growth rates for all transplanted individuals was greater than those for their nontransplanted counterparts as evidenced by larger values for slope (table 32). This indicates that transplanted individuals are growing faster on the ground than plants growing epiphytically. This could have resulted from the fact that the forest floor plot was sunny and the plants could have increased their photosynthetic output.

It is interesting to consider why Vriesia incurva and Tillandsia complanata do not occur naturally on the

forest floor. Since even the tiniest seedlings of both do well when planted on the forest floor, the problem may lie at the seed stage of the life cycle. There may be no "safe sites" (sensu Harper 1977). The pH of the forest floor is between 2.8 and 3.5 (Tanner, 1977b). The lowest bark pH I recorded was 3.7 for Alchornea latifolia. Only 5.1% (N = 380) of the total number of bromeliads was observed on A. latifolia (table 8). I speculate that the very low pH of the forest floor may inhibit the germination of the seeds of Tillandsia complanata and Vriesia incurva.

My data indicate that predation may also reduce the rate of seedling establishment. The leaves of the smaller T. complanata transplanted to the forest floor were constantly eaten. Twenty five percent of the tiny seedlings and over 50% of the small seedlings were consumed. Tiny seedlings of Vriesia incurva did well on the forest floor for more than a year but after a prolonged dry period many of them died. Dessication may be another barrier to establishment of T. complanata and V. incurva on the forest floor.

## COLONIZATION EXPERIMENTS

### INTRODUCTION

Cook (1979) has stated that "ecologists wishing to explain the correlation between habitat and abundance and distribution of species have stressed the crucial role of seed and seedling environment in determining the subsequent dynamics of adult populations." This aspect of population biology has also been stressed by others (Sager and Harper 1961, Harper and White 1974). Harper (1977) gave several examples which show that species distributions are contingent on events in the seedling stage.

In order to evaluate the effect of events at the seedling stage on the ultimate distribution of the three species of bromeliads, I performed colonization experiments.

### MATERIALS AND METHODS

One 10 m X 5 m plot was established in Site 1. All trees with trunks greater than 2 cm DBH were marked and identified. One half of the 46 trees in the plot were randomly selected for complete epiphyte removal (vascular as well as nonvascular epiphytes). The remaining trees had only the vascular epiphytes removed. All bromeliads were removed from all the trees in this plot thus preventing seeds from being

shed directly downward. The trees destined for total epiphyte removal were thoroughly cleaned of bryophytes and lichens up to a height of 2 m. Many of the trees in this type of forest were too small to climb or to support a ladder, and therefore accurate observations could not be made at heights greater than 2 m. The bark was cleaned of lichens by scrubbing with a brush. The reason for not removing some nonvascular epiphytes is that the mats formed by mosses and other nonvascular plants may be a favourable growing site for bromeliad seedlings.

An artificial tree was erected in the plot. The tree was constructed using branches from outside the site. It was 2 m tall and had one vertical and one horizontal branch as well as two branches attached at an angle of 45 degrees. Initially all trees in the plot were carefully observed once per month. The height above ground was noted for any seeds found on the bark. The states of the seeds were recorded once per month initially and then once every other month. If the seeds germinated, the seedlings were numbered. A numbered stick pin was placed in the bark near the seedling.

In addition four 1 m X 1 m plots were cleared on the forest floor and colonization of these sites was observed. One 10 m X 5 m control plot for the colonization was set up in the site. The trees were

not stripped or disturbed in any way. A control plot was also set up for the forest floor colonization. Seeds scored as dead when they were no longer brown and plump, but instead were flat and gray.

#### RESULTS

In the colonization plot, 117 seeds became attached to the trees. Of these 51 (43.59%) germinated and 15 (12.82%) died. Of the germinants, 2 (3.9%) died within 2 months of germination. Most of the seeds (53.9%) and germinants (58.8%) were found on trees which had only the vascular epiphytes removed. Likewise, all of the germinants which died and 93.3% of the seeds which died were found on the trees which had only the vascular epiphytes removed (table 33).

In the control plot 89 seeds and 57 germinants were observed. Eleven (12.4%) of the seeds germinated, and 31 (34.8%) died. Of the seeds which germinated none died. Of the germinants 14 (24.6%) died (table 34). No seeds were found on the artificial tree. No seeds germinated in the plots cleared on the forest floor.

## DISCUSSION

In the colonization plot all the germinants belonged to the same species, Vriesia sintenisii. Some of the ungerminated seeds may have been from Tillandsia complanata. None of the seeds came from V. incurva. Over 769 individuals of this species were observed and no flower spikes were seen.

All the germinants in the control plot were also Vriesia sintenisii. It is very difficult to distinguish between the seeds of V. sintenisii and Tillandsia complanata, so the species to which the seeds belong could only be identified upon germination.

One reason for the lack of colonization in the experimental plot may have been a lack of seeds. Another reason may have been a lack of "safe sites." Harper (1977) describes a "safe site" as a set of conditions which provide all the necessary stimuli for germination and establishment of the seed. Some of these conditions could be the microtopography of the substrate, sufficient water and oxygen and absence of predators or competitors. "A population of a particular species may be absent from an area either

because it offers no safe sites even though seed is abundantly, or because seed is absent although safe sites are abundant" (Harper 1977).

## BARK STUDIES

### INTRODUCTION

The properties of bark (relief, porosity and chemical composition) affect epiphytes (Johansson, 1974). The texture (roughness) of bark varies with the age of trees. Bark relief may be important in the colonization of new sites by bromeliads as deep fissures may provide suitable microclimates for germination of seeds. Additionally, fissures may prevent the removal of seeds by stem flow. Johansson (1974) observed that older trees with rougher bark supported more epiphytes.

The porosity of the bark affects its water holding capacity. Voth (1939) observed that the absorptive capacity of bark varied from tree to tree depending on age and species. The water content of bark depends also on rainfall and the amount of evaporation. The water content of bark is further affected by the fact that water does not flow evenly over the bark but is channeled through "rain tracts" or drainage channels (Richards, 1964; Yarranton, 1967).

When investigating bark pH and its possible influence on past colonization or establishment of seedlings, it must be kept in mind that the pH of a specific piece of bark might have changed drastically since seedlings were established. For slow growing

species like bromeliads, this consideration is even more important.

The pH of bark is quite variable even on individual trees, decreasing from the base of the tree to the top (Johansson, 1974). The pH of bark can be affected by exudates. The acidity of bark may influence seed germination or affect the growth of established plants (Pessin, 1925). Acidity can also affect nitrification since this process is pH dependent (Barkman, 1958).

#### MATERIALS AND METHODS

##### Bark Texture and Capillarity

The quantification of bark texture was made by displacement of water in a small steel box with one open side clamped to the side of the trees. The rougher the bark, the greater the volume of water displaced from the box. The displaced volume was then used as a "roughness number" by which the textures of the barks of the several support species were compared.

The steel box was oblong (19 mm X 19 mm X 76 mm) and, including its drain and fill tubes, had a volume of 22.1 ml. The edges of its open side were filed to a knife edge which cut into the bark to form a water tight seal when the clamp was tightened. The clamp

consisted of a chain which wrapped around the tree and hooked onto a block of steel through which was threaded a rod which would be turned to press the box onto the side of the tree. The box was fitted with a port at each end, one for filling and one for draining the chamber. The interior of the box was coated with a thin film of paraffin to render it hydrophobic and ensure that it would drain completely.

Measurements of bark texture were made on representative areas where the trunk was straight and locally nearly flat. The drain port was closed with a short rubber tube and a pinch clamp. The position of the pinch clamp was controlled at a standard location on the hose by a plastic ring slipped over the tube proximal to the clamp. The filling port was temporarily fitted with another tube, the free end of which was held in the mouth. As the clamp was tightened and the box pressed against the bark, air was blown into the box through the tube. The clamp was tightened only as far as necessary to eliminate leakage between the edges of the box and the tree bark. Once the box was sealed to the bark, a measured volume of water was poured into the box. The difference between the volume required to fill the box on the tree and the total volume of the box (22.1 ml) was the volume of bark intruded within the box. The water was then drained from the box into a graduated cylinder. The

difference between the volume of water needed to fill the box and the volume which was subsequently drained from it is the volume of water which is held by capillary action on the surface of the bark.

#### Bark pH

Bark from the 10 most common support trees was removed from living examples of these trees. Bark was taken from areas between the ground and 2 m high. The samples were dried in an oven for four days and stored in a moisture free environment until the pH could be measured. Prior to pH measurement, the bark was pulverized and all samples from the same taxon were mixed together. Distilled water ten times the weight of each sample was added. All bark samples weighed 3 gm, therefore 30 ml of water was added to each. The mixtures were left to stand for 24 hrs before pH was measured.

### RESULTS

#### Bark Texture and Capillarity

Water displacement and capillarity are shown on table 35. Clethra occidentalis with a mean water displacement of 4.3 ml had the roughest bark while Vaccinium meridionale with a mean displacement of 1.96 ml was the smoothest (table 36). The bark of Vaccinium meridionale is very flaky but the flakes are large and their individual surfaces are quite smooth.

The bark of Lyonia octandra had the greatest capillarity, 1.28 ml. Clusia havetioides had the lowest, 0.26 ml (table 37). The roughness of Clusia, Cyrilla and Lyonia barks fell halfway between the roughest Clethra occidentalis and the smoothest Vaccinium meridionale.

The bark of Clusia was the only one which felt smooth to the touch. Clusia did not, however, score as the smoothest because the bark is frequently interrupted by protrusions. Some of these protrusions are the beginnings of prop roots.

#### Bark pH

The choosing of bark for pH measurements was subjective. No dead, corky pieces of bark were chosen since they are known to give higher pH values than living bark (Johansson, 1974). Moreover, dead, corky portions of bark tend to be shed, and any bromeliads which might be recruited to these areas would be lost when the bark was shed.

Du Rietz (1945) (after Johansson 1974) distinguished three types of bark based on pH measurements: "rich bark" (pH 5 - 7), "intermediate bark" (pH 4 - 5) and "extremely poor bark" (pH < 4). The range for mean bark pH was 3.7 - 5.1 (table 38). Alchornea latifolia (mean pH of 3.7) had the lowest pH, and Clusia havetioides (mean pH of 5.1) had the

highest. One species, Alchornea latifolia (pH 3.7), had poor bark by the classification of Du Rietz, while eight had intermediate bark and one, Clusia havetioides (pH 5.1) had rich bark.

#### DISCUSSION

Clusia havetioides, the preferred support of Tillandsia complanata had medium textured bark with low capillarity. On the other hand, Clethra occidentalis which is also well liked by T. complanata has the roughest bark in the study area but also low capillarity, while the third most liked tree, Cyrilla racemiflora, has medium textured bark and high capillarity (tables 35, 36, 37). No strong preferences for bark type or capillarity is shown by T. complanata. Clusia havetioides does have the highest pH of all the support trees (table 38) but here once again T. complanata does not show any strong preferences for a particular range of pH values.

Vriesia incurva prefers Cyrilla racemiflora and Chaetocarpus globosus. These two plants have medium textured to smooth bark and fairly high capillarity (tables 36, 37). Clusia havetioides, which is also liked by V. incurva, has medium textured bark and the lowest capillarity of the group. While V. incurva is more successful on species with medium to smooth bark, the capillarity tolerance of this species is quite

wide. The pH tolerance of this bromeliad is also quite wide (table 38).

Vriesia sintenisii plants prefer species with smooth bark (Chaetocarpus, Cyrilla and Lyonia) and higher capillarity (tables 36, 37). The range of pH tolerance for this species is also wide (table 38).P

## STEM FLOW

### INTRODUCTION

Stem flow characteristics of six support trees were investigated. The volume and nutrient content of the stem flow might be important to establishment of seedlings.

### MATERIALS AND METHODS

Stem flow collars similar to those of Likens and Eaton (1970), were installed on trees at a height no greater than 1 m. Water was collected in 5 gallon buckets which were covered by plastic in order to keep out debris. Rainfall was also measured. The volume, pH, and conductivity of the stem flow were derived.

### RESULTS

This experiment was beset with problems partially due to poor design. The stem flow collars were in many cases not wide enough to handle the volume of heavy downpours. Many of the storage buckets overflowed or overturned and therefore the volumes are inaccurate. Small pieces of plant debris, dead insects, insect larvae and worms were washed into the storage buckets. The water was measured once per month and usually contained the rotted remains of the debris. Because of

this, the pH and conductivity measurements are suspect but provide baseline data. The experiment had only been running for three months when vandals stole most of the storage buckets. There is stem flow volume data for only five species for the period March 1985 to June 1985.

Stem flow volume, mean pH and mean conductivity are shown in table 39.

## GENERAL DISCUSSION

Three hypotheses were tested in an effort to identify and characterize the factors affecting the distribution of Tillandsia complanata, Vriesia sintenisii and Vriesia sintenisii.

1. Is distribution controlled by events at the seedling stage?

Data from the population census showed that seedlings (tiny seedlings, small seedlings, seedlings) constituted the largest size class. A large number of plants die before they reach maturity. Seedlings of all three species are found from very close to the ground to the top of the canopy, but the mean height above ground is well defined for each species.

Vriesia incurva with a mean height of 2.7 m attains the greatest vertical height. Vriesia sintenisii (mean height 1.8 m) is the next highest and Tillandsia complanata (mean height 1.6 m) grows closest to the ground. Since the overall populations of each species sort themselves by vertical height it is obvious that most seedlings which occur at heights very different from the mean of its particular species, do not survive to adulthood. Factors such as bark texture or bark chemistry may be the cause of juvenile death. The tiny seedlings of all three species are

atmospheric, having a dense trichome cover and no water impounding leaves. Once the seedling morphology changes to the more adult, water impounding form, they may not then be able to live in microhabitats (eg. hotter) which supported the atmospheric seedlings. The changes from seedling to adult morphology may play a large role in the final distribution of each species. For Vriesia incurva, which has many atmospheric qualities as an adult, the morphological changes may not be as detrimental as for V. sintenisii and Tillandsia complanata. Seedlings of V. incurva which occur in the more moist parts of the habitat may not do as well as those in the more preferred, exposed, drier microsites. Vriesia incurva mainly reproduces by vegetative means, so the distribution of vegetative propagules (suckers) of this species is greatly affected by the distribution of adults.

A small fraction of the population of Vriesia sintenisii grows on the forest floor. The plants are mainly adults or small adults along with the occasional seedling. there were very few small and almost no tiny seedlings (only one was observed). These plants may or may not have been derived from seeds which had landed on the forest floor. Since so few tiny seedlings and no new germinants were observed on the forest floor, very little germination may actually take place there. The plants growing on the ground, may have fallen there

as tiny or small seedlings attached to flakes of bark or small branches. Indeed, many plants were observed to have fallen to the ground in this manner. Many of these plants survived for the duration of the study and were growing quite vigorously at the conclusion of the field work. This may be how the few Tillandsia complanata and Vriesia incurva on the forest floor got there.

From the results of the transplant experiment, it is apparent that all three species can do well initially if planted on the forest floor. Only Vriesia sintenisii is routinely found growing on the ground. The duration of the transplant experiment (approximately two years), was not enough to observe the ultimate response of these species. If Vriesia sintenisii plants do fall to the ground on pieces of bark or small branches, then its distribution on the forest floor is at least partially affected by events at all stages from tiny seedling to adult.

Many individuals of Vriesia sintenisii and Tillandsia complanata were observed to have dispersed most of their seeds very close to the parent plant. In many cases, this was on their own support trees or on nearby ones. Although few seeds seem to be dispersed far from their source, this may still be an excess with respect to available niches.

The results of the colonization experiment indicate that the presence of other vascular epiphytes on a particular substrate may affect the seeds and germinants adversely. Only 12.8% of the seeds which landed on trees which had had vascular epiphytes removed died as compared to 34.9% on undisturbed control trees. For newly germinated seeds only 3.9% of those on experimental trees (vascular epiphytes removed) died as opposed to 24.6% on control trees.

2. Is distribution the result of interspecific competition?

Plants compete for limited resources (Werner, 1979). These resources could be, among other things, pollinators or space. In many cases, the present distribution of co-occurring species may be explained by whether or not they are still competing or have eliminated or reduced competition by partitioning available resources. It must be borne in mind that, "even when resources are mobile or when plants are ubiquitous, competition can still only be inferred from the distributional patterns of species seen in the field" (Werner, 1979).

In my opinion, space is the likely resource for which epiphytic bromeliads may be competing. The three species, Tillandsia complanata, Vriesia incurva and V. sintenisii have partitioned the space in their

environment. Even though the ranges overlap, there are significant differences in mean heights above ground (table 18). The only indication that there might be some amount of interference competition (Werner 1979) is in the results from Site 1. In that site, there is no significant difference in mean height above ground between Tillandsia complanata and Vriesia sintenisii. When all three sites are combined, there are no significant differences in mean height between these two taxa.

Vriesia sintenisii produces a larger inflorescence than does Tillandsia complanata. Vriesia sintenisii also produces more and larger fruits per plant than does T. complanata. If more seeds of V. sintenisii are broadcast into the environment this species might have the edge in seedling recruitment. This may be the strategy of V. sintenisii. It produces more biomass per year than the other two species. Larger investments in vegetative growth could supply more energy for reproduction. This could explain the larger numbers of V. sintenisii I observed in the study area. There were 4804 (64.5% of the bromeliads) individuals of V. sintenisii observed, compared with 1880 (25.2%) T. complanata and 769 (10.3%) V. incurva (table 12).

As was mentioned above, many seeds are shed close to the parent plant. There might be competition for

space among the seeds of the same species instead of between different species.

The only visitors I observed to the flowers of Tillandsia complanata and Vriesia sintenisii were hummingbirds. No detailed observations of the pollination biology of these two species were made but the fact that V. sintenisii is self compatible might indicate that competition for pollinators may not be important.

There were no significant differences in relative growth rates among bromeliads growing epiphytically and among those transplanted to the ground (tables 28, 31). There were differences in absolute growth with Vriesia sintenisii showing the greatest increase in size and V. incurva the smallest (figure 15). The faster growth of V. sintenisii would increase its competitive ability. The lack of significant differences in rates of relative growth between the three species (tables 28, 31), may indicate that these plants are not presently in competition, or else the results may simply indicate that the general climate and environment of the area controls growth rates.

### 3. Is distribution is determined by support trees?

The three bromeliad species have preferred support trees. Their distribution is therefore highly influenced by these trees. For example, one of the

preferred support trees of Vriesia sintenisii is Chaetocarpus globosus. This species represents only 5.3% of the support trees but is preferred over Lyonia octandra (16.4%) and Clusia havetioides (14.2%), the most common trees. The texture, capillarity and pH of bark do not seem to greatly influence support tree preference, with the possible exception of Vriesia sintenisii. This bromeliad prefers trees with smooth bark and higher capillarity.

As was pointed out earlier, the pH, texture and capillarity of bark change over time. These three characteristics which do not seem important to established bromeliads, may have been very important for initial colonization. More detailed studies of support trees are needed in order to more fully explain bromeliad preferences.

TABLE 1. FREQUENCY TABLE OF SUPPORT SPECIES. SITE 1.

SUPPORT SPECIES	FREQUENCY	PERCENT	FAMILY
<u>Clusia havetioides</u>	40	14.55	Clusiaceae
<u>Lyonia octandra</u>	37	13.45	Ericaceae
<u>Cyrilla racemiflora</u>	29	10.55	Cyrillaceae
<u>Ilex macfadyenii</u>	22	8.00	Aquifoliaceae
<u>Clethra occidentalis</u>	20	7.27	Clethraceae
Dead trees	20	7.27	*****
<u>Ilex obcordata</u>	16	5.82	Aquifoliaceae
<u>Podocarpus urbanii</u>	13	4.73	Podocarpaceae
<u>Vaccinium meridionale</u>	12	4.36	Ericaceae
<u>Calyptranthes rigida</u>	11	4.00	Myrtaceae
<u>Mecranium purpurascens</u>	10	3.64	Melastomataceae
<u>Chaetocarpus globosus</u>	9	3.27	Euphorbiaceae
<u>Wallenia subverticillata</u>	9	3.27	Myrsinaceae
<u>Schefflera sciadophyllum</u>	8	2.91	Celastraceae
<u>Alchornea latifolia</u>	7	2.55	Euphorbiaceae
<u>Persea alpigena</u>	4	1.45	Lauraceae
<u>Psychotria corymbosa</u>	4	1.45	Rubiaceae
<u>Dendropanax pendulus</u>	3	1.09	Araliaceae
<u>Eugenia virgultosa</u>	1	0.36	Myrtaceae

TOTAL

275

TABLE 2. FREQUENCY TABLE OF SUPPORT SPECIES. SITE 2

<u>SUPPORT SPECIES</u>	<u>FREQUENCY</u>	<u>PERCENT</u>	<u>FAMILY</u>
<u>Clusia havetioides</u>	28	16.77	Clusiaceae
<u>Lyonia octandra</u>	28	16.77	Ericaceae
<u>Cyrilla racemiflora</u>	26	15.57	Cyrillaceae
<u>Blakea trinervia</u>	15	8.98	Melastomataceae
<u>Chaetocarpus globosus</u>	12	7.19	Euphorbiaceae
<u>Clethra occidentalis</u>	9	5.39	Clethraceae
<u>Ilex macfadyenii</u>	9	5.39	Aquifoliaceae
<u>Vaccinium meridionale</u>	9	5.39	Ericaceae
<u>Alchornea latifolia</u>	8	4.79	Euphorbiaceae
<u>Schefflera sciadophyllum</u>	8	4.79	Celastraceae
Dead trees	4	2.40	*****
<u>Podocarpus urbanii</u>	3	1.80	Podocarpaceae
<u>Calyptranthes rigida</u>	2	1.80	Myrtaceae
<u>Ilex obcordata</u>	2	1.80	Aquifoliaceae
<u>Persea alpigena</u>	2	1.80	Lauraceae
<u>Hedyosmum arborescens</u>	1	0.60	Chloranthaceae
<u>Dendropanax pendulus</u>	1	0.60	Araliaceae
 TOTAL	 167		

TABLE 3. FREQUENCY TABLE OF SUPPORT SPECIES. SITE 3

SUPPORT SPECIES	FREQUENCY	PERCENT	FAMILY
<u>Lyonia octandra</u>	41	19.90	Ericaceae
<u>Cyrilla racemiflora</u>	27	13.11	Cyrillaceae
<u>Clusia havetioides</u>	24	11.65	Clusiaceae
<u>Alchornea latifolia</u>	18	8.74	Euphorbiaceae
<u>Vaccinium meridionale</u>	18	8.74	Ericaceae
Dead trees	16	7.77	*****
<u>Chaetocarpus globosus</u>	13	6.31	Euphorbiaceae
<u>Clethra occidentalis</u>	13	6.31	Clethraceae
<u>Ilex obcordata</u>	8	3.88	Aquifoliaceae
<u>Podocarpus urbanii</u>	8	3.88	Podocarpaceae
<u>Schefflera sciadophyllum</u>	8	3.88	Celastraceae
<u>Schradera involucrata</u>	4	1.94	Rubiaceae
<u>Ilex macfadyenii</u>	3	1.46	Aquifoliaceae
<u>Persea alpigena</u>	3	1.46	Lauraceae
TOTAL	206		

