

INFORMATION TO USERS

This material was produced from a microfilm copy of the original document. While the most advanced technological means to photograph and reproduce this document have been used, the quality is heavily dependent upon the quality of the original submitted.

The following explanation of techniques is provided to help you understand markings or patterns which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting thru an image and duplicating adjacent pages to insure you complete continuity.
2. When an image on the film is obliterated with a large round black mark, it is an indication that the photographer suspected that the copy may have moved during exposure and thus cause a blurred image. You will find a good image of the page in the adjacent frame.
3. When a map, drawing or chart, etc., was part of the material being photographed the photographer followed a definite method in "sectioning" the material. It is customary to begin photoing at the upper left hand corner of a large sheet and to continue photoing from left to right in equal sections with a small overlap. If necessary, sectioning is continued again — beginning below the first row and continuing on until complete.
4. The majority of users indicate that the textual content is of greatest value, however, a somewhat higher quality reproduction could be made from "photographs" if essential to the understanding of the dissertation. Silver prints of "photographs" may be ordered at additional charge by writing the Order Department, giving the catalog number, title, author and specific pages you wish reproduced.
5. PLEASE NOTE: Some pages may have indistinct print. Filmed as received.

University Microfilms International

300 North Zeeb Road
Ann Arbor, Michigan 48106 USA
St. John's Road, Tyler's Green
High Wycombe, Bucks, England HP10 8HR

7820424

ERIKSEN, FLEMMING ISKOV
THE EFFECT OF SHADING ON MORPHOLOGY, YIELD
AND NITROGENASE ACTIVITY OF GRAIN LEGUMES AND
TROPICAL FORAGE GRASSES AND LEGUMES,

UNIVERSITY OF HAWAII, PH.D., 1977

THE EFFECT OF SHADING ON MORPHOLOGY, YIELD AND NITROGENASE
ACTIVITY OF GRAIN LEGUMES AND TROPICAL FORAGE GRASSES AND LEGUMES.

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

AGRONOMY AND SOIL SCIENCE

MAY 1978

By

Flemming Iskov Eriksen

Dissertation Committee:

A. Sheldon Whitney, Chairman
Duane P. Bartholomew
Charles M. Campbell
Donald L. Plucknett
Peter P. Rotar
Yusuf N. Tamimi

ACKNOWLEDGEMENT

The faculty members and staff of the University of Hawaii, College of Tropical Agriculture, have been very helpful in my graduate program, particularly members of the Department of Agronomy and Soil Science (including the NIFTAL Project). Their help is greatly appreciated.

I am thankful to Dr. J. C. Nolan for his advice and for serving on my committee during Dr. C. M. Campbell's sabbatical leave.

I wish to acknowledge the assistance of the field staff of the Maui Agricultural Experiment Station, Kula and the NIFTAL Project, Hamakuapoko, Maui.

I want to thank Dr. D. T. C. Friend for his advice on plant physiological aspects of my experiments and to Mr. W. Y. Toma for his help in the computer analysis of data.

I wish to express my appreciation for financial support provided by the Hawaii Agricultural Experiment Station (assistsanship: Pasture Improvement Project) and the NIFTAL Project (supplies, and field and laboratory facilities).

I cherish the faithful assistance of Ms. Itiuna Vaia'oga Eriksen who helped me in numerous tasks and typed this dissertation.

To my family and friends, thank you for your support.

ABSTRACT

Six tropical forage legumes and six forage grasses were evaluated over a 20-month period and three grain legumes were evaluated over summer and cool seasons on an Oxic Haplustoll in Hawaii (100 meters above sea level) under four light regimes (100, 70, 45 and 27% daylight using polypropylene netting) in the field.

Forage legumes evaluated were: *Centrosema pubescens*, *Desmodium canum*, *Desmodium intortum*, *Leucaena leucocephala*, *Macroptilium atropurpureum*, and *Stylosanthes guyanensis*. Dry matter (DM) yields decreased with decreasing light intensity. DM yields in T/ha/yr in full daylight were highest for *L. leucocephala* (23.5) and *D. intortum* (20.0) and lowest for *D. canum* (12.2) and *M. atropurpureum