TABLE 4. FREQUENCY TABLE OF SUPPORT SPECIES - COMBINED SITES

SUPPORT SPECIES	FREQUENCY	PERCENT	FAMILY
<u>Lyonia octandra</u>	106	16.40	Ericaceae
<u>Clusia havetioides</u>	92	14.20	Clusiaceae
<u>Cyrilla racemiflora</u>	82	12.65	Cyrillaceae
<u>Clethra occidentalis</u>	42	6.48	Clethraceae
Dead trees	40	6.17	*****
<u>Vaccinium meridionale</u>	39	6.02	Ericaceae
<u>Chaetocarpus globosus</u>	34	5.25	Euphorbiaceae
<u>Ilex macfadyenii</u>	34	5.25	Aquifoliaceae
<u>Alchornea latifolia</u>	33	5.09	Euphorbiaceae
<u>Ilex obcordata</u>	26	4.01	Aquifoliaceae
<u>Podocarpus urbanii</u>	24	3.70	Podocarpaceae
<u>Schefflera sciadophyllum</u>	24	3.70	Celastraceae
<u>Blakea trinervia</u>	15	2.31	Melastomataceae
<u>Calyptranthes rigida</u>	13	2.01	Myrtaceae
<u>Mecranium purpurascens</u>	10	1.54	Melastomataceae
<u>Persea alpigena</u>	9	1.39	Lauraceae
<u>Wallenia subverticillata</u>	9	1.39	Myrsinaceae
<u>Schradera involucrata</u>	5	0.77	Rubiaceae
<u>Psychotria corymbosa</u>	4	0.62	Rubiaceae
<u>Dendropanax pendulus</u>	3	0.46	Araliaceae
<u>Miconia rigida</u>	2	0.31	Melastomataceae
<u>Eugenia virgultosa</u>	1	0.15	Myrtaceae
<u>Hedyosmum arborescens</u>	1	0.15	Chloranthaceae
TOTAL	648		

TABLE 5. FREQUENCY TABLE OF BROMELIADS ON SUPPORT SPECIES. SITE 1

<u>SUPPORT SPECIES</u>	<u>FREQUENCY</u>	<u>PERCENT</u>	<u>FAMILY</u>
<u>Clusia havetioides</u>	620	21.6	Clusiaceae
<u>Cyrilla racemiflora</u>	464	16.2	Cyriaceae
<u>Lyonia octandra</u>	422	14.7	Ericaceae
<u>Clethra occidentalis</u>	280	9.8	Clethraceae
Forest floor	193	6.3	*****
<u>Ilex macfadyenii</u>	148	5.2	Aquifoliaceae
<u>Chaetocarpus globosus</u>	118	4.1	Euphorbiaceae
Dead trees	115	4.0	*****
<u>Ilex obcordata</u>	90	3.1	Aquifoliaceae
<u>Podocarpus urbanii</u>	90	3.1	Podocarpaceae
<u>Alchornea latifolia</u>	85	3.0	Euphorbiaceae
<u>Vaccinium meridionale</u>	61	2.1	Ericaceae
<u>Mecranium purpurascens</u>	40	1.4	Melastomataceae
<u>Schefflera sciadophyllum</u>	36	1.3	Celastraceae
<u>Calyptranthes rigida</u>	34	1.2	Myrtaceae
<u>Wallenia subverticillata</u>	25	0.9	Myrsinaceae
<u>Dendropanax pendulus</u>	19	0.7	Araliaceae
<u>Persea alpigena</u>	18	0.6	Lauraceae
<u>Psychotria corymbosa</u>	12	0.4	Rubiaceae
<u>Eugenia virgultosa</u>	2	0.1	Myrtaceae
TOTAL	2872		

TABLE 6. FREQUENCY TABLE OF BROMELIADS ON SUPPORT SPECIES. SITE 2

<u>SUPPORT SPECIES</u>	<u>FREQUENCY</u>	<u>PERCENT</u>	<u>FAMILY</u>
<u>Lyonia octandra</u>	535	26.6	Ericaceae
<u>Cyrtilla racemiflora</u>	418	20.8	Cyrtillaceae
<u>Clusia havetioides</u>	227	11.3	Clusiaceae
<u>Chaetocarpus globosus</u>	115	7.7	Euphorbiaceae
Forest floor	136	6.8	*****
<u>Alchornea latifolia</u>	96	4.8	Euphorbiaceae
<u>Blakea trinervia</u>	89	4.4	Melastomataceae
<u>Clethra occidentalis</u>	79	3.9	Clethraceae
<u>Ilex macfadyenii</u>	74	3.7	Aquifoliaceae
<u>Vaccinium meridionale</u>	63	3.1	Ericaceae
<u>Schefflera sciadophyllum</u>	37	1.8	Celastraceae
<u>Podocarpus urbanii</u>	25	1.2	Podocarpaceae
<u>Ilex obcordata</u>	20	1.0	Aquifoliaceae
Dead trees	19	0.9	*****
<u>Calyptranthes rigida</u>	18	0.9	Myrtaceae
<u>Schradera involucrata</u>	10	0.5	Rubiaceae
<u>Persea alpigena</u>	9	0.5	Lauraceae
<u>Hedyosmum arborescens</u>	2	0.1	Chloranthaceae
TOTAL	2012		

TABLE 7. FREQUENCY TABLE OF BROMELIADS ON SUPPORT SPECIES  
SITE 3.

<u>SUPPORT SPECIES</u>	<u>FREQUENCY</u>	<u>PERCENT</u>	<u>FAMILY</u>
<u>Lyonia octandra</u>	654	25.5	Ericaceae
<u>Cyrilla racemiflora</u>	485	18.9	Cyrillaceae
<u>Clusia havetioides</u>	353	13.7	Clusiaceae
<u>Chaetocarpus globosus</u>	248	9.7	Euphorbiaceae
<u>Alchornea latifolia</u>	199	7.7	Euphorbiaceae
<u>Clethra occidentalis</u>	136	5.3	Clethraceae
<u>Vaccinium meridionale</u>	123	4.8	Ericaceae
Dead trees	96	3.7	*****
<u>Ilex obcordata</u>	76	3.0	Aquifoliaceae
Forest Floor	58	2.3	*****
<u>Schefflera sciadophyllum</u>	42	1.6	Celastraceae
<u>Ilex macfadyenii</u>	38	1.5	Aquifoliaceae
<u>Podocarpus urbanii</u>	35	1.4	Podocarpaceae
<u>Miconia rigida</u>	10	0.4	Melastomataceae
<u>Schradera involucrata</u>	10	0.4	Rubiaceae
<u>Persea alpigena</u>	7	0.3	Lauraceae
TOTAL	2570		

TABLE 8. FREQUENCY TABLE OF BROMELIADS ON SUPPORT SPECIES  
COMBINED SITES.

SUPPORT SPECIES	FREQUENCY	PERCENT	FAMILY
<u>Lyonia octandra</u>	1611	21.6	Ericaceae
<u>Cyrtilla racemiflora</u>	1367	18.3	Cyrtillaceae
<u>Clusia havetioides</u>	1200	16.1	Clusiaceae
<u>Chaetocarpus globosus</u>	521	7.0	Euphorbiaceae
<u>Clethra occidentalis</u>	495	6.7	Clethraceae
Forest Floor	387	5.2	*****
<u>Alchornea latifolia</u>	380	5.1	Euphorbiaceae
<u>Ilex macfadyenii</u>	260	3.5	Aquifoliaceae
<u>Vaccinium meridionale</u>	247	3.3	Ericaceae
Dead trees	230	3.1	*****
<u>Ilex obcordata</u>	186	2.5	Aquifoliaceae
<u>Podocarpus urbanii</u>	150	2.0	Podocarpaceae
<u>Schefflera sciadophyllum</u>	115	1.5	Celastraceae
<u>Blakea trinervia</u>	89	1.2	Melastomataceae
<u>Calyptranthes rigida</u>	52	0.7	Myrtaceae
<u>Mecranium purpurascens</u>	40	0.5	Melastomataceae
<u>Persea alpigena</u>	34	0.5	Lauraceae
<u>Wallenia subverticillata</u>	25	0.3	Myrsinaceae
<u>Schradera involucrata</u>	20	0.3	Rubiaceae
<u>Dendropanax pendulus</u>	19	0.3	Araliaceae
<u>Psychotria corymbosa</u>	12	0.2	Rubiaceae
<u>Miconia rigida</u>	10	0.1	Melastomataceae
<u>Eugenia virgultosa</u>	2	0.03	Myrtaceae
<u>Hedyosmum arborescens</u>	2	0.03	Chloranthaceae
TOTAL	7454		

TABLE 9. FREQUENCY TABLE OF BROMELIAD SPECIES BY SIZE CLASS  
SITE 1

A=adult, SA=small adult, S=seedling, SS=small seedling, TS=tiny seedling.

BROMELIAD SPECIES	CLASS					TOTAL
	A	SA	S	SS	TS	
<u>T. complanata</u>	94 3.3%	44 1.5	248 8.6	292 10.2	472 16.4	1150 40.0
<u>V. incurva</u>	99 3.5	31 1.1	165 5.8	187 6.5	119 4.1	601 20.9
<u>V. sintenisii</u>	296 10.3	51 1.8	185 6.4	233 8.1	356 12.4	1121 39.0
TOTAL	489 17.0	126 4.4	598 20.8	712 24.8	947 33.0	2872 100

TABLE 10. FREQUENCY TABLE OF BROMELIAD SPECIES BY SIZE CLASS  
SITE 2

A=adult, SA=small adult, S=seedling, SS=small seedling, TS=tiny seedling.

BROMELIAD SPECIES	CLASS					TOTAL
	FREQUENCY PERCENT	A	SA	S	SS	
<u>T. complanata</u>	38 1.9%	9 0.5	48 2.4	76 3.8	276 13.7	447 22.2
<u>V. incurva</u>	28 1.3	4 0.2	17 0.8	19 0.9	16 0.8	84 4.2
<u>V. sintenisii</u>	339 16.9	85 4.2	119 5.9	323 16.1	614 31.0	1480 73.6
TOTAL	405 20.2	98 4.9	184 9.2	418 20.8	906 45.0	2011 100

TABLE 11. FREQUENCY TABLE OF BROMELIAD SPECIES BY SIZE CLASS  
SITE 3

A=adult, SA=small adult, S=seedling, SS=small seedling, TS=tiny seedling.

BROMELIAD SPECIES	CLASS					TOTAL
	A	SA	S	SS	TS	
FREQUENCY PERCENT						
<u>T. complanata</u>	8 0.3%	4 1.2	9 0.4	34 1.3	228 8.9	283 11.1
<u>V. incurva</u>	8 0.3	2 0.08	16 0.6	35 1.4	23 0.9	84 3.3
<u>V. sintenisii</u>	260 10.1	49 1.9	135 5.3	308 12.0	1451 56.5	2203 85.7
TOTAL	276 10.4	55 2.1	160 6.2	377 14.7	1102 66.2	2570 100

TABLE 12. FREQUENCY TABLE OF BROMELIAD SPECIES BY SIZE CLASS  
COMBINED SITES

A=adult, SA=small adult, S=seedling, SS=small seedling, TS=tiny seedling.

BROMELIAD SPECIES	CLASS					TOTAL
	A	SA	S	SS	TS	
FREQUENCY PERCENT						
<u>T. complanata</u>	108 1.9%	57 0.8	305 4.1	402 5.4	976 13.1	1880 25.2
<u>V. incurva</u>	135 1.8	37 0.5	198 2.7	241 3.2	158 2.1	769 10.3
<u>V. sintenisii</u>	895 12.0	185 2.5	439 5.9	864 11.6	2421 32.5	4804 64.5
TOTAL	1170 15.7	279 3.7	942 12.6	1507 20.2	3555 47.7	7453 100

TABLE 13. FREQUENCY TABLE OF BROMELIAD SPECIES BY SITE

BROMELIAD SPECIES

FREQUENCY PERCENT	SITE 1	SITE 2	SITE 3	COMB. SITES
<u>T. complanata</u>	1150 40.0%	447 22.2	283 11.1	1880 25.2
<u>V. incurva</u>	601 20.9	84 4.2	84 3.3	769 10.3
<u>V. sintenisii</u>	1121 39.3	1480 73.6	2203 85.7	4804 64.4
TOTAL	2872 38.5	2011 27.0	2570 34.5	7453 100

TABLE 14. FREQUENCY TABLE FOR PLOT BY BROMELIAD SPECIES SITE 1

The frequencies are the number of individual plants censused in each 5 m x 5 m plot.

PLOT #	BROMELIAD SPECIES			TOTAL ROW %
	<u>T. complanata</u>	<u>V. incurva</u>	<u>V. sintenisii</u>	
1	205	98	153	456 15.9
2	40	44	134	218 7.8
3	19	45	151	215 7.5
4	55	146	226	427 14.9
5	114	59	113	286 10.0
6	174	45	100	319 11.1
7	230	43	130	403 14.0
8	150	28	33	211 7.4
9	129	69	65	263 9.2
10	34	24	16	74 2.6
TOTAL COL. %	1150 40.0	601 20.9	1121 39.0	2872 100

TABLE 15. FREQUENCY TABLE FOR PLOT BY BROMELIAD SPECIES SITE 2

The frequencies are the number of individual plants censused in each 5 m x 5 m plot.

PLOT #	BROMELIAD SPECIES			TOTAL ROW %
	<u>T. complanata</u>	<u>V. incurva</u>	<u>V. sintenisii</u>	
1	27	5	145	187 9.3
2	57	14	143	214 10.6
3	52	9	87	148 7.4
4	62	13	144	219 10.9
5	21	7	95	123 6.1
6	60	12	179	215 12.5
7	59	5	172	236 11.7
8	63	2	205	270 13.4
9	19	3	97	119 12.1
10	17	14	213	244 12.1
TOTAL	447	84	1480	2011
COL. %	22.2	4.2	73.6	100

TABLE 16. FREQUENCY TABLE FOR PLOT BY BROMELIAD SPECIES SITE 3

The frequencies are the number of individual plants censused in each 5 m x 5 m plot.

PLOT #	BROMELIAD SPECIES			TOTAL ROW %
	<u>T. complanata</u>	<u>V. incurva</u>	<u>V. sintenisii</u>	
1	14	6	404	424 16.5
2	2	1	282	285 11.1
3	28	8	210	246 9.6
4	24	9	115	148 5.8
5	22	20	188	230 9.0
6	19	5	136	160 6.2
7	37	8	171	216 8.4
8	55	11	220	286 11.3
9	53	14	354	421 11.4
10	29	2	123	154 6.0
TOTAL COL. %	283 11.0	84 3.3	2203 85.7	2570 100

TABLE 17. FREQUENCY TABLE FOR PLOT BY BROMELIAD SPECIES  
COMBINED SITES.

The frequencies are the number of individual plants  
censused in each 5 m x 5 m plot.

PLOT #	BROMELIAD SPECIES			TOTAL ROW %
	<u>T. complanata</u>	<u>V. incurva</u>	<u>V. sintenisii</u>	
1	256	109	702	1067 14.3
2	99	59	559	717 9.6
3	99	62	448	609 8.2
4	141	168	485	794 10.7
5	157	86	396	639 8.6
6	253	62	415	730 9.8
7	326	56	473	855 11.5
8	268	41	458	767 10.3
9	201	86	516	803 10.8
10	80	40	352	452 6.0
TOTAL	1880	769	4804	7454
COL. %	25.2	10.3	64.5	100

TABLE 18. TWO-WAY ANOVA ( NO REPLICATION ) On the variable height (m) above ground across the three study sites. The descriptive statistics for each cell of the two-way design are entered below.

BROMELIAD SPECIES

	<u>T. complanata</u>	<u>V. incurva</u>	<u>V. sintenisii</u>	Overall	
SITE 1	<u>Mean</u>	1.3	2.4	1.3	1.5
	<u>SD</u>	0.8	1.3	1.1	1.1
	<u>N</u>	1150	601	1121	2872
SITE 2	<u>Mean</u>	2.0	3.6	1.8	1.9
	<u>SD</u>	1.3	1.6	1.4	1.4
	<u>N</u>	447	84	1480	2012
SITE 3	<u>Mean</u>	1.9	3.8	2.1	2.1
	<u>SD</u>	1.1	2.2	1.3	1.4
	<u>N</u>	283	84	2203	2570
OVERALL	<u>Mean</u>	1.6	2.7	1.8	1.8
	<u>SD</u>	1.1	1.6	1.3	1.3
	<u>N</u>	1880	769	4804	7454

\*\*\*\*\*

TWO-WAY ANOVA TABLE

SOURCE OF VARIATION	df	SS	F	
Among Epiphyte Species	2	4.7	41	*
Among Study Sites	2	.76	13	*

\* p < .05

TABLE 19. STATISTICS FOR HEIGHT OF TILLANDSIA COMPLANATA  
BY SIZE CLASS FOR COMBINED SITES

<u>CLASS</u>	<u>MEAN</u>	<u>SD</u>	<u>N</u>
ADULT	2.7	1.5	140
SMALL ADULT	1.8	1.0	57
SEEDLING	1.5	1.1	305
SMALL SEEDLING	1.4	1.0	402
TINY SEEDLING	1.5	0.9	976

\*\*\*\*\*

TABLE 20. STATISTICS FOR HEIGHT OF VRIESIA INCURVA  
BY SIZE CLASS FOR COMBINED SITES

<u>CLASS</u>	<u>MEAN</u>	<u>SD</u>	<u>N</u>
ADULT	3.5	1.9	135
SMALL ADULT	3.2	1.5	37
SEEDLING	3.0	1.6	198
SMALL SEEDLING	2.5	1.4	241
TINY SEEDLING	1.8	0.8	158

TABLE 21. STATISTICS FOR HEIGHT OF VRIESIA SINTENISII  
BY SIZE CLASS FOR COMBINED SITES

<u>CLASS</u>	<u>MEAN</u>	<u>SD</u>	<u>N</u>
ADULT	2.2	1.8	895
SMALL ADULT	1.6	1.5	185
SEEDLING	1.6	1.4	439
SMALL SEEDLING	1.8	1.3	864
TINY SEEDLING	1.8	1.1	2421

\*\*\*\*\*

TABLE 22. SPEARMAN CORRELATION FOR HEIGHT vs SIZE CLASS COMBINED  
SITES

BROMELIAD SPECIES	<u>r</u>	<u>N</u>	<u>P</u>
<u>T. complanata</u>	0.11	1880	0.0001 ***
<u>V. incurva</u>	0.37	769	0.0001 ***
<u>V. sintenisii</u>	0.02	4804	0.14 NS

\*\*\* p < .001

TABLE 23. SPEARMAN CORRELATION FOR HEIGHT vs SIZE CLASS BY SITE

	<u>T. complanata</u>	<u>V. incurva</u>	<u>V. sintenisii</u>
SITE 1	0.10 ***	0.31 ***	-0.06 NS
SITE 2	0.45 ***	0.68 ***	0.08 **
SITE 3	0.24 ***	0.61 ***	0.18 ***

\*\* p < .01

TABLE 24. PLOT ANALYSIS OF BROMELIAD SPECIES ON SUPPORT TREES

TC = T. complanata, VI = V. incurva, VS = V. sintenisii  
 TREES (N) = total number of individuals of tree species  
 N = number of bromeliads per tree species, MEAN = mean  
 number of bromeliads per individual tree. Only the 10  
 most abundant support trees were analyzed.

SUPPORT SPECIES (N)	TC		VS		V		RGM
	N	MEAN	N	MEAN	N	MEAN	
<u>Lyonia octandra</u> (106)	336	3.2	121	1.1	1154	10.9	5.1
<u>Clusia havetioides</u> (92)	399	4.3	159	1.7	642	7.0	4.4
<u>Cyrilla racemiflora</u> (82)	303	3.7	146	1.8	918	11.2	5.6
<u>Clethra occidentalis</u> (42)	160	3.8	54	1.3	281	6.7	3.9
<u>Vaccinium meridionale</u> (39)	46	1.2	24	0.6	177	4.5	2.1
<u>Chaetocarpus globosus</u> (34)	80	2.4	59	1.7	380	11.2	5.0
<u>Ilex macfadyenii</u> (34)	103	3.0	25	0.7	132	3.9	2.6
<u>Alchornea latifolia</u> (33)	91	2.8	39	1.2	250	7.6	3.8
<u>Ilex obcordata</u> (26)	35	1.4	31	1.2	120	4.6	2.4
<u>Podocarpus urbanii</u> (24)	39	1.6	24	1.0	87	3.6	2.1
COLUMN GRAND MEAN		2.7		1.2		7.1	

\*\*\*\*\*

TWO WAY ANOVA (NO REPLICATION) FOR ABOVE DATA

SOURCE OF VARIATION	F	V1, V2	P	
AMONG BROMELIAD SPECIES	35.1	2, 9	0.0001	***
AMONG SUPPORT TREES	2.0	9, 18	0.1008	NS

TABLE 25. RANKED SUPPORT TREE PREFERENCES

Among the 10 most abundant trees. # and ## indicate very close or equal preference.

TREES	<u>T. COMPLANATA</u>	<u>V. INCURVA</u>	<u>V. SINTENISII</u>
<u>Lyonia octandra</u>	4	7	3
<u>Clusia havetioides</u>	1	3 #	5
<u>Cyrilla racemiflora</u>	3	1	2 ##
<u>Clethra occidentalis</u>	2	4	6
<u>Vaccinium meridionale</u>	10	10	8
<u>Chaetocarpus globosus</u>	7	2 #	1 ##
<u>Ilex macfadyenii</u>	5	9	9
<u>Alchornea latifolia</u>	6	6	4
<u>Ilex obcordata</u>	9	5	7
<u>Podocarpus urbanii</u>	8	8	10

TABLE 26. MEAN NUMBER OF LEAVES PRODUCED (# PROD) AND MEAN  
STANDING CROP OF LEAVES (MSC)

TC = T. complanata, VI = V. incurva, VS = V. sintenisii  
 No data were collected for small adults of V. incurva  
 because no individuals in this group fell within the  
 random coordinates used to select the plants studied.  
 Sample sizes for adults, small adults, seedlings, small  
 seedlings, tiny seedlings and total population are for  
 TC: 11, 5, 8, 27, 11, 62; VI: 4, 0, 9, 21, 8, 42;  
 VS: 22, 6, 16, 16, 24, 8, 76.

	TC		VI		VS	
	# PROD.	MSC	# PROD.	MSC	#. PROD.	MSC
ADULT	16	38	9	39	23	35
SMALL ADULT	10	21	-	-	21	28
SEEDLING	9	18	7	29	15	19
SMALL SEEDLING	7	13	7	24	10	11
TINY SEEDLING	6	15	6	19	8	13
TOTAL POPULATION	9	19	7	26	16	21

TABLE 27. CALCULATED MEAN LEAF LIFE IN DAYS

BROMELIAD SPECIES

	<u>T. COMPLANATA</u>	<u>V. INCURVA</u>	<u>V. SINTENISII</u>
TOTAL POP.	724	1274	450
ADULT	815	1486	522
SMALL ADULT	720	----	475
SEEDLING	686	1421	434
SMALL SEEDLING	637	1176	377
TINY SEEDLING	858	1086	557

TABLE 28. PAIRED COMPARISONS OF REGRESSION SLOPES (LINEAR LEAST SQUARES MODEL; SOKAL AND ROHLF, 1981 BOX 14.8) OF RELATIVE GROWTH CURVES FOR EPIPHYTICALLY GROWING BROMELIADS

TC = T. complanata

VI = V. incurva

VS = V. sintenisii

Degrees of freedom: V1, V2 = 1, 18 No data were collected for small adults of V. incurva because no individuals in this group fell within the random coordinates used to select the plants studied.

NS means that the two slopes are not significantly different ( $p > .05$ ).

<u>TOTAL POPULATION</u>			<u>SLOPES</u> (% INCREASE/ MONTH)			<u>F STATISTIC</u>	
TC	vs	VS	9.06	-	9.18	0.08	NS
TC	vs	VI	9.06	-	8.81	0.20	NS
VS	vs	VI	9.18	-	8.81	0.63	NS
<u>ADULT</u>							
TC	vs	VS	9.16	-	9.19	5.72-E03	NS
TC	vs	VI	9.16	-	9.14	5.75-E04	NS
VS	vs	VI	9.19	-	9.14	9.53-E03	NS
<u>SMALL ADULT</u>							
TC	vs	VS	8.88	-	9.04	0.23	NS
TC	vs	VI	---		--		
VS	vs	VI	---		--		
<u>SEEDLING</u>							
TC	vs	VS	8.97	-	9.20	0.40	NS
TC	vs	VI	9.97	-	8.71	0.28	NS
VS	vs	VI	9.20	-	8.71	1.13	NS
<u>SMALL SEEDLING</u>							
TC	vs	VS	8.96	-	9.27	0.39	NS
TC	vs	VI	8.96	-	8.93	1.99	NS
VS	vs	VI	9.27	-	8.93	0.33	NS
<u>TINY SEEDLING</u>							
TC	vs	VS	8.82	-	9.16	0.39	NS
TC	vs	VI	8.82	-	8.22	0.75	NS
VS	vs	VI	9.16	-	8.22	2.24	NS

TABLE 29. MEAN NUMBER OF LEAVES PRODUCED (# PROD) AND MEAN STANDING CROP OF LEAVES (MSC) FOR TRANSPLANTED BROMELIADS

TC = T. complanata, VI = V. incurva, VS = V. sintenisii  
 Sample sizes for adults, small adults, seedlings, small seedlings, tiny seedlings and total population are for TC: 5, 5, 5, 3, 2, 20; VI: 5, 5, 5, 5, 5, 25; VS: 5, 5, 5, 5, 4, 24.

	TC		VI		VS	
	# PROD.	MSC	# PROD.	MSC	#. PROD.	MSC
ADULT	15	38	11	37	17	25
SMALL ADULT	10	21	12	36	19	23
SEEDLING	9	18	9	30	14	18
SMALL SEEDLING	10	14	9	21	8	11
TINY SEEDLING	8	22	4	10	6	10
TOTAL POPULATION	11	24	9	27	13	18

TABLE 30. MEAN LEAF LIFE (DAYS) FOR TRANSPLANTED BROMELIADS

	BROMELIAD SPECIES		
	<u>T. COMPLANATA</u>	<u>V. INCURVA</u>	<u>V. SINTENISII</u>
TOTAL POP.	624	858	396
ADULT	725	962	421
SMALL ADULT	601	858	346
SEEDLING	572	953	368
SMALL SEEDLING	400	667	393
TINY SEEDLING	787	715	477

TABLE 31. PAIRED COMPARISONS OF REGRESSION SLOPES (LINEAR LEAST SQUARES MODEL; SOKAL AND ROHLF, 1981 BOX 14.8) OF RELATIVE GROWTH CURVES FOR TRANSPLANTED BROMELIADS

TC = T. complanata

VI = V. incurva

VS = V. sintenisii

Degrees of freedom: V1, V2 = 1, 14

<u>TOTAL POPULATION</u>	<u>SLOPES</u> (% INCREASE/ MONTH)		<u>F STATISTIC</u>	
TC vs VS	10.97	- 11.24	1.92	NS
TC vs VI	10.97	- 11.18	1.88	NS
VS vs VI	11.24	- 11.18	0.01	NS
<u>ADULT</u>				
TC vs VS	10.85	- 11.58	1.58	NS
TC vs VI	10.85	- 11.17	0.40	NS
VS vs VI	11.58	- 11.17	0.53	NS
<u>SMALL ADULT</u>				
TC vs VS	11.06	- 11.76	1.55	NS
TC vs VI	10.06	- 11.04	1.56	NS
VS vs VI	11.76	- 11.04	1.72	NS
<u>SEEDLING</u>				
TC vs VS	10.77	- 11.38	0.97	NS
TC vs VI	10.77	- 11.40	0.81	NS
VS vs VI	11.38	- 11.40	9.37E=04	NS
<u>SMALL SEEDLING</u>				
TC vs VS	11.17	- 11.01	0.05	NS
TC vs VI	11.01	- 11.31	0.02	NS
VS vs VI	11.01	- 11.31	0.14	NS
<u>TINY SEEDLING</u>				
TC vs VS	11.03	- 10.93	0.03	NS
TC vs VI	11.03	- 10.66	0.28	NS
VS vs VI	10.93	- 10.66	0.15	NS

TABLE 32. PAIRED COMPARISONS OF REGRESSION SLOPES (LINEAR LEAST SQUARES MODEL; SOKAL AND ROHLF, 1981 BOX 14.8) OF RELATIVE GROWTH CURVES FOR EPIPHYTIC X TRANSPLANTED BROMELIADS

TC = T. complanata

VI = V. incurva

VS = V. sintenisii

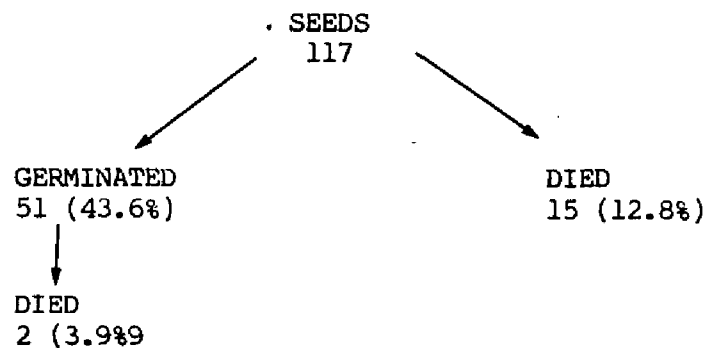
TC-T, VS-T, VI-T refer to transplanted bromeliads.

Degrees of freedom: V1, V2 = 1, 16

<u>TOTAL POPULATION</u>			<u>SLOPES</u> (; INCREASE/ MONTH)		<u>F STATISTIC</u>	
TC	vs	TC-T	9.06	- 10.97	13.46	**
VS	vs	VS-T	9.18	- 11.24	17.80	***
VI	vs	VI-T	8.81	- 11.18	15.78	**
<u>ADULT</u>						
TC	vs	TC-T	9.16	- 10.52	8.56	**
VS	vs	VS-T	9.19	- 11.58	30.09	***
VI	vs	VI-T	9.14	- 11.17	10.38	**
<u>SMALL ADULT</u>						
TC	vs	TC-T	8.88	- 11.06	22.55	***
VS	vs	VS-T	9.04	- 11.76	38.45	***
<u>SEEDLING</u>						
TC	vs	TC-T	8.97	- 10.77	11.03	**
VS	vs	VS-T	9.20	- 11.38	27.78	***
VI	vs	VI-T	8.71	- 11.40	11.50	**
<u>SMALL SEEDLING</u>						
TC	vs	TC-T	8.96	- 11.17	12.17	**
VS	vs	VS-T	9.27	- 11.01	10.59	**
VI	vs	VI-T	8.93	- 11.31	8.17	*
<u>TINY SEEDLING</u>						
TC	vs	TC-T	8.82	- 11.03	10.95	**
VS	vs	VS-T	9.16	- 10.93	10.24	**
VI	vs	VI-T	8.22	- 10.66	9.60	**

TABLE 33. COLONIZATION - EXPERIMENTAL PLOT

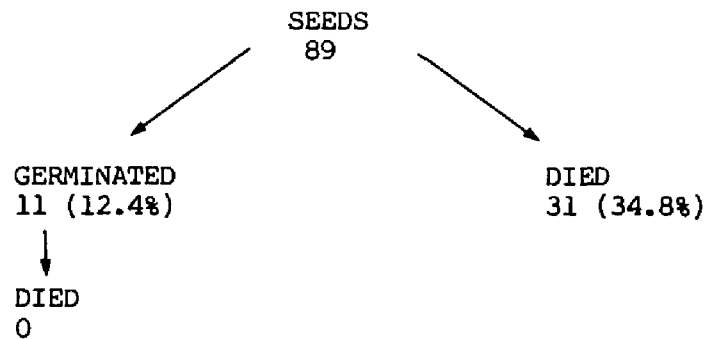
Naturally dispersed seeds



\*\*\*\*\*

TABLE 34. COLONIZATION - CONTROL PLOT

Naturally dispersed seeds



NEWLY GERMINATED SEEDS

57

DIED  
14 (24.6%)

TABLE 35. BARK TEXTURE AND CAPILLARITY

The sample size for water displacement and capillarity is 5 trees per taxon.

SUPPORT TREES	WATER DISPLACEMENT		CAPILLARITY	
	<u>Mean</u>	<u>SD</u>	<u>Mean</u>	<u>SD</u>
<u>Lyonia octandra</u>	3.3	0.8	1.3	0.7
<u>Clusia havetioides</u>	3.3	0.7	0.3	0.5
<u>Cyrilla racemiflora</u>	3.3	1.2	1.2	0.4
<u>Clethra occidentalis</u>	4.3	2.0	0.6	0.2
<u>Vaccinium meridionale</u>	2.0	0.8	1.3	0.3
<u>Chaetocarpus globosus</u>	2.1	1.0	1.1	1.9
<u>Ilex macfadyenii</u>	3.7	1.6	0.5	0.4
<u>Alchornea latifolia</u>	3.2	1.0	0.9	0.1
<u>Ilex obcordata</u>	4.0	#	0.7	#
<u>Podocarpus urbanii</u>	3.5	1.8	0.8	0.2

# only 1 measurement was made.

TABLE 36. BARK TEXTURE GRADIENT

ROUGHER	<u>Clethra occidentalis</u>
	<u>Ilex obcordata</u>
	<u>Ilex macfadyenii</u>
	<u>Podocarpus urbanii</u>
	# <u>Clusia havetioides</u>
	# <u>Cyrilla racemiflora</u>
	# <u>Lyonia octandra</u>
	<u>Alchornea latifolia</u>
	<u>Chaetocarpus globosus</u>
SMOOTHER	<u>Vaccinium meridionale</u>

# indicates similar texture

TABLE 37. BARK CAPILLARITY GRADIENT

GREATER CAPILLARITY



Lyonia octandra

Vaccinium meridionale

Cyrilla racemiflora

Chaetocarpus globosus

Alchornea latifolia

Podocarpus urbanii

Ilex obcordata

Clethra occidentalis

Ilex macfadyenii

LESS CAPILLARITY

Clusia havetioides

TABLE 38. BARK pH GRADIENT AND TYPE

N refers to replicate aliquots of ground bark.

SUPPORT TREES	MEAN pH	N	SD	BARK TYPE
<u>Alchornea latifolia</u>	3.7	3	0	Poor
<u>Cyrilla racemiflora</u>	3.9	3	0.6	Intermediate
<u>Vaccinium meridionale</u>	4.2	3	0	Intermediate
<u>Chaetocarpus globosus</u>	4.2	3	0.6	Intermediate
<u>Clethra occidentalis</u>	4.3	3	0.6	Intermediate
<u>Ilex obcordata</u>	4.7	3	0	Intermediate
<u>Podocarpus urbanii</u>	4.8	3	0	Intermediate
<u>Lyonia octandra</u>	4.9	3	0.6	Intermediate
<u>Ilex macfadyenii</u>	5.0	3	0	Intermediate
<u>Clusia havetioides</u>	5.1	3	0	Rich

TABLE 39. STEM FLOW DATA

The sample size for the volume, pH and conductivity is 4 trees per taxon.

TREE SPECIES	MEAN VOLUME (ml)	MEAN pH	MEAN CONDUCTIVITY (mV)
<u>Clusia havetioides</u>	42122	6.4	+ 73.2
<u>Alchornea latifolia</u>	22210	6.0	+ 82.5
<u>Lyonia octandra</u>	45500	6.4	+ 55
<u>Clethra occidentalis</u>	43632	6.4	+ 62.5
<u>Cyrilla racemiflora</u>	42790	6.5	+ 50.0
Rain Water	4.0	6.7	+ 40

FIGURE 1. MAPS

- a, Map of a section of the Blue Mountain Range between Silver Hill Peak and St. Helen's Gap (contours in feet) showing the approximate positions of the three study sites (arrows indicate Sites 1, 2 and 3). The map was reproduced from Sheet L, Survey Department of Jamaica.
- b, Outline map of Jamaica (from Grubb and Tanner 1976).

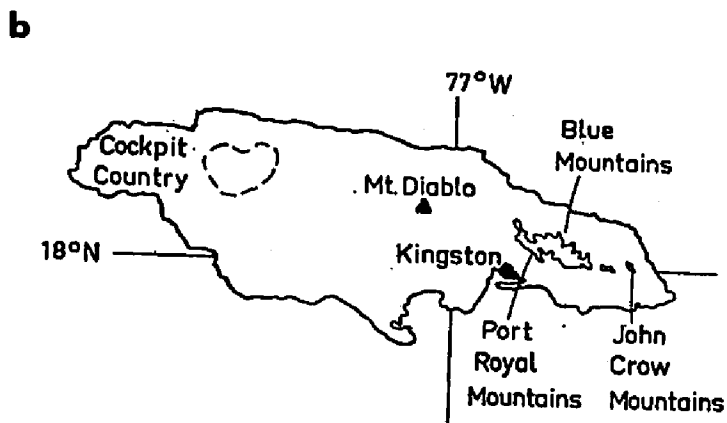
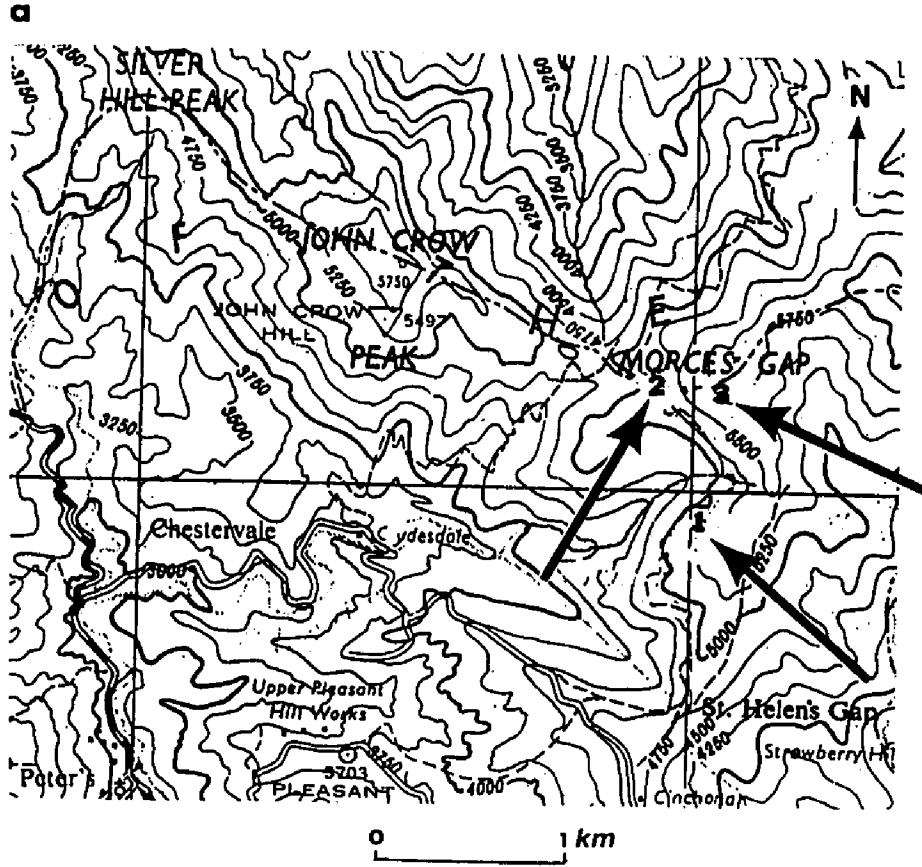


FIGURE 2. MEAN HEIGHT ABOVE GROUND.

TC = Tillandsia complanata

VI = Vriesia incurva

VS = Vriesia sintenisii

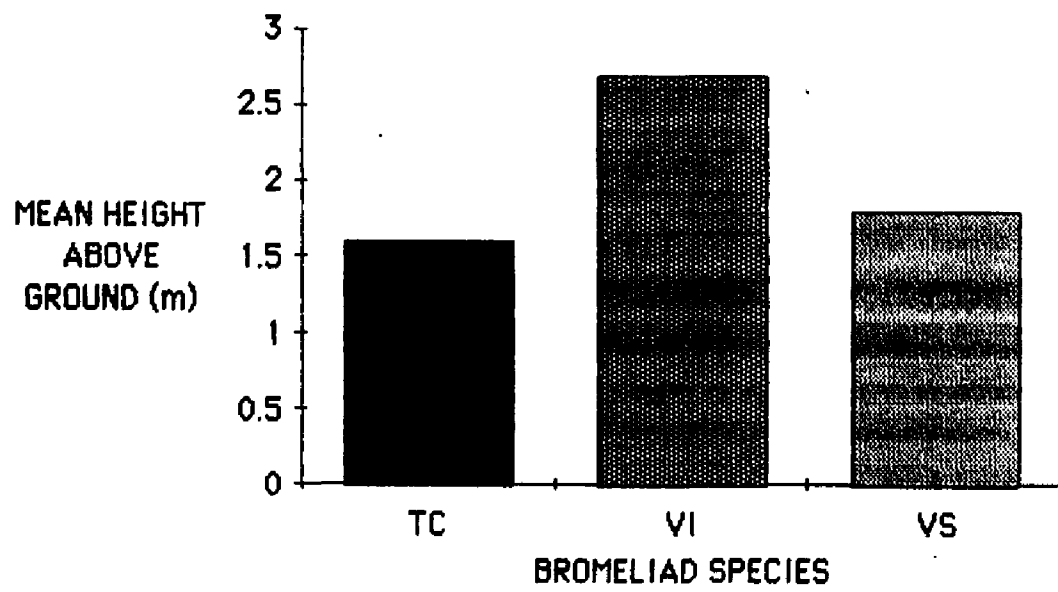


FIGURE 3. FREQUENCY DISTRIBUTION OF BROMELIAD HEIGHTS.

T. complanata in Site 1, N = 1150 plants.

Arrow indicates end of frequency distribution on this and subsequent graphs of frequency distributions.

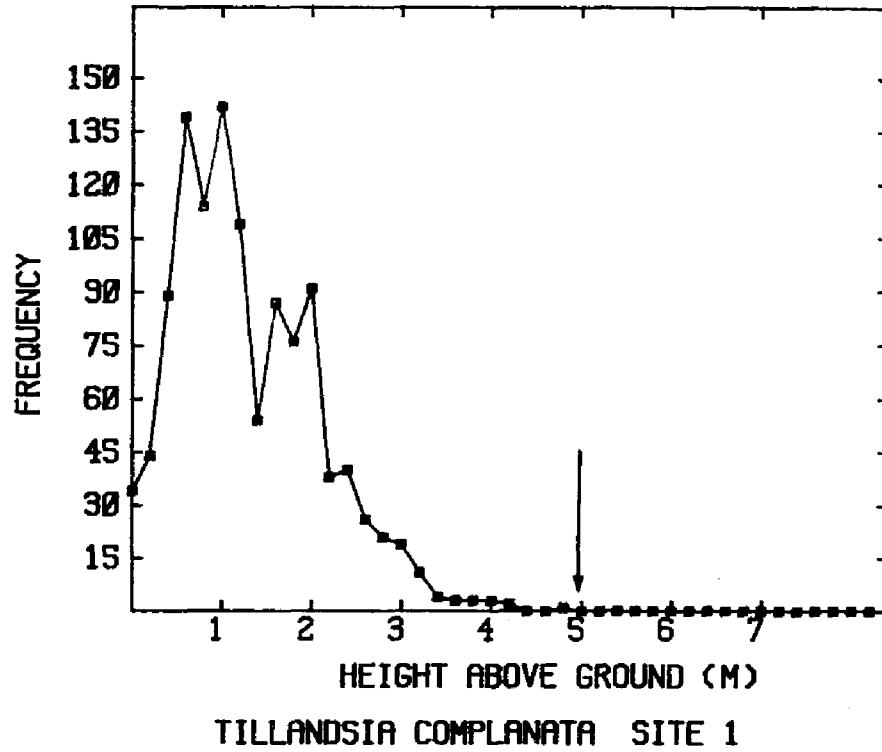


FIGURE 4. FREQUENCY DISTRIBUTION OF BROMELIAD HEIGHTS.

V. incurva in Site 1, N = 601.

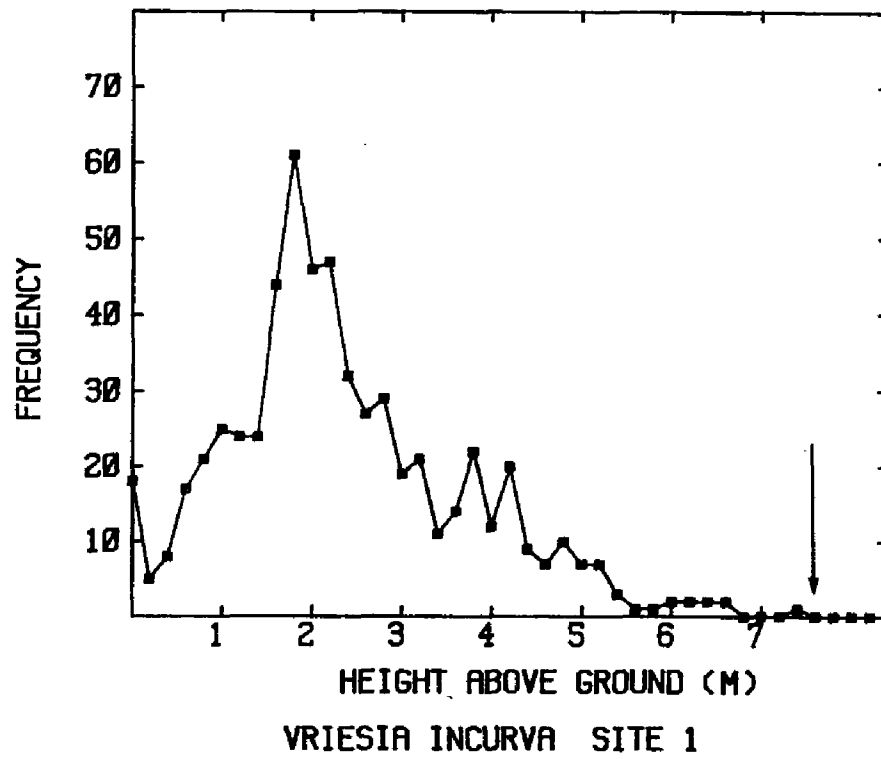


FIGURE 5. FREQUENCY DISTRIBUTION OF BROMELIAD HEIGHTS.

V. sintenisii in Site 1, N = 1121.

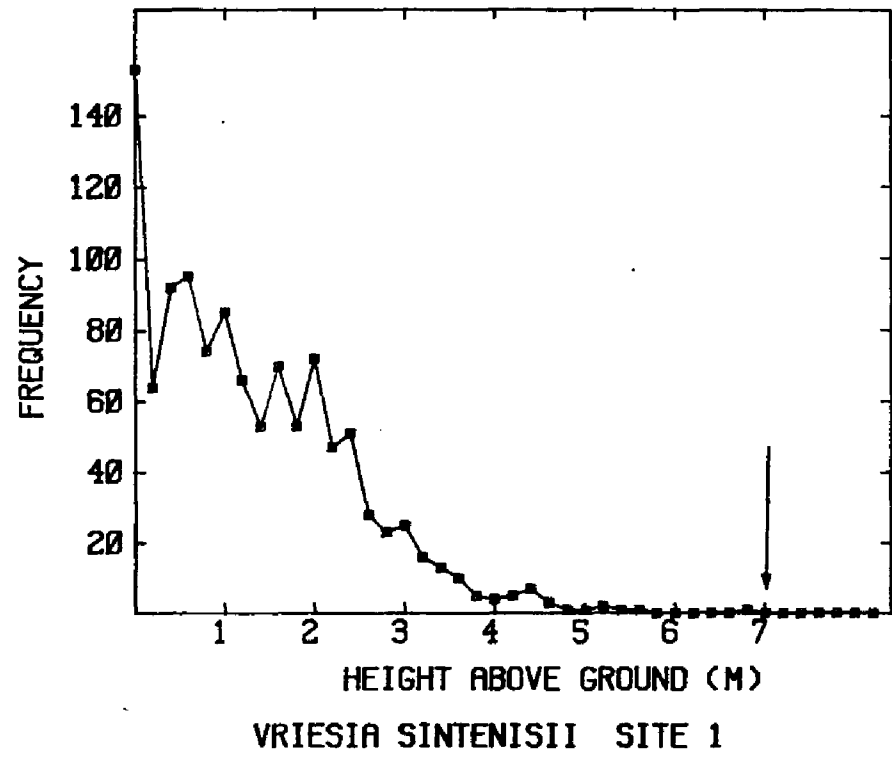


FIGURE 6. FREQUENCY DISTRIBUTION OF BROMELIAD HEIGHTS.

T. complanata in Site 2, N = 447.

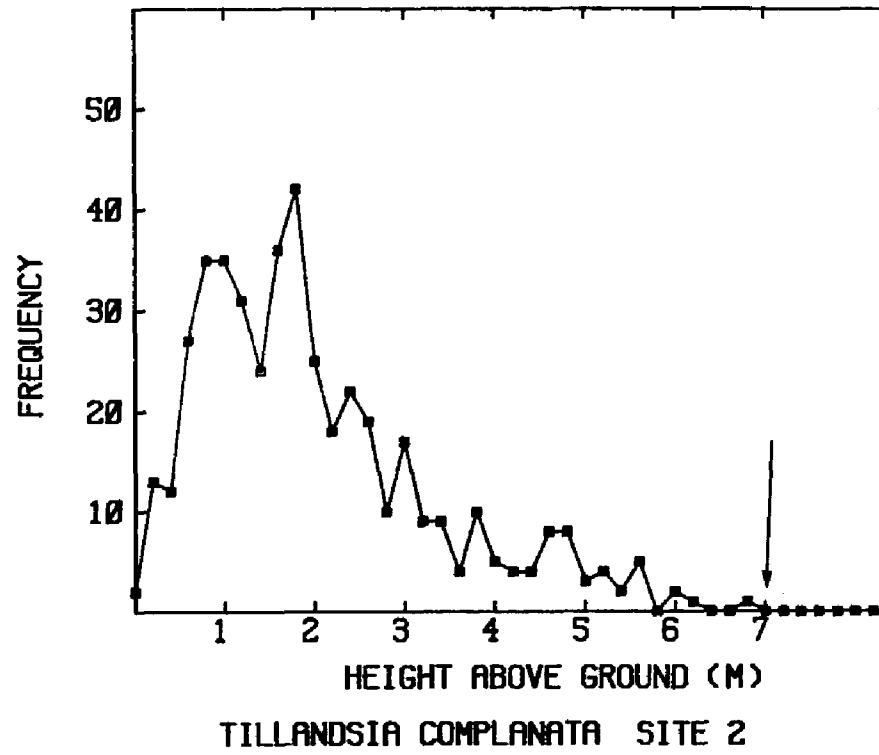


FIGURE 7. FREQUENCY DISTRIBUTION OF BROMELIAD HEIGHTS.

V. incurva in Site 2, N = 84.

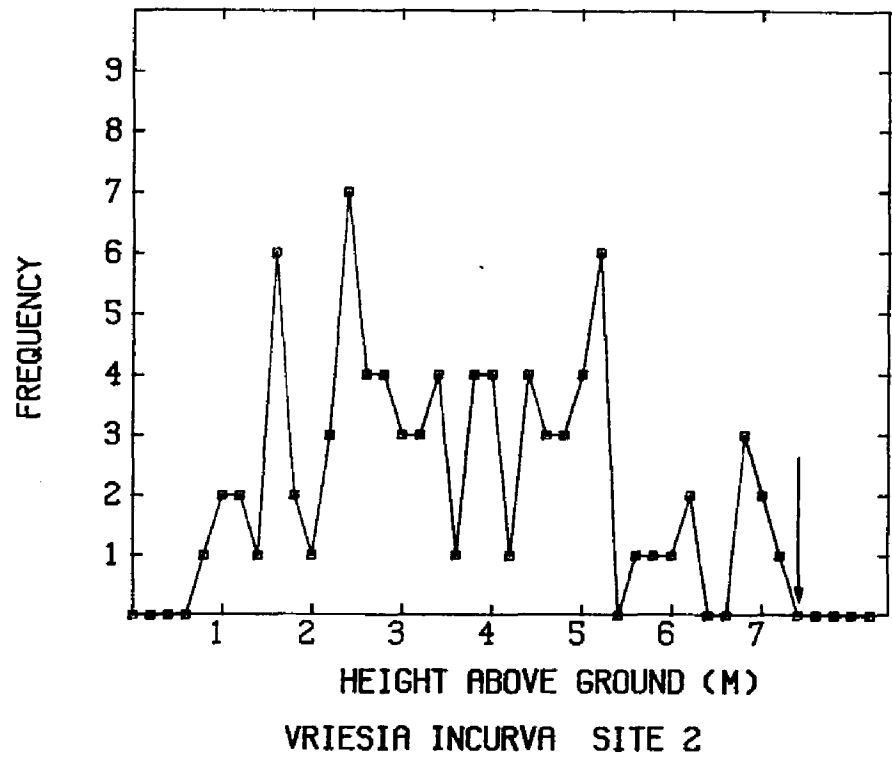


FIGURE 8. FREQUENCY DISTRIBUTION OF BROMELIAD HEIGHTS.

V. sintenisii in Site 2, N = 1480.

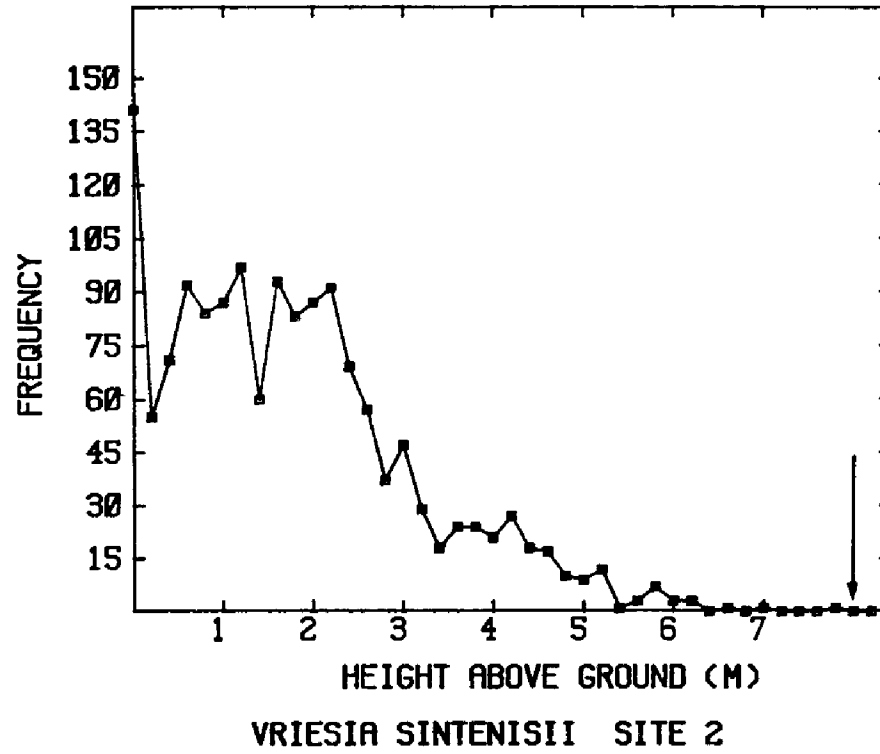


FIGURE 9. FREQUENCY DISTRIBUTION OF BROMELIAD HEIGHTS.

T. complanata in Site 3, N = 283.

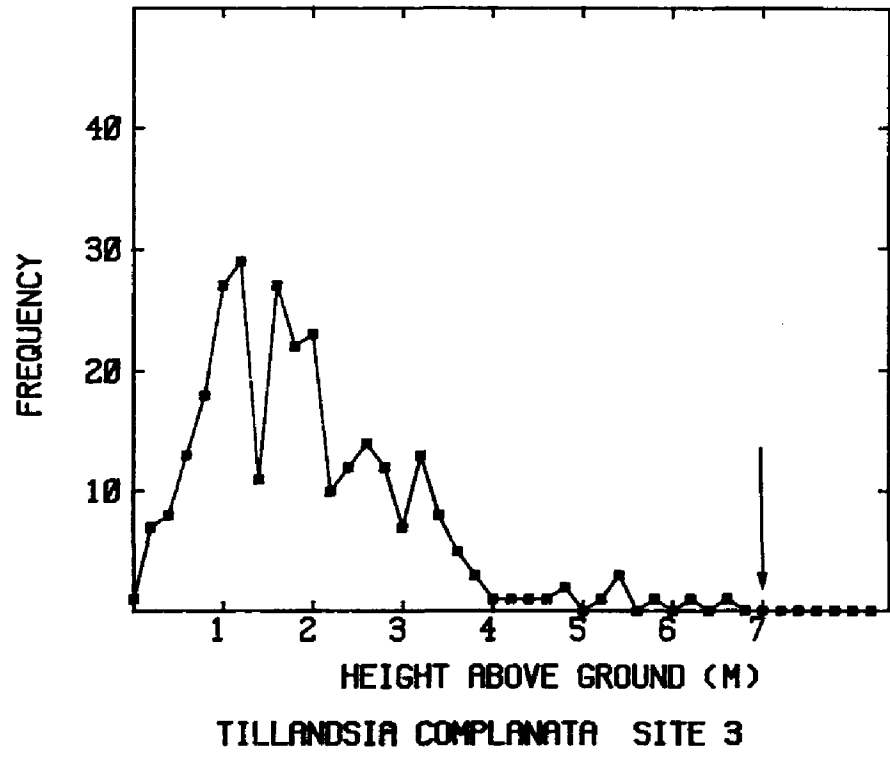


FIGURE 10. FREQUENCY DISTRIBUTION OF BROMELIAD HEIGHTS.

V. incurva in Site 3, N = 84.

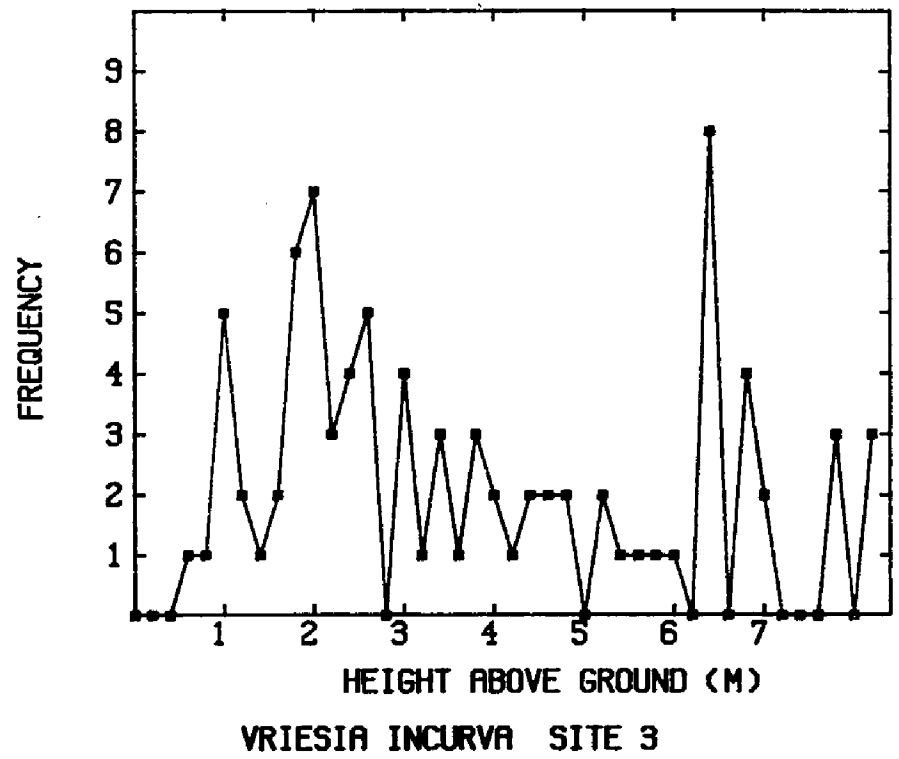
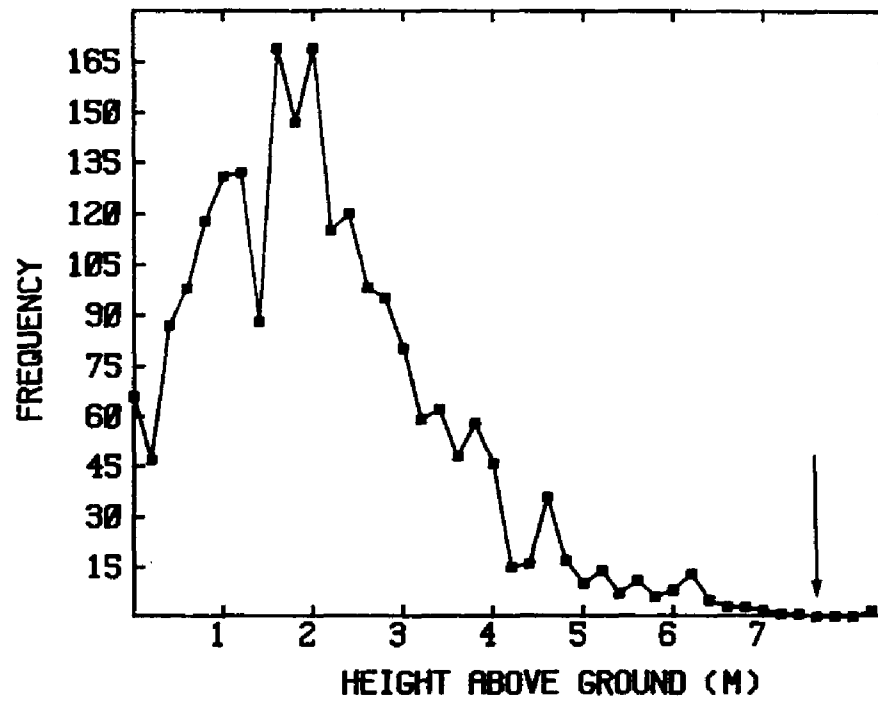


FIGURE 11. FREQUENCY DISTRIBUTION OF BROMELIAD HEIGHTS.

V. sintenisii in Site 3, N = 2203.



VRIESIA SINTENISII SITE 3

FIGURE 12. FREQUENCY DISTRIBUTION OF BROMELIAD HEIGHTS.

T. complanata -- Combined Sites, N = 1880.

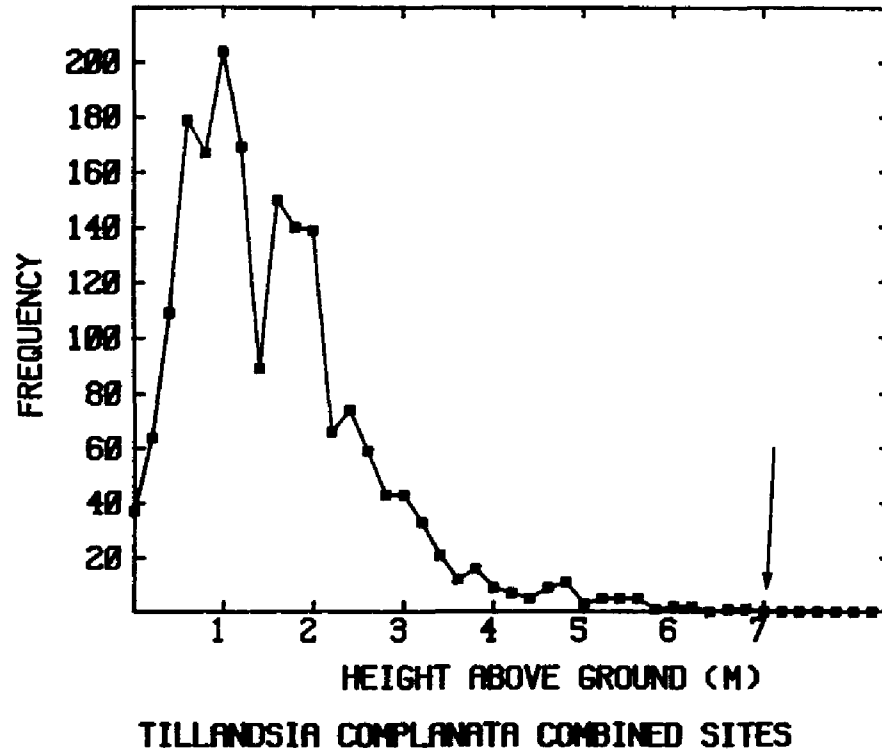


FIGURE 13. FREQUENCY DISTRIBUTION OF BROMELIAD HEIGHTS.

V. incurva -- Combined Sites, N = 769.

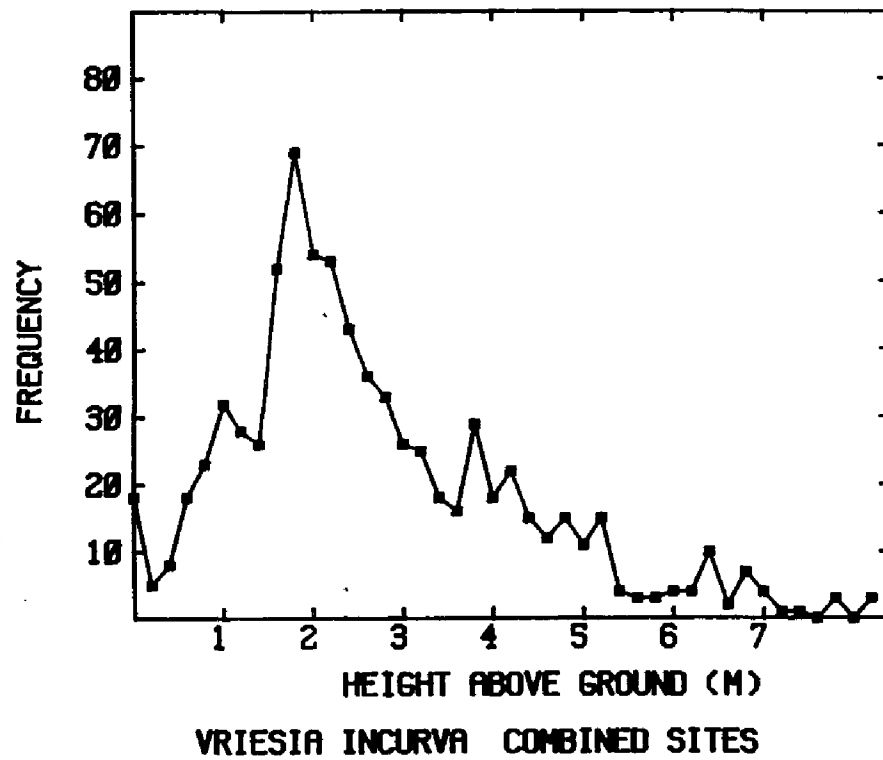


FIGURE 14. FREQUENCY DISTRIBUTION OF BROMELIAD HEIGHTS.

V. sintenisii -- Combined Sites, N = 4804.

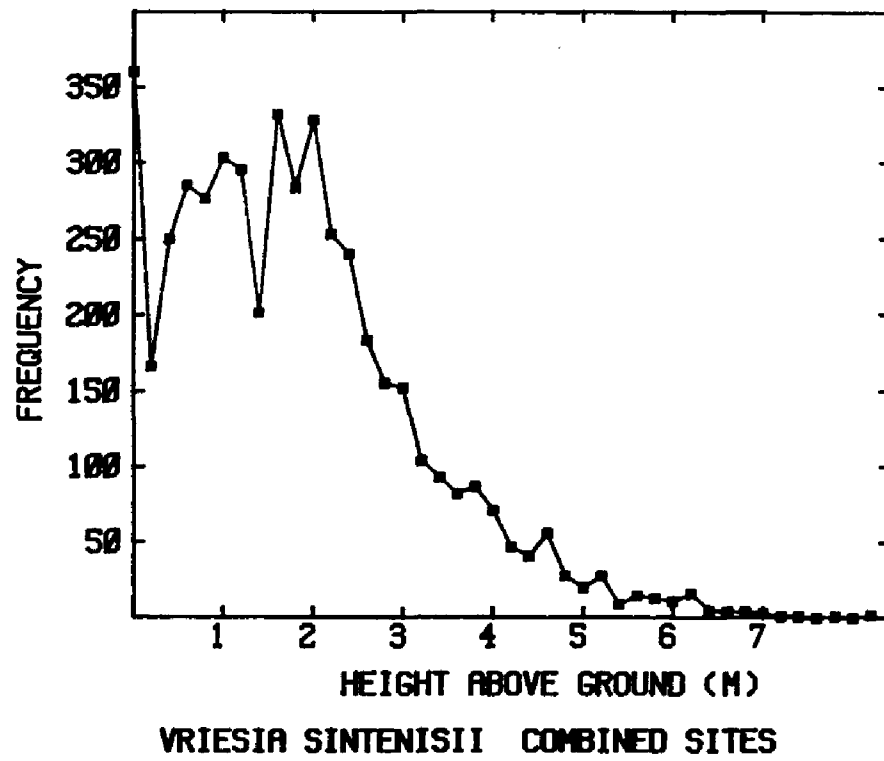


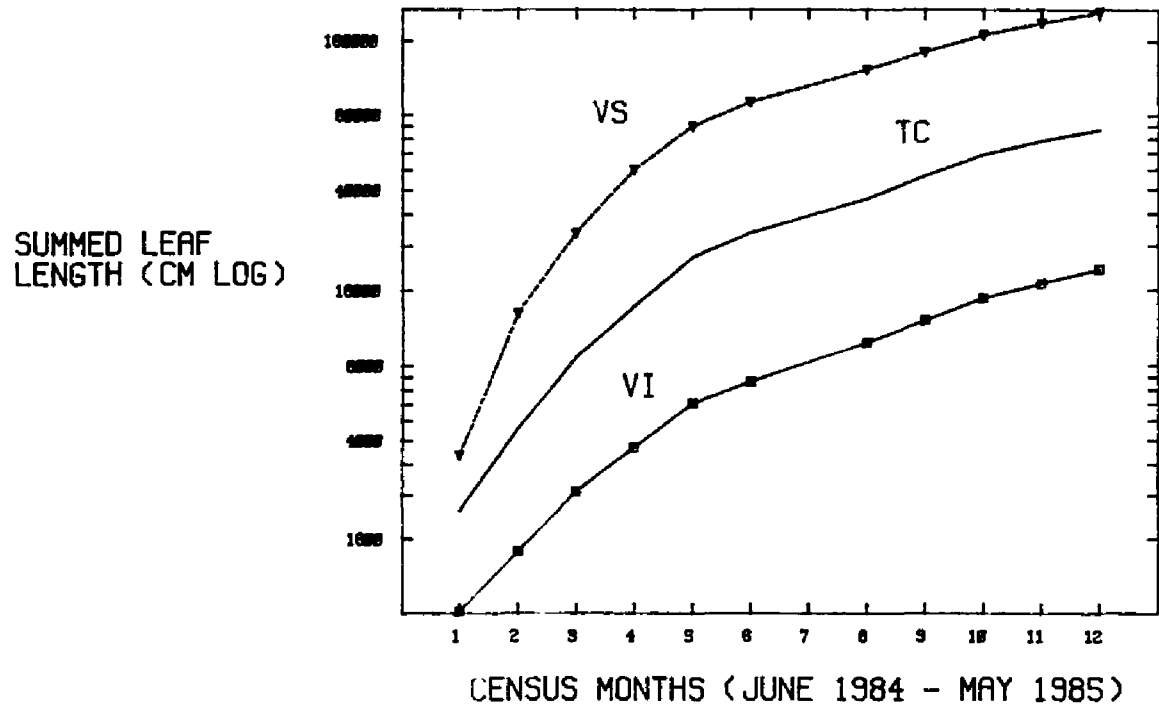
FIGURE 15. ABSOLUTE GROWTH OF T. COMPLANATA, V. INCURVA AND  
V. SINTENISII.

TC = Tillandsia complanata # of leaves = 554.

VI = Vriesia incurva # of leaves = 287.

VS = Vriesia sintenisii # of leaves = 1178.

Growth = change in leaf length over time. The leaf lengths used were the summed leaf lengths per month. The tic marks along the x-axis are the census months June 1984 - May 1985. No data were collected in December 1984.



ABSOLUTE GROWTH OF *T. COMPLANATA* - *V. INCURVA* - *V. SINTENISII*

FIGURE 16. RELATIVE GROWTH OF T. COMPLANATA

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. No data were collected in December 1984.

The # of leaves = 554.

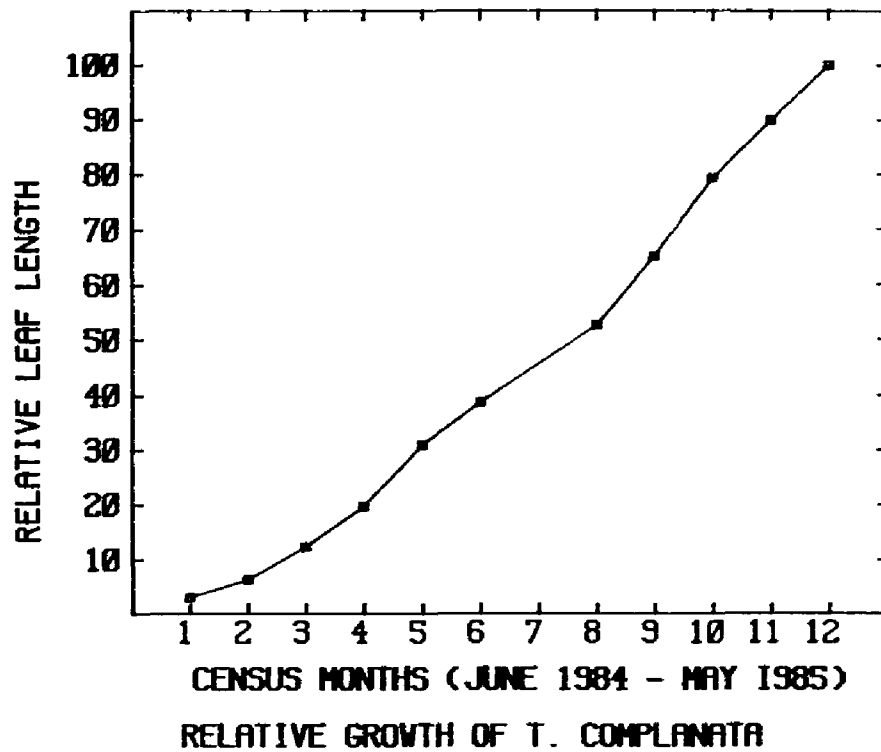


FIGURE 17. RELATIVE GROWTH OF T. COMPLANATA ADULTS

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 172.

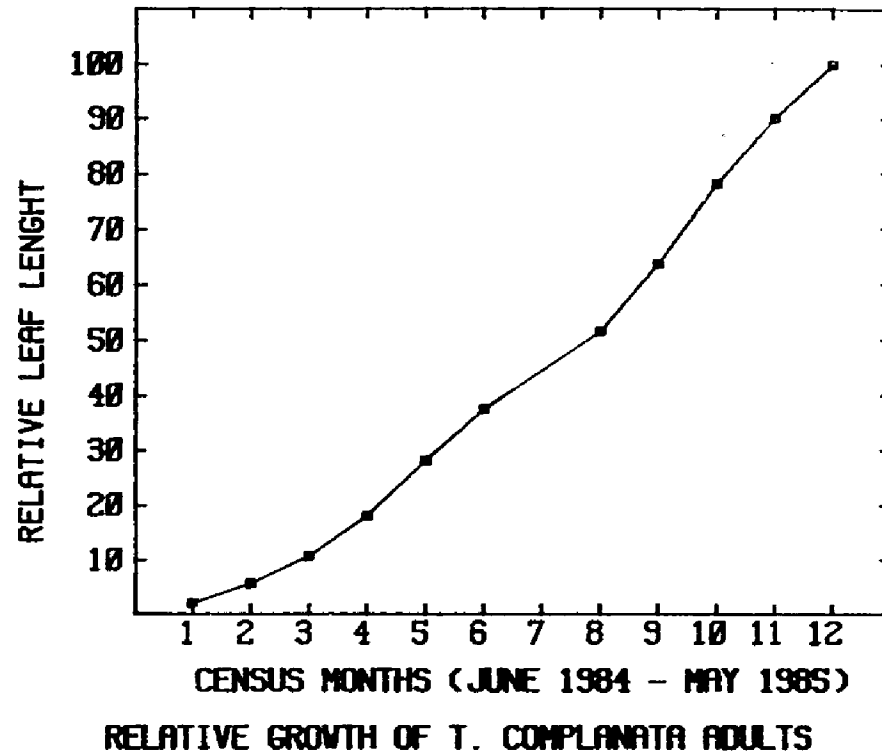


FIGURE 18. RELATIVE GROWTH OF T. COMPLANATA SMALL ADULTS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 49.

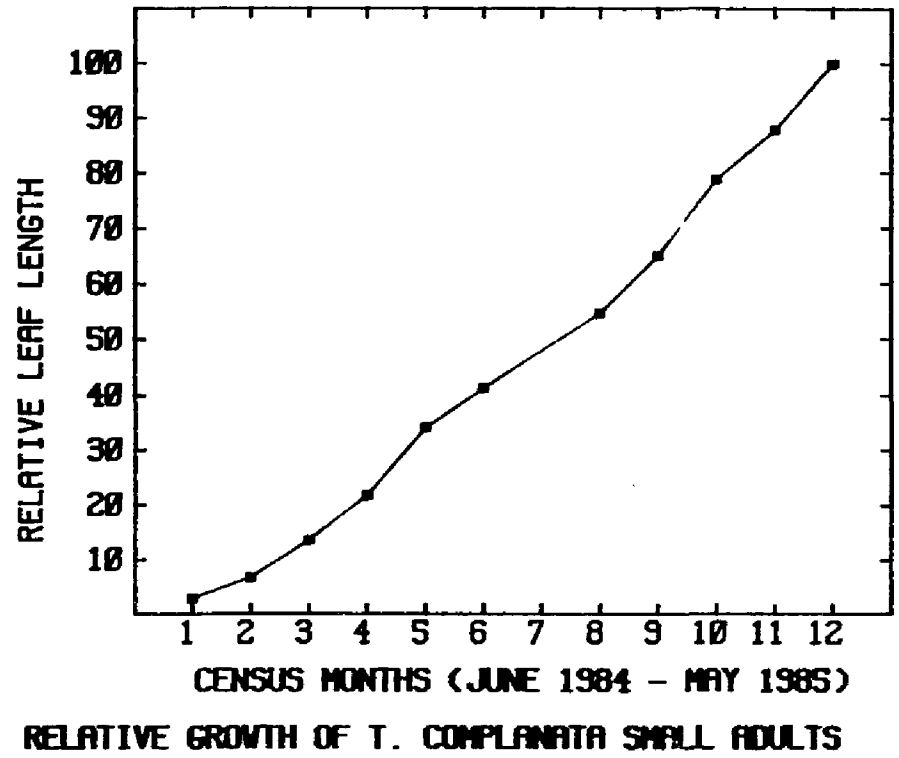
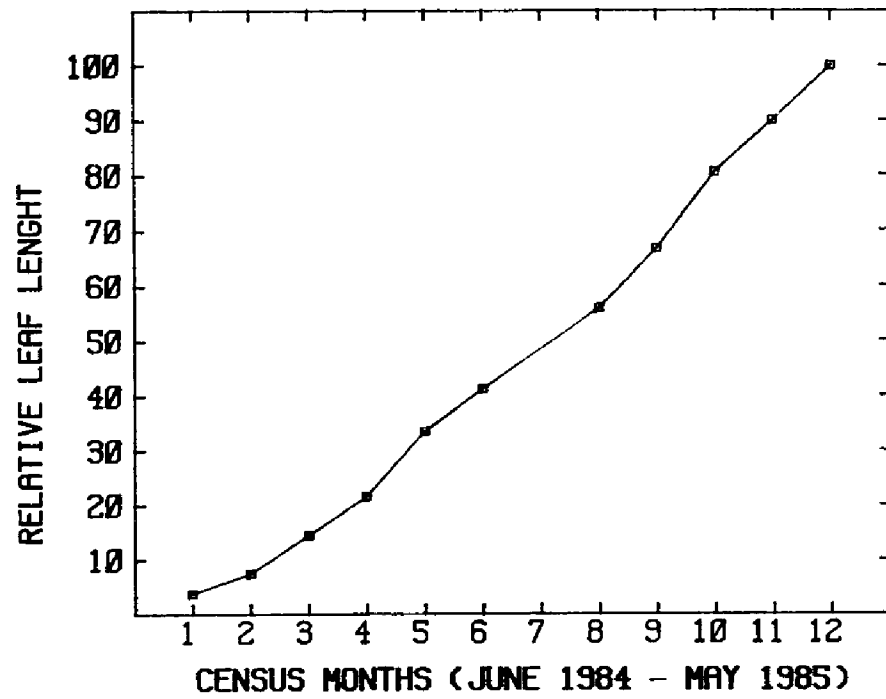


FIGURE 19. RELATIVE GROWTH OF T. COMPLANATA SEEDLINGS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 71.



RELATIVE GROWTH OF *T. COMPLANATA* SEEDLINGS

FIGURE 20. RELATIVE GROWTH OF T. COMPLANATA SMALL SEEDLINGS

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 192.

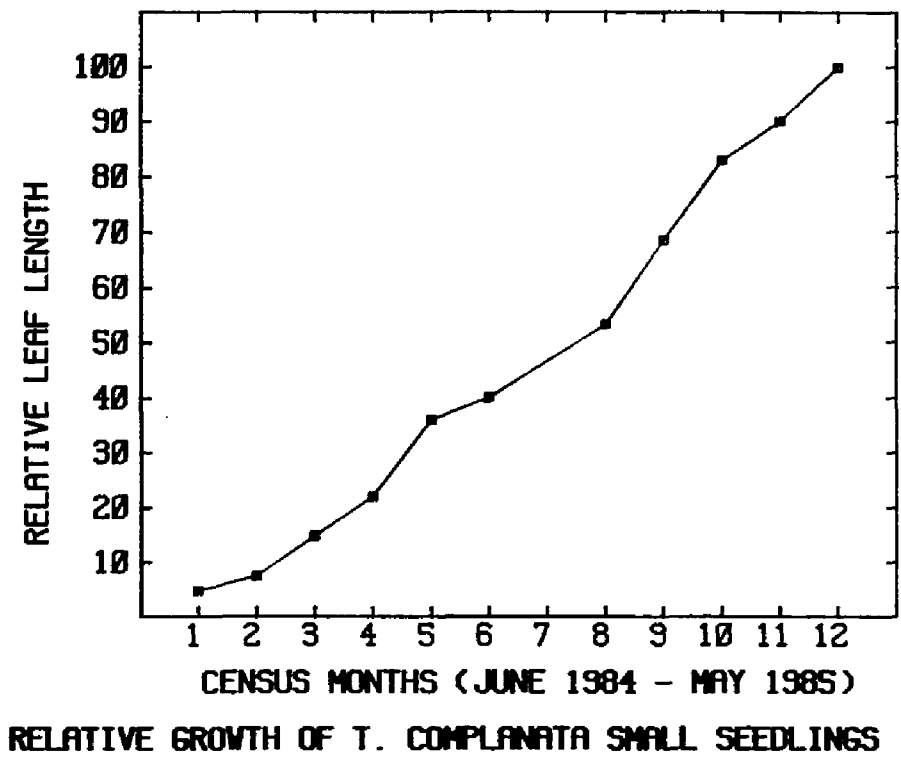


FIGURE 21. RELATIVE GROWTH OF T. COMPLANATA TINY SEEDLINGS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 70.

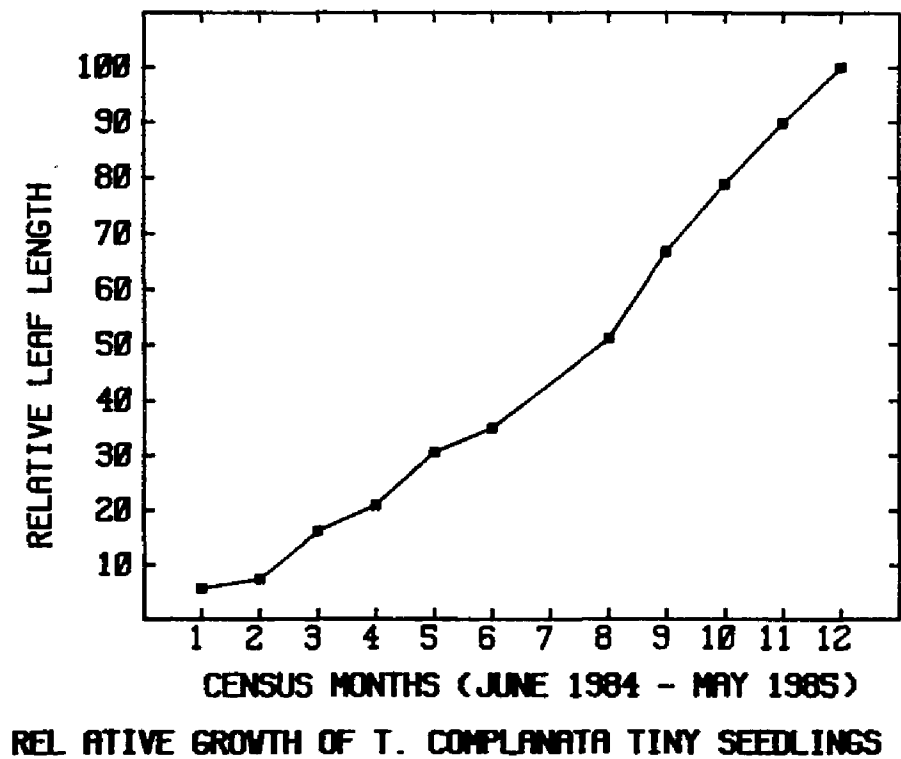


FIGURE 22. RELATIVE GROWTH OF V. INCURVA.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 287.

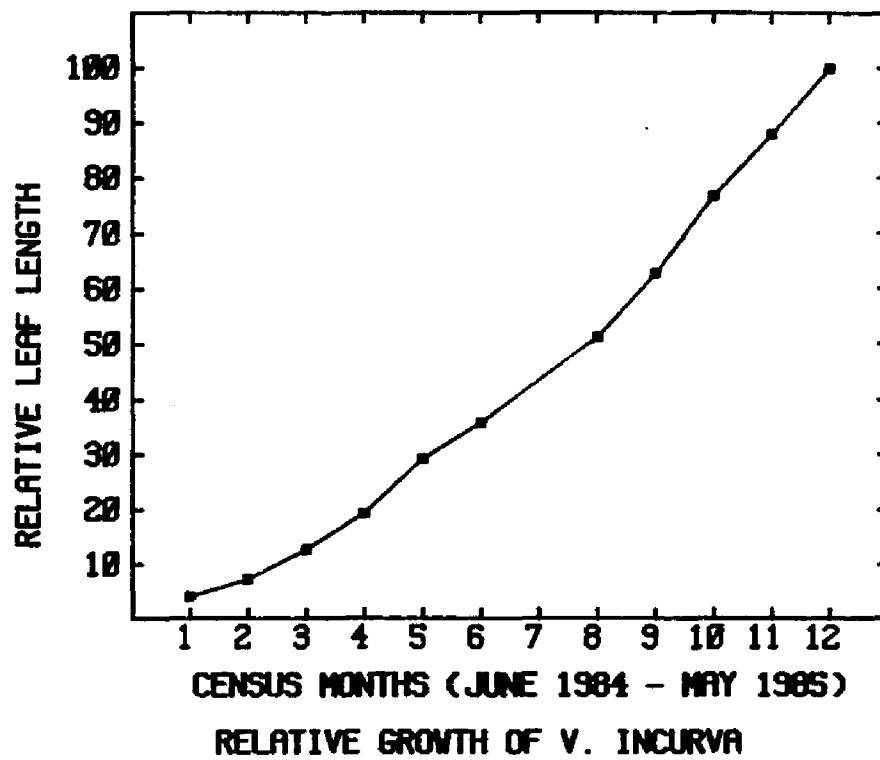


FIGURE 23. RELATIVE GROWTH OF V. INCURVA ADULTS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 34.

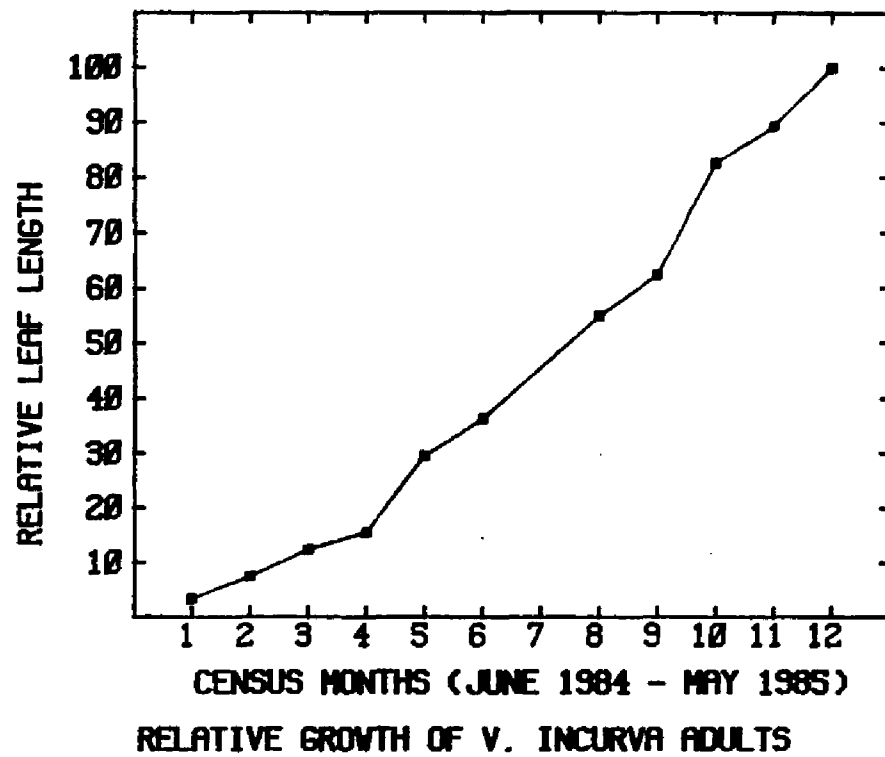


FIGURE 24. RELATIVE GROWTH OF V. INCURVA SEEDLINGS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 65.

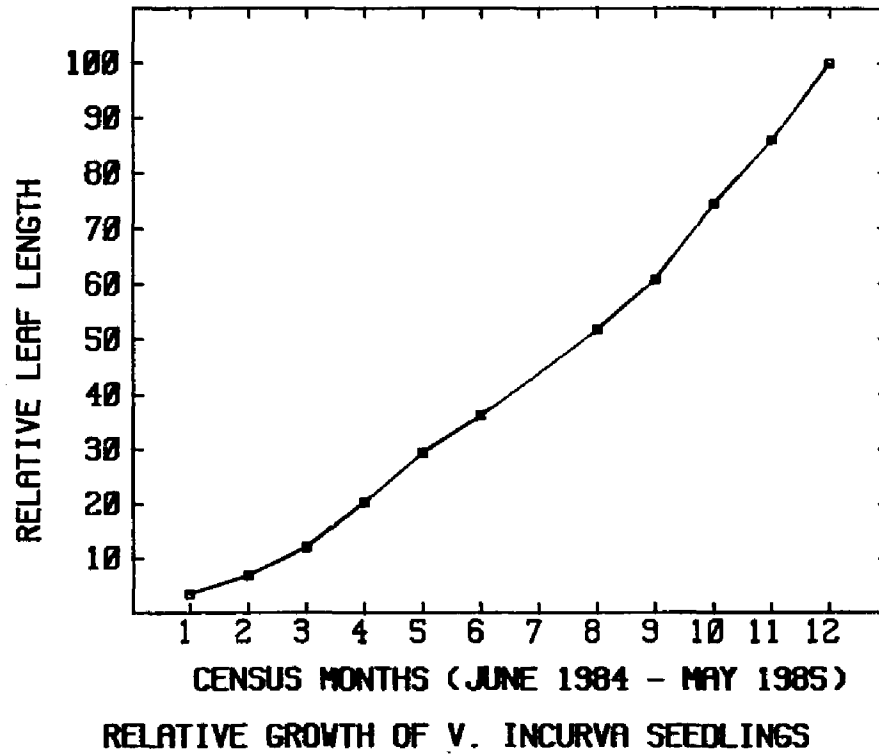


FIGURE 25. RELATIVE GROWTH OF V. INCURVA SMALL SEEDLINGS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 144.

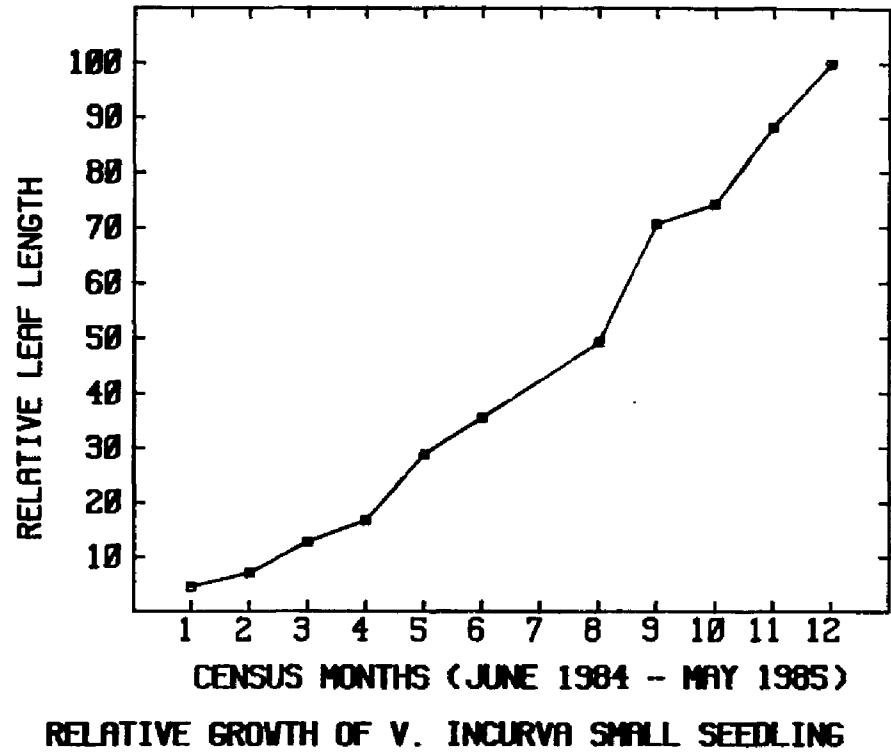
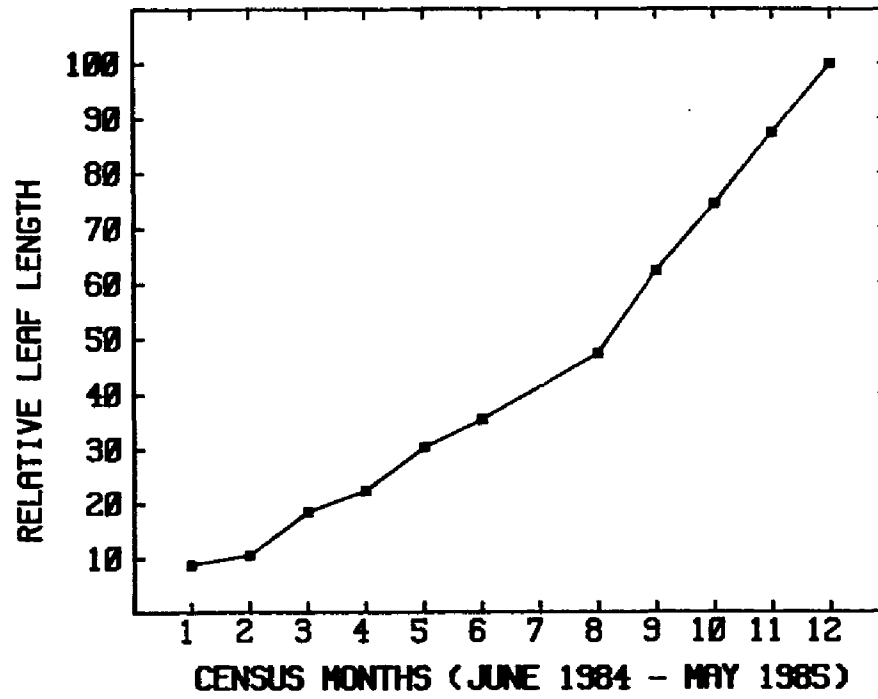


FIGURE 26. RELATIVE GROWTH OF V. INCURVA TINY SEEDLINGS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 44.



RELATIVE GROWTH OF *V. INCURVA* TINY SEEDLINGS

FIGURE 27. RELATIVE GROWTH OF V. SINTENISII.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 1178.

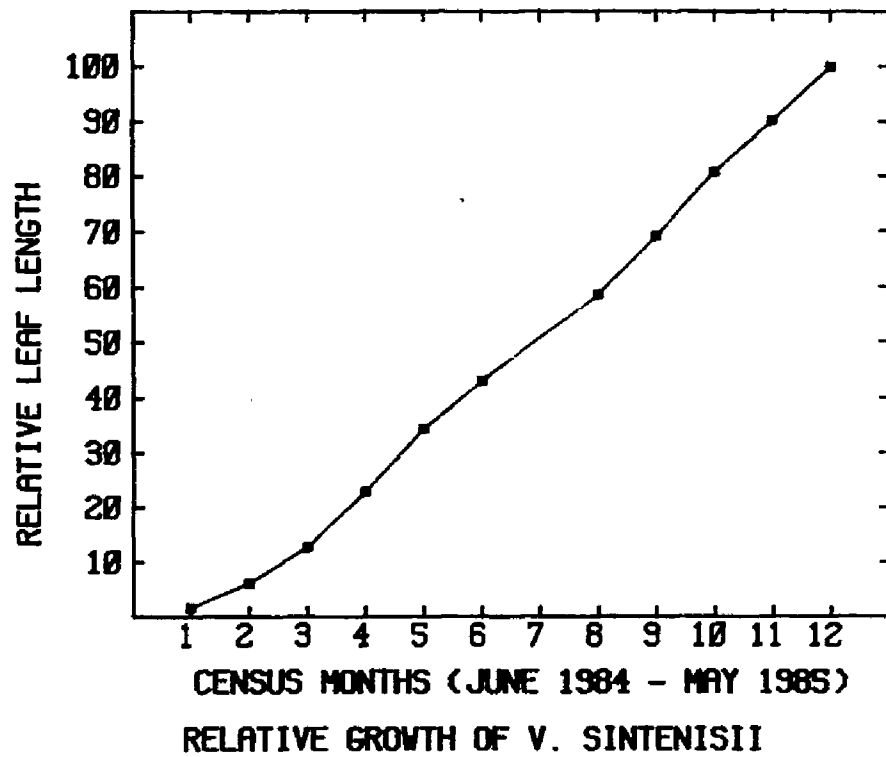


FIGURE 28. RELATIVE GROWTH OF V. SINTENISII ADULTS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 513.

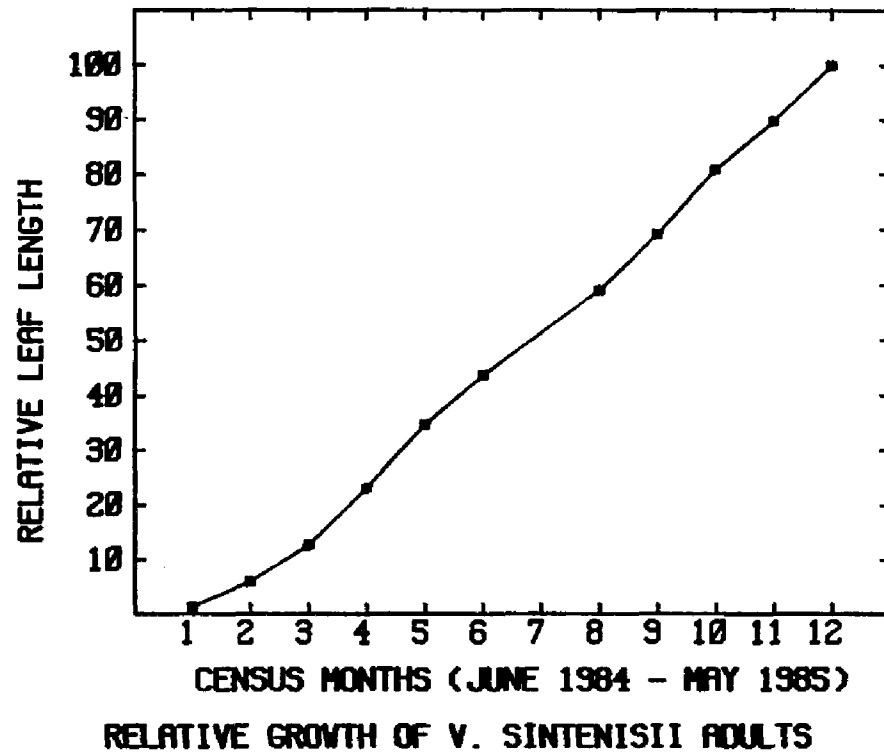
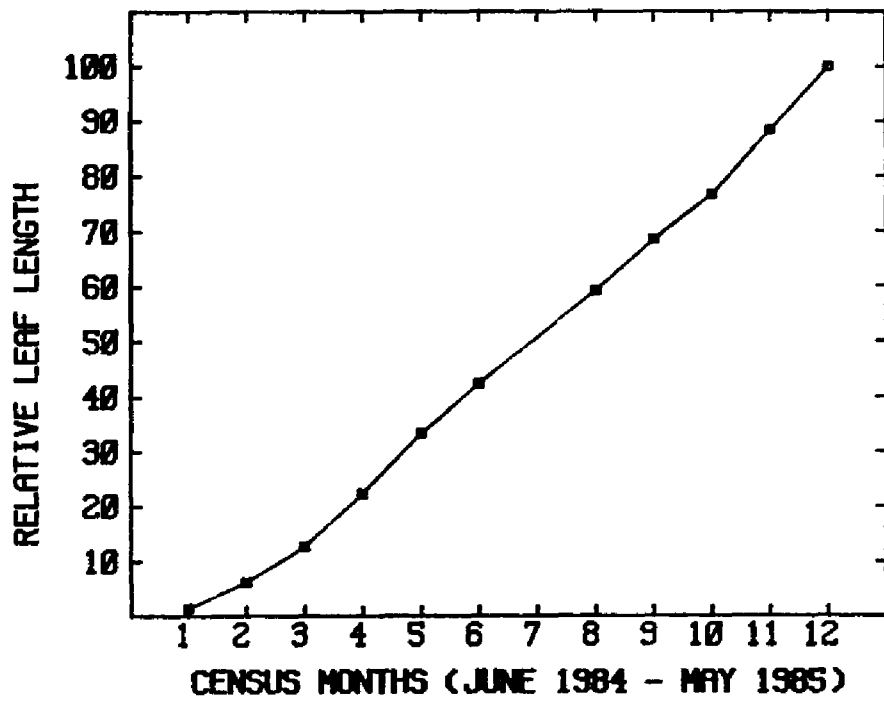


FIGURE 29. RELATIVE GROWTH OF V. SINTENISII SMALL ADULTS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 126.



RELATIVE GROWTH OF *V. SINTENISII* SMALL ADULTS

FIGURE 30. RELATIVE GROWTH OF V. SINTENISII SEEDLINGS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 245.

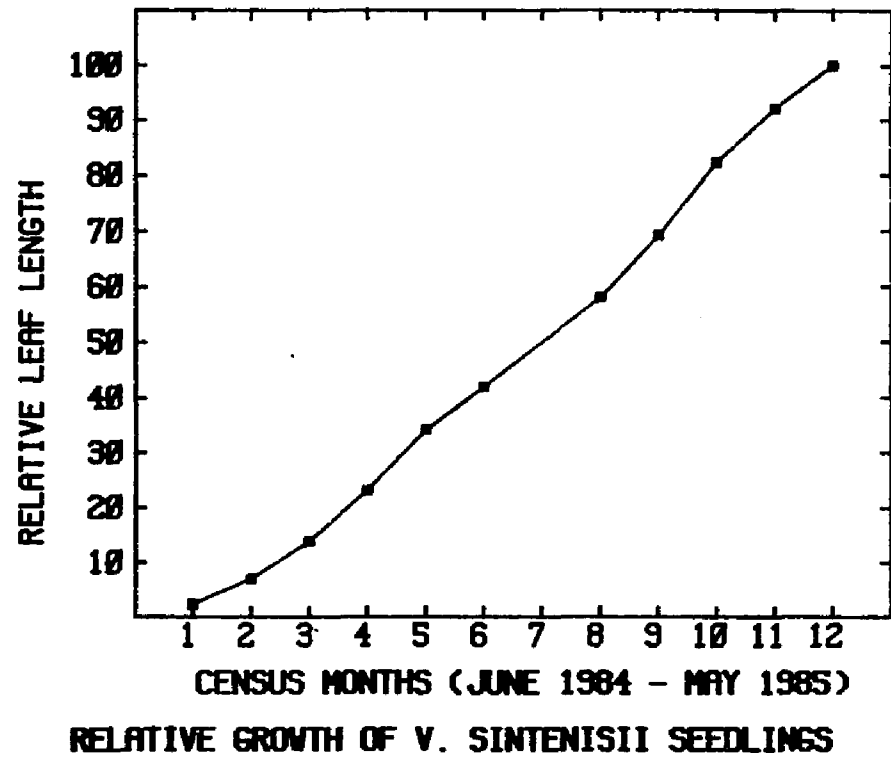


FIGURE 31. RELATIVE GROWTH OF V. SINTENISII SMALL SEEDLINGS

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 231.

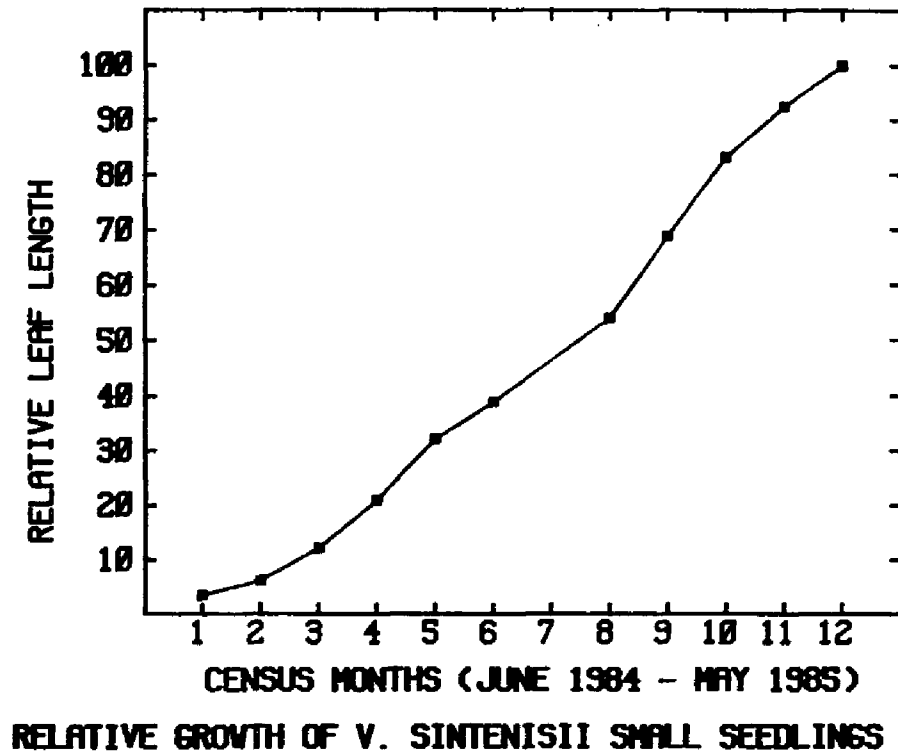
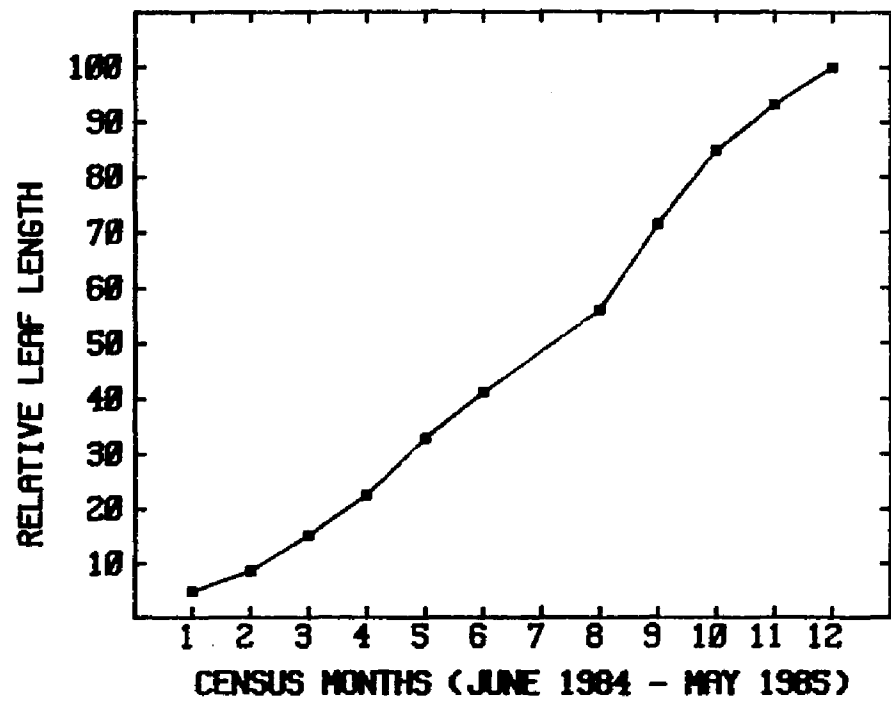


FIGURE 32. RELATIVE GROWTH OF V. SINTENISII TINY SEEDLINGS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 63.



RELATIVE GROWTH OF *V. SINTENISII* TINY SEEDLINGS

FIGURE 33. RELATIVE GROWTH OF T. COMPLANATA TRANSPLANTS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 213.

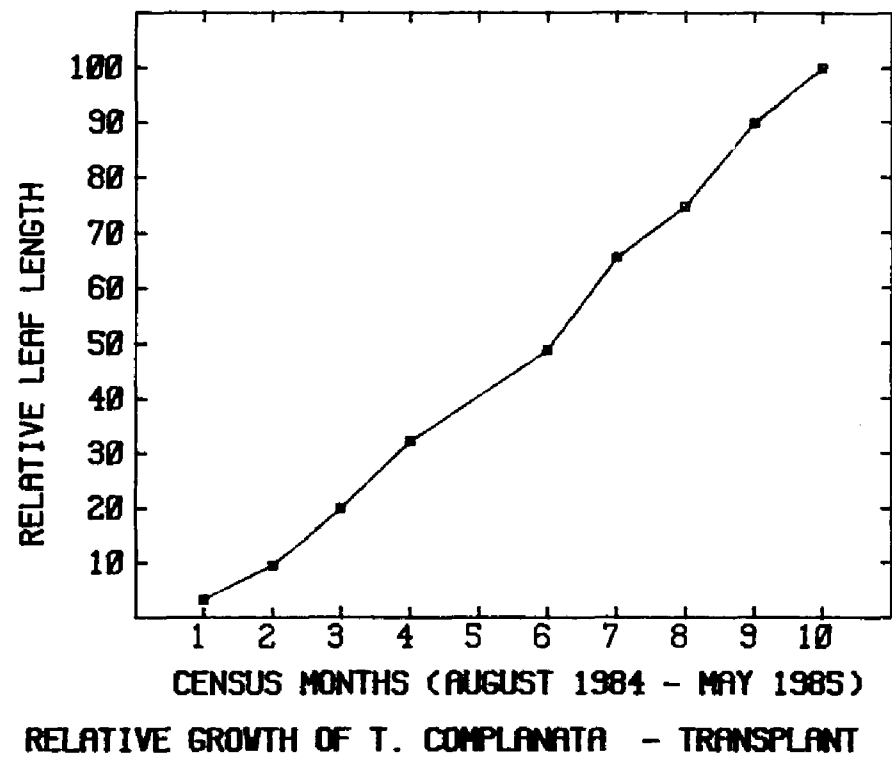
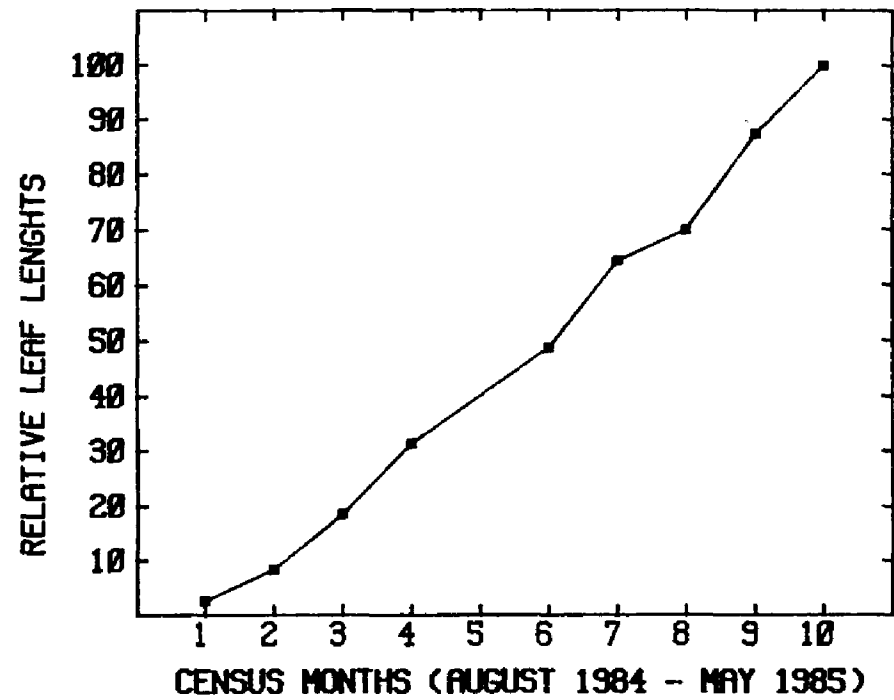


FIGURE 34. RELATIVE GROWTH OF T. COMPLANATA ADULTS -  
TRANSPLANTS.

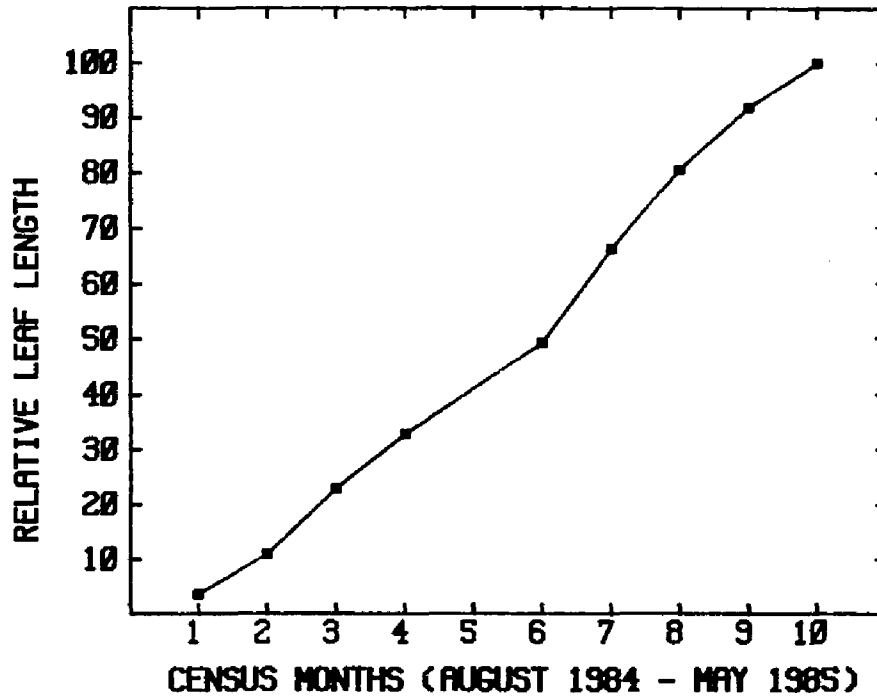
Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 74.



RELATIVE GROWTH OF *T. COMPLANATA* ADULTS - TRANSPLANT

FIGURE 35. RELATIVE GROWTH OF T. COMPLANATA SMALL ADULTS -  
TRANSPLANTS.

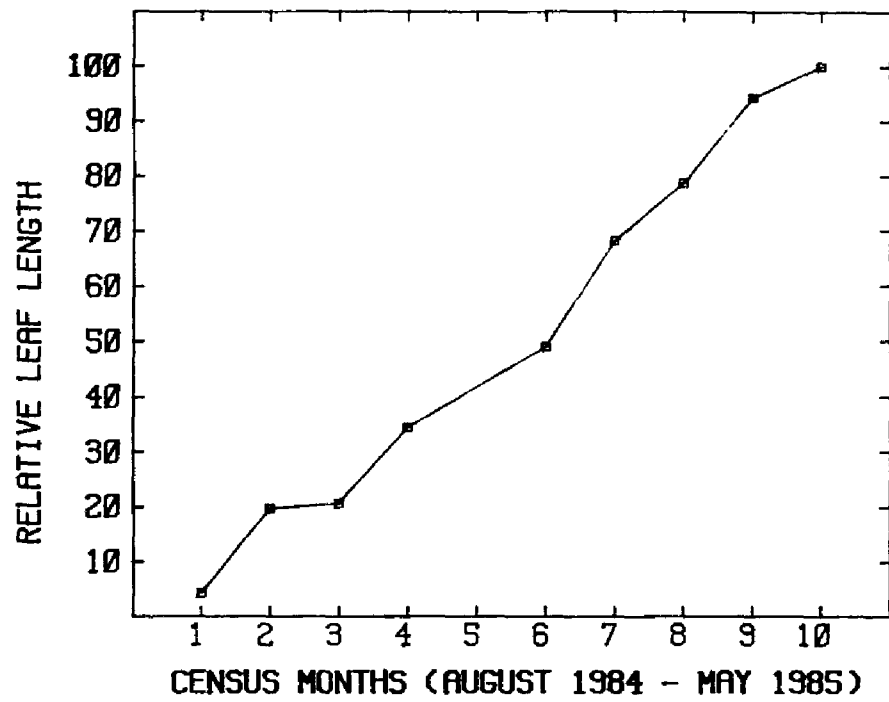
Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 51.



RELATIVE GROWTH OF *T. COMPLANATA* SMALL ADULTS - TRANSPLANT

FIGURE 36. RELATIVE GROWTH OF T. COMPLANATA SEEDLINGS -  
TRANSPLANTS.

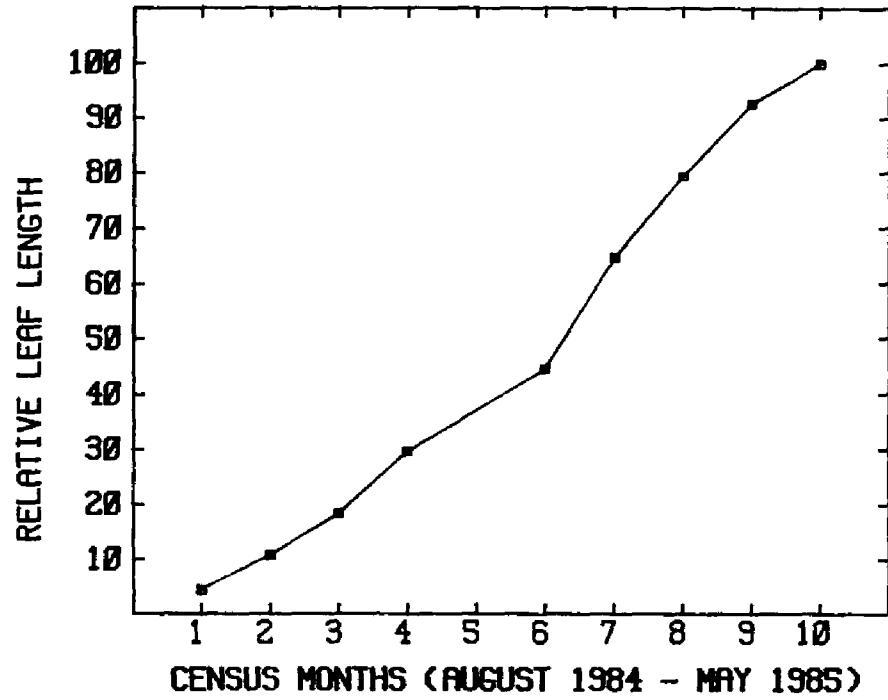
Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 43.



RELATIVE GROWTH OF *T. COMPLANATA* SEEDLINGS - TRANSPLANT

FIGURE 37. RELATIVE GROWTH OF T. COMPLANATA SMALL SEEDLINGS  
- TRANSPLANTS.

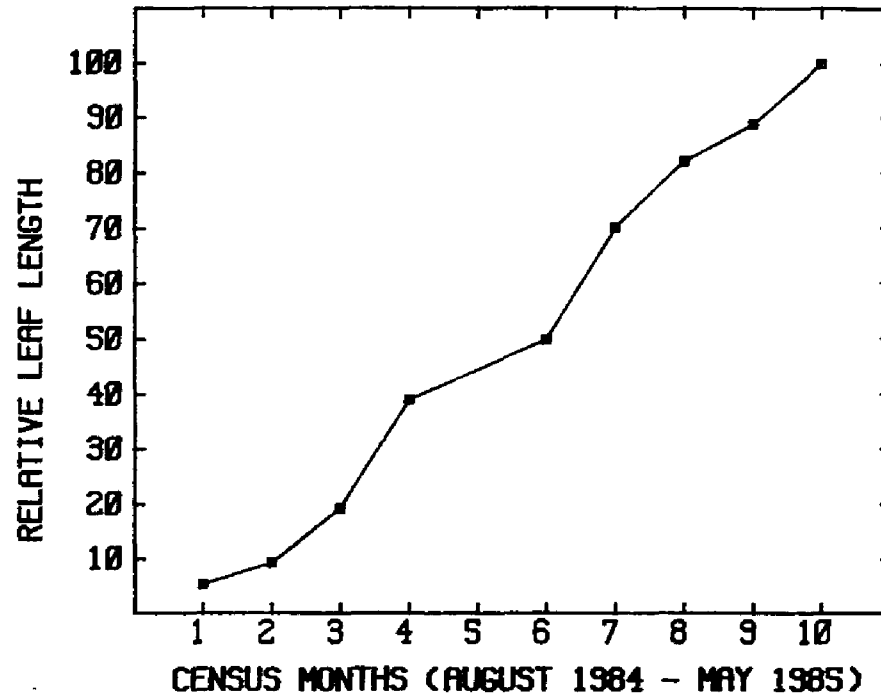
Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 29.



RELATIVE GROWTH OF *T. COMPLANATA* SMALL SEEDLINGS - TRANSPLANT

FIGURE 38. RELATIVE GROWTH OF T. COMPLANATA TINY SEEDLINGS  
- TRANSPLANTS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 16.



RELATIVE GROWTH OF *T. COMPLANATA* TINY SEEDLING - TRANSPLANT

FIGURE 39. RELATIVE GROWTH OF V. INCURVA - TRANSPLANTS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 225.

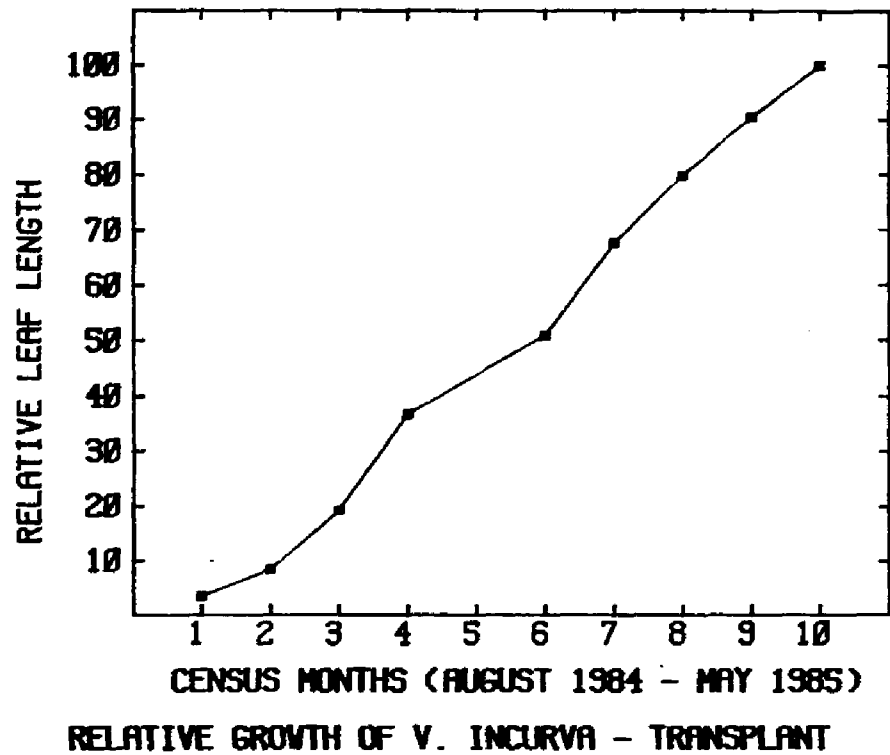


FIGURE 40. RELATIVE GROWTH OF V. INCURVA ADULTS -  
TRANSPLANTS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 56.

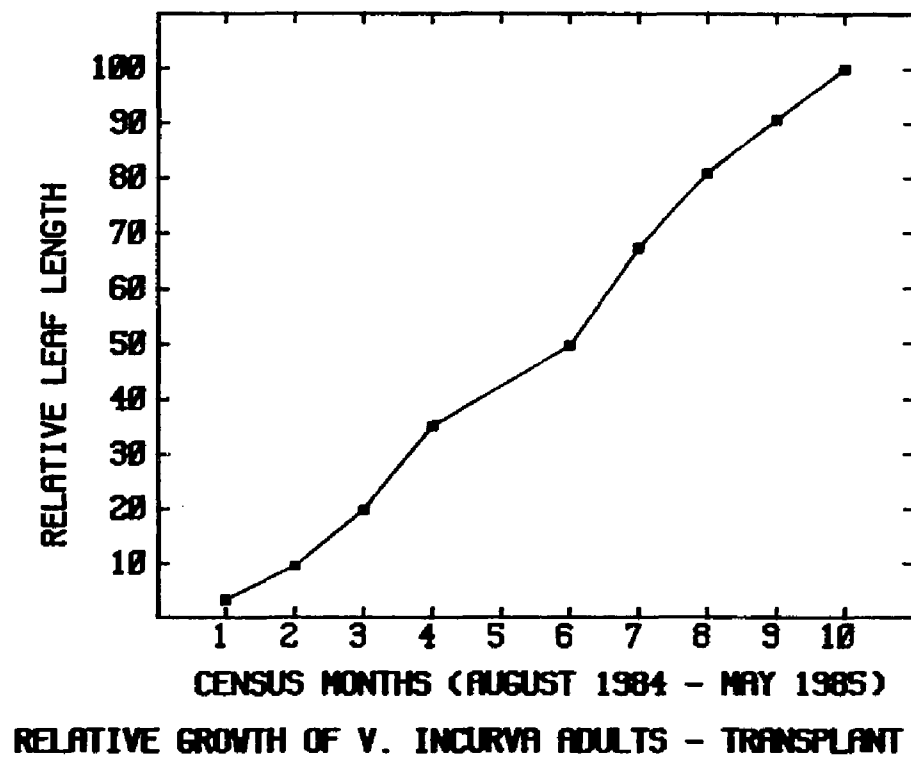
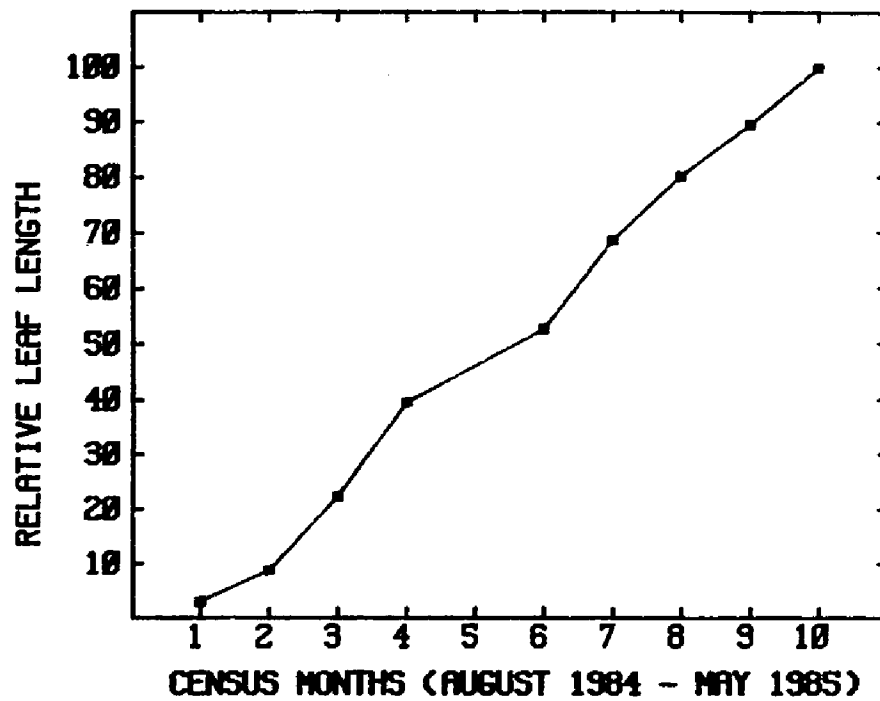


FIGURE 41. RELATIVE GROWTH OF V. INCURVA SMALL ADULTS -  
TRANSPLANTS.

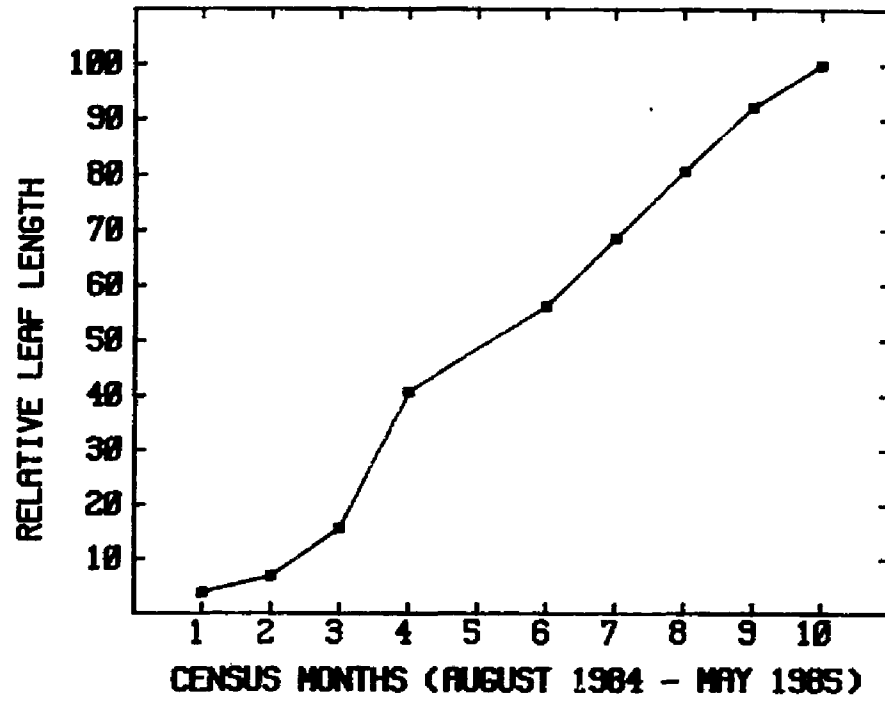
Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 59.



RELATIVE GROWTH OF *V. INCURVA* SMALL ADULTS - TRANSPLANT

FIGURE 42. RELATIVE GROWTH OF V. INCURVA SEEDLINGS -  
TRANSPLANTS.

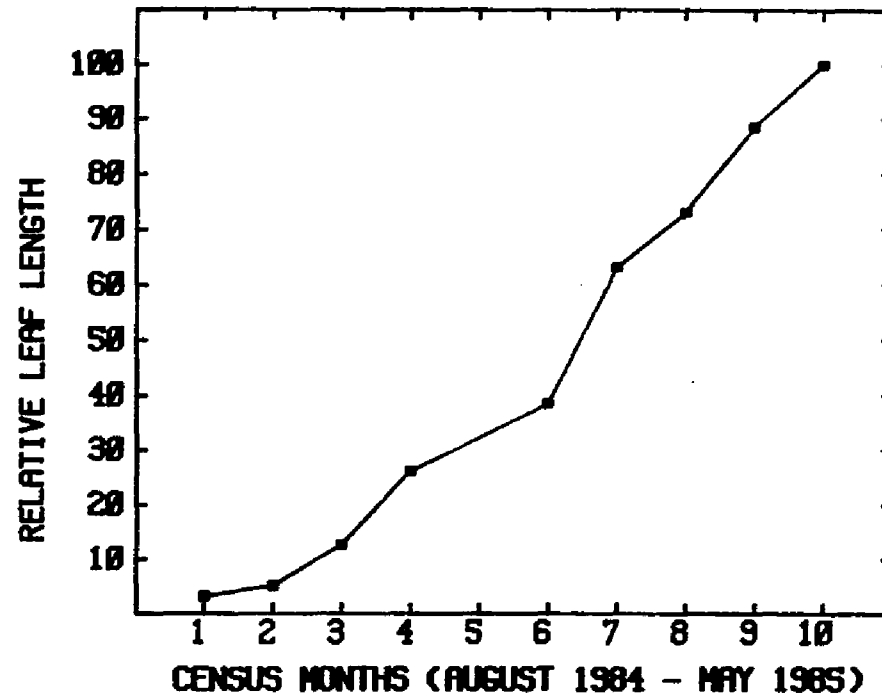
Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 45.



RELATIVE GROWTH OF *V. INCURVA* SEEDLINGS - TRANSPLANT

FIGURE 43. RELATIVE GROWTH OF V. INCURVA SMALL SEEDLINGS -  
TRANSPLANTS.

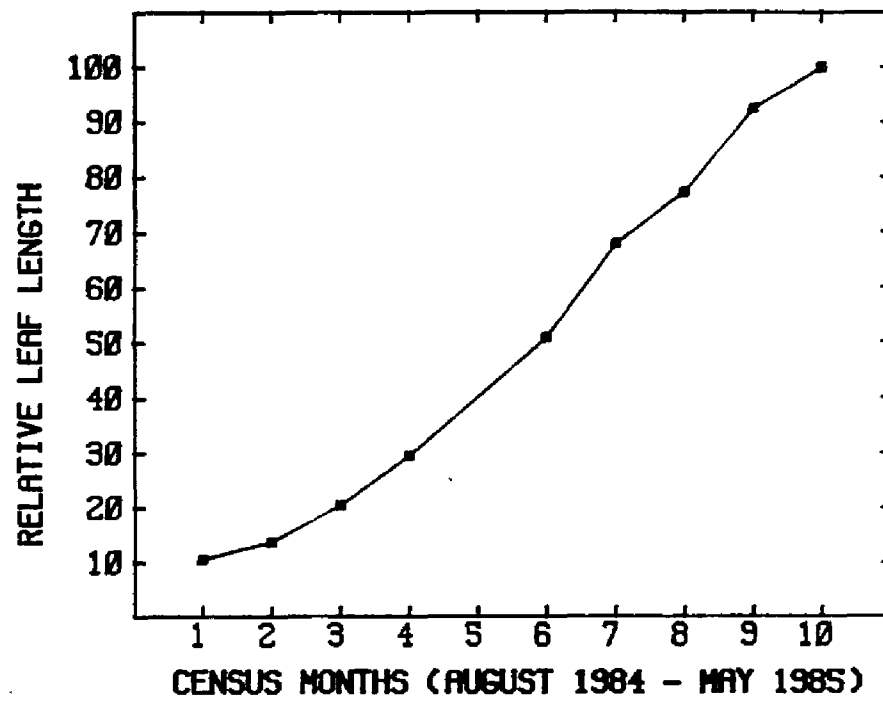
Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 43.



RELATIVE GROWTH OF *V. INCURVA* SMALL SEEDLINGS - TRANSPLANT

FIGURE 44. RELATIVE GROWTH OF V. INCURVA TINY SEEDLINGS -  
TRANSPLANTS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 22.



RELATIVE GROWTH OF *V. INCURVA* TINY SEEDLINGS - TRANSPLANT

FIGURE 45. RELATIVE GROWTH OF V. SINTENISII - TRANSPLANTS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 313.

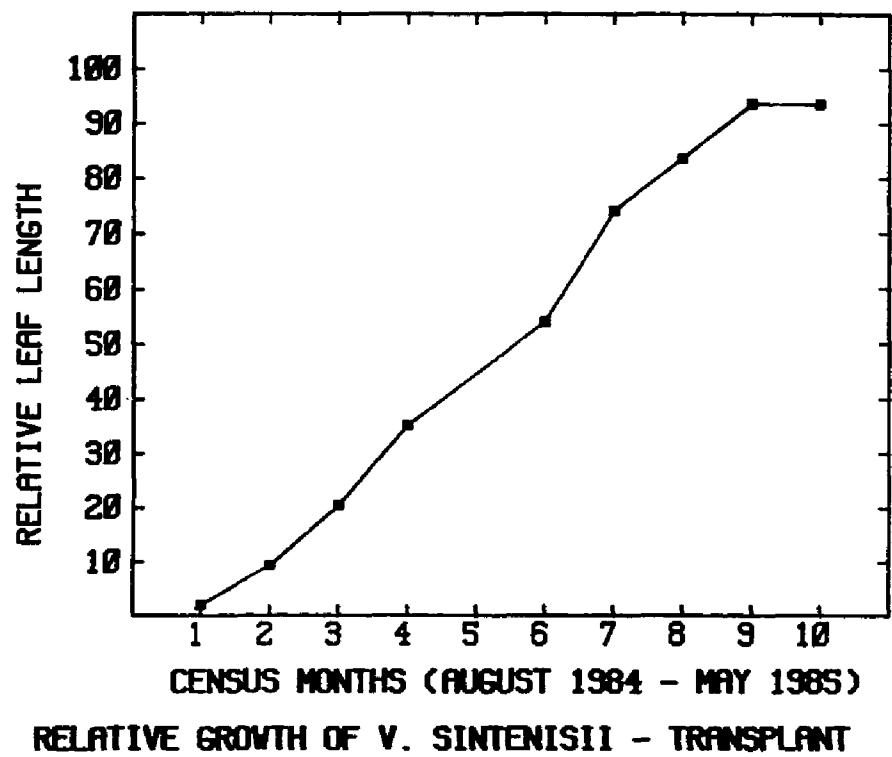
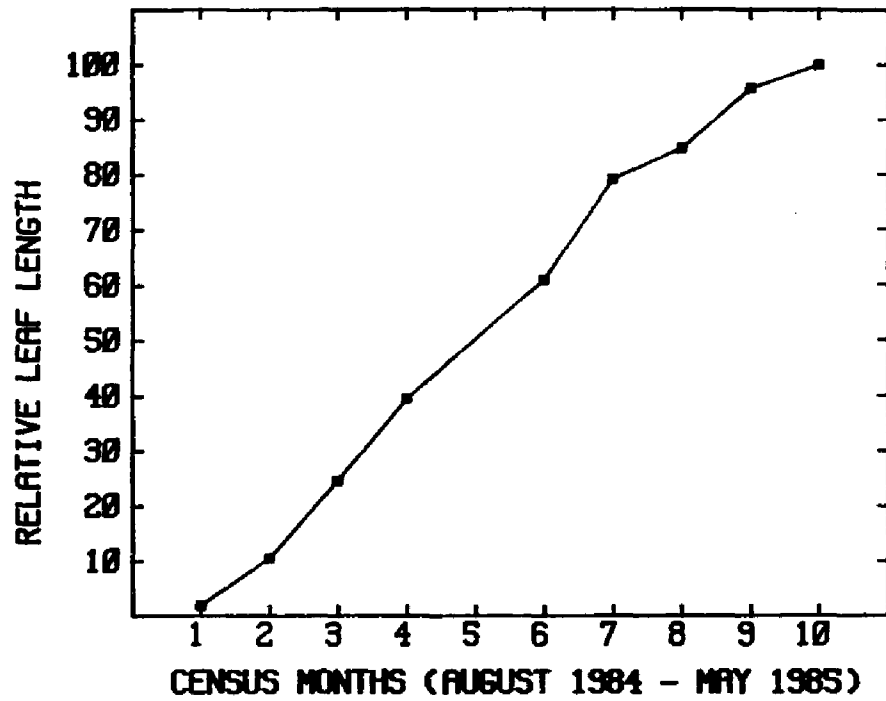


FIGURE 46. RELATIVE GROWTH OF V. SINTENISII ADULTS -  
TRANSPLANTS.

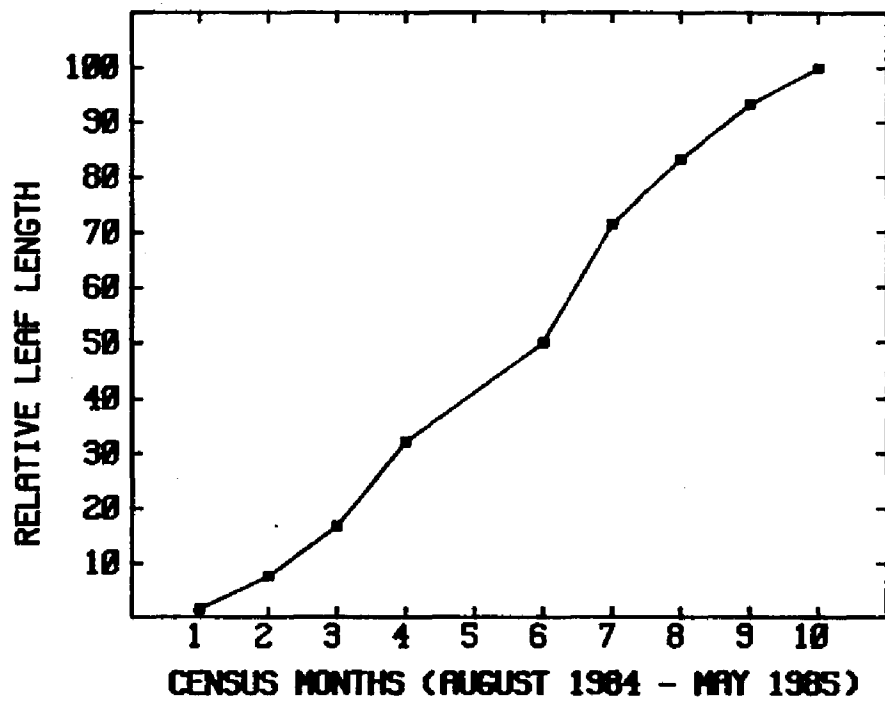
Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 85.



RELATIVE GROWTH OF *V. SINTENISII* ADULTS - TRANSPLANT

FIGURE 47. RELATIVE GROWTH OF V. SINTENISII SMALL ADULTS -  
TRANSPLANTS.

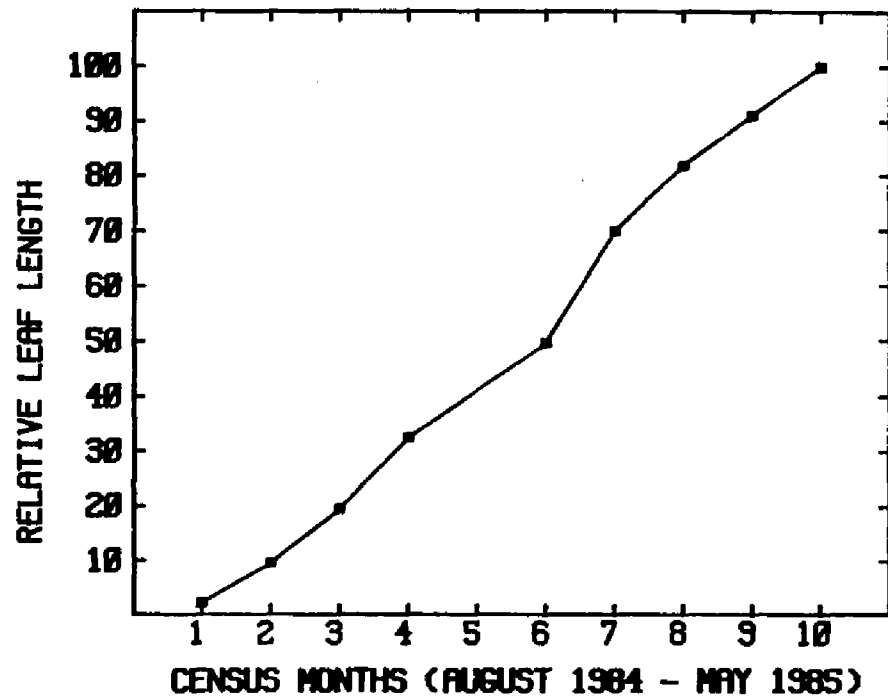
Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 93.



RELATIVE GROWTH OF *V. SINTENISII* SMALL ADULTS - TRANSPLANT

FIGURE 48. RELATIVE GROWTH OF V. SINTENISII SEEDLINGS -  
TRANSPLANTS.

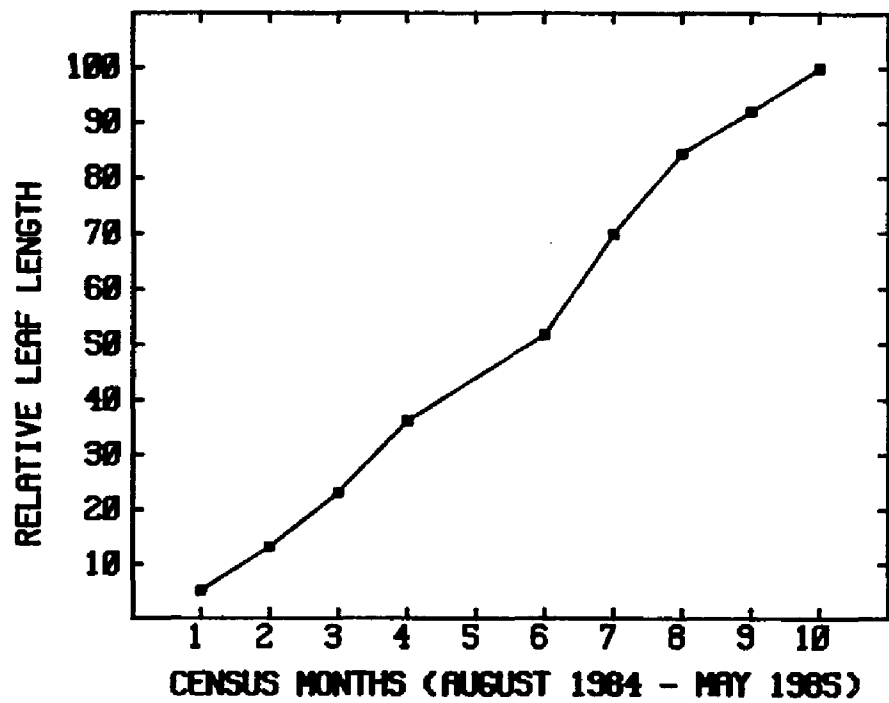
Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 72.



RELATIVE GROWTH OF *V. SINTENISII* SEEDLINGS - TRANSPLANT

FIGURE 49. RELATIVE GROWTH OF V. SINTENISII SMALL SEEDLINGS  
- TRANSPLANTS.

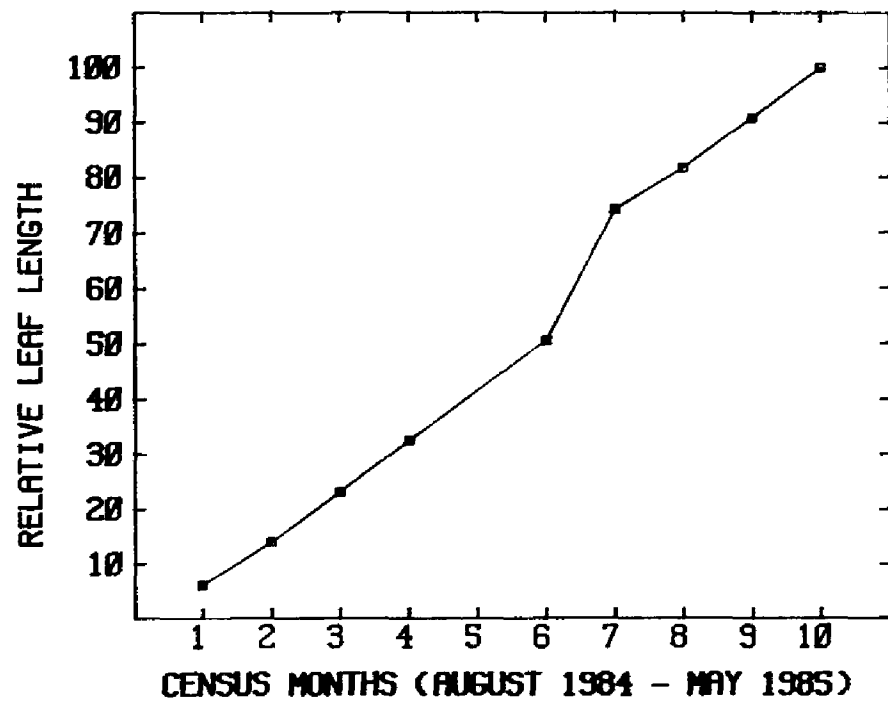
Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985. The # of leaves = 38.



RELATIVE GROWTH OF *V. SINTENISII* SMALL SEEDLINGS - TRANSPLANT

FIGURE 50. RELATIVE GROWTH OF V. SINTENISII TINY SEEDLINGS  
- TRANSPLANTS.

Relative growth = percent of total leaf growth achieved at any period of time. The relative leaf length was derived by dividing the summed leaf lengths for each month by the summed leaf length of the final month on the census. The tic marks along the x-axis are the census months June 1984 - May 1985.  
The # of leaves = 25.



RELATIVE GROWTH OF *V. SINTENISII* TINY SEEDLINGS - TRANSPLANT

LITERATURE CITED

- Adams, C. D. 1972. Flowering plants of Jamaica. University of The West Indies. Mona, Jamaica.
- Adams, W. W., and C. E. Martin. 1986. Morphological changes accompanying the transition from juvenile (atmospheric) to adult (tank) forms in the Mexican epiphyte Tillandsia deppeana (Bromeliaceae). Amer. J. Bot. 73: 1207-1214.
- Asprey, G. F., and R. G. Robbins. 1953. The vegetation of Jamaica. Ecological Monographs 23: 359-412.
- Barkman, J. J. 1958. Phytosociology and ecology of cryptogamic epiphytes. Van Gorcum and Co. Assen.
- Benzing D. H. 1970. Foliar permeability and absorption of minerals and organic nitrogen by certain tank bromeliads. Bot. Gaz. 131(1): 23-31.
- \_\_\_\_\_ 1973. The Monocotyledons: their evolution and comparative biology I. Mineral nutrition and related phenomena in the Bromeliaceae and Orchidaceae. Quart. Rev. Biol. 48: 277-290.
- \_\_\_\_\_ 1976. Bromeliad trichomes: structure, function, and ecological significance. Selbyana 1: 330-348.
- \_\_\_\_\_ 1978a. The life history profile of Tillandsia circinnata (Bromeliaceae) and the rarity of extreme epiphytism among the angiosperms. Selbyana 2: 325-337.
- \_\_\_\_\_ 1978b. Germination and early establishment of Tillandsia circinnata Schlecht. (Bromeliaceae) on some of its hosts and other supports in southern Florida. Selbyana 5: 95-106.
- \_\_\_\_\_ 1981. The population dynamics of Tillandsia circinnata (Bromeliaceae): Cypress crown colonies in southern Florida. Selbyana 5(3-4): 256-263.
- \_\_\_\_\_ and K. M. Burt. 1970. Foliar permeability among twenty species of Bromeliaceae. Bull. Torrey Bot. Club 97: 269-279.
- \_\_\_\_\_ and E. Davidson. 1979. Oligotrophic Tillandsia circinnata Schlecht. (Bromeliaceae): an assessment of its patterns of mineral allocation and reproduction. Amer. J. Bot. 66:386-397.

\_\_\_\_\_ and A. Renfrow. 1971. The biology of the epiphytic bromeliad Tillandsia circinnata Schlecht. I. The nutrient status of populations in south Florida. Amer. J. Bot. 58(9): 867-873.

\_\_\_\_\_ and \_\_\_\_\_ 1980. The nutritional dynamics of Tillandsia circinnata in southern Florida and the origin of the "air plant" strategy. Bot. Gaz. 141: 165-172.

\_\_\_\_\_, K. Henderson, B. Kessel and J. Sulak. 1976. The absorptive capacities of bromeliad trichomes. Amer. J. Bot. 63(7): 1009-1014.

Cook, R. E. 1979. Patterns of juvenile mortality and recruitment in plants. In O. T. Solbrig, S. Jain, G. B. Johnson and P. H. Raven, (eds.), Topics in plant population biology. Columbia University Press, New York.

Downs, W. G. and C. S. Pittendrigh. 1946. Bromeliad malaria in Trinidad, British West Indies. Amer. J. Tropical Medicine 26: 47-66.

Du Rietz, G. E. 1945. Om fattiggark- och rikbarksamhallen. Svensk Bot. Tidskr. 39: 147-150.

Eaton, T. S., G. E. Likens, and F. H. Borman. 1973. Throughfall and stem flow chemistry in a northern hardwood forest. J. Ecol. 61:495-508.

Fish, D. 1976. Structure and composition of the aquatic invertebrate community inhabiting epiphytic bromeliads in south Florida and the discovery of an insectivorous bromeliad. Ph.D. Thesis, University of Florida, Gainesville.

Frank, J. H. and G. A. Curtis. 1977a. On the bionomics of bromeliad-inhabiting mosquitoes. III. The probable strategy of larval feeding in Wyeomyia vanduzeei and Wy. medioalbipes. Mosquito News 37: 200-206.

\_\_\_\_\_ and \_\_\_\_\_ 1977b. On the bionomics of bromeliad-inhabiting mosquitoes. IV. Egg mortality of Wyeomyia vanduzeei caused by rainfall. Mosquito News 37: 239-245.

Gilmartin, A. J. 1973. Trans-Andean distribution of Bromeliads in Ecuador. Ecology 54: 1389-1393.

Grubb, P. J., J. R. Lloyd, T. D. Pennington and T. C. Whitmore. 1963. A comparison of montane and lowland rain forest in Ecuador, I. The forest structure, physiognomy and floristics. J. Ecol. 51: 567-601.

- \_\_\_\_\_ and E. V. J. Tanner. 1976. The montane forests and soils of Jamaica: A reassessment. *J. Arnold Arboretum* 57(3):313-368.
- \_\_\_\_\_ and T. C. Whitmore. 1966. A comparison of montane and lowland rain forest in Ecuador, II. The climate and its effects on the distribution and physiognomy of the forests. *J. Ecol.* 54: 303-333.
- Harberd, D. 1961. Observations on population structure and longevity of Festuca rubra L. *New Phytol.* 60: 184-206.
- Harper, J. L. 1977. Population biology of plants. Academic Pres. London.
- \_\_\_\_\_ and J. White. 1974. The demography of plants. *Ann. Rev. Ecol. Syst.* 5: 419-463.
- Holtum, R. E. 1960. The ecology of tropical epiphytic orchids. *Proc. Third World Orch. Conference.* London.
- Hosokawa, T. 1943. Studies on the life-forms of vascular epiphytes and the epiphyte flora of Ponape, Micronesia. *Trans. Nat. Hist. Soc. Taiwan* 33: 35-55, 71-89, 113-141.
- \_\_\_\_\_ 1952. A plant-sociological study in the mossy forests of Micronesian islands. *Mem. Fac. Sci. Kyushu Univ. E* (1): 65-82.
- Johansson, D. 1974. Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeographica Suecica* 59: 1-129.
- Laessle, A. M. 1961. A micro-limnological study of Jamaican bromeliads. *Ecology* 42: 499-517.
- Lieske, R. 1914. Die Heterophyllie epiphytischer, rosettenbildender Bromeliaceen. *Jb. wiss. Bot.* 53: 502-510.
- Likens, G. E., and T. S. Eaton. 1970. A polyurethane stem flow collector for trees and shrubs. *Ecology* 51:938-939.
- Madison, M. 1977. Vascular epiphytes: their systematic occurrence and salient features. *Selbyana* 2: 1-13.
- Mez, C. 1904. Physiologische Bromeliaceen-Studien 1. Die Wasserökonomie der extrem atmosphärischen Tillandsien. *Jb. wiss. Bot.* 40: 157-229.

Moreau, W. M., and R. E. Moreau. 1943. An introduction to the epiphytic orchids of East Africa. East Africa Nat. Hist. Soc. Nairobi.

Morris, B. 1970. The epiphytic orchids of Malawi. The Society of Malawe, Balantyre.

Oye, P. van. 1921. Influence des facteurs climatiques sur la repartition des epiphytes a la surface des troncs d'arbres a Java. Rev. Gen. Bot 33: 161-176.

\_\_\_\_\_ 1924. Sur l'ecologie des epiphytes a la surface des troncs d'arbres a Java. Ibid. 36: 1-30, 68-83.

Pessin, L. J. 1925. An ecological study of the polypody fern Polypodium polypodioides as an epiphyte in Mississippi. Ecology 6: 17-38.

Picado, C. 1913. Les Bromeliacees epiphytes, considerees comme milieu biologique. Bull. Scient. Fr. Belg. Ser. 7, 47: 215-360.

Pittendrigh, C. S. 1948. The bromeliad-Anopheles-malaria complex in Trinidad. I.- The bromeliad flora. Evolution 2: 58-89.

Proctor, G. R. 1985. Ferns of Jamaica: a guide to the pteridophytes. British Museum of Natural History. London.

Putwain, P. D., D. Machin and J. L. Harper. 1968. Studies on the dynamics of plant populations. II. Components and regulation of a natural population of Rumex acetosella L. J. Ecol. 56: 421-431.

Richards, P. W. 1952. The tropical rain forest: an ecological study. Cambridge University Press, Cambridge.

\_\_\_\_\_ 1964. The tropical rain forest. Cambridge Univ. Press, London.

Sager, G. R. and J. L. Harper. 1961. Controlled interference with natural populations of Plantago lanceolata, P. major and P. media. Weed Res. 1: 163-176.

Sanford, W. W. 1968. Distribution of epiphytic orchids in semi-deciduous tropical forest in Southern Nigeria. J. Ecol. 56: 697-705.

\_\_\_\_\_ 1969. The distribution of epiphytic orchids in Nigeria in relation to each other and to geographic location and climate, type of vegetation and tree species. Biol. J. Linn. Soc. 1: 247-285.

Schimper, A. F. W. 1888. Die epiphytische vegetation Amerikas. Bot. Mitteil. aus den Tropen No. 2, Fisher Verlag, Jena.

\_\_\_\_\_ 1903. Plant-geography upon a physiological basis (transl. by W. R. Fisher). Clarendon Press, Oxford.

Shreve, F. 1914. A montane rain forest. A contribution to the physiological plant geography of Jamaica. Publ. Carnegie Inst. 199: 1-110.

Smith, L. B. and R. J. Downs. 1974. Pitcairnioideae (Bromeliaceae). Flora Neotropica Monograph No. 14 Part 1.

\_\_\_\_\_ and \_\_\_\_\_ 1977. Tillandsioideae (Bromeliaceae). Flora Neotropica Monograph No. 14 Part 2.

\_\_\_\_\_ and \_\_\_\_\_ 1979. Bromelioideae (Bromeliaceae). Flora Neotropica Monograph No. 14 Part 3.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. 2nd ed. W. H. Freeman and Company., San Francisco.

Sugden, A. M. 1981. Aspects of the ecology of vascular epiphytes in two Colombian cloud forests, II. Habitat preferences of Bromeliaceae in the Serrania de Macuira. Selbyana 5(3-4): 264-273.

\_\_\_\_\_ and R. J. Robbins. 1979. Aspects of the ecology of vascular epiphytes in Colombian cloud forests, I. The distribution of the epiphytic flora. Biotropica 11(3): 173-188.

Tamm, C. O. 1972. Survival and flowering of perennial herbs. III. The behavior of of Primula veris on permanent polts. Oikos 23: 159-166.

Tanner, E. V. J. 1977a. Mineral cycling in montane rain forests of Jamaica. Ph.D. Dissertation, University of Cambridge.

\_\_\_\_\_ 1977b. Four montane rain forests in Jamaica: A quantitative characterization of the floristics, the soils and the foliar mineral levels,

and a discussion of the interrelations. J. Ecol. 65: 883-918.

\_\_\_\_\_ 1980a. Studies on the biomass and productivity in a series of montane rain forests in Jamaica. J. Ecol 68: 573-588.

\_\_\_\_\_ 1980b. Litterfall in montane rain forests of Jamaica and its relation to climate. J. Ecol. 68: 833-848.

\_\_\_\_\_ 1981. The decomposition of leaf litter in Jamaican montane rain forests. J. Ecol. 69: 263-275.

\_\_\_\_\_ 1982. Species diversity and reproductive mechanisms in Jamaican trees. Biol. J. Linn. Soc. 18: 263-278.

\_\_\_\_\_ 1983. Leaf demography and growth of the tree-fern Cyathea pubescens Mett. ex Kuhn in Jamaica. Biol. J. Linn. Soc. 87: 213-227.

\_\_\_\_\_ and V. Kapos. 1982. Leaf structure of Jamaican upper montane rain-forest trees. Biotropica 14(1): 16-24.

Thomas, A. G. and H. M. Dale. 1975. The role of seed reproduction in the dynamics of established populations of Hieracium floribundum and a comparison with that of vegetative reproduction. Canad. J. Bot. 53: 3022-3031.

Tietze, M. 1906. Physiologische Bromeliaceen Studien II. Die Entwicklung der Wasseraunehmunden Bromeliaceen Trichome. Z. Naturwiss. 78: 1-49.

Vogel, S. 1970. Convective cooling at low airspeeds and the shapes of broad leaves. J. Exp. Bot. 21(66): 91-101.

Voth, P. H. 1939. Conduction of rainfall by plant stem in a tropical rain forest. Bot. Gaz. 101: 328-340.

Vrizo de Santo A. A., A. Alfani and P. de Lucia. 1976. Water vapour uptake from the atmosphere by some Tillandsia species. Ann. Bot. (London) 40: 391-394.

Went, F. W. 1931. Over de sociologie der Epiphyten. Handel. 6 Ned. Ind. Nautrw. Congr.: 381-387. Bandoeng.

\_\_\_\_\_ 1940. Soziologie der Epiphyten eines tropischen Urwaldes. Ann. Jard. Bot. Buitenz. 50: 1-98.

Werner, P. A. 1979. Competition and coexistence of similar species. In O. T. Solbrig, S. Jain, G. B. Johnson and P. H. Raven, (eds.), Topics in plant population biology. Columbia University Press, New York.

Yarranton, G. A. 1967. An instrument for measuring the microrelief of bark. Can. J. Bot. 45 (8): 1173-1178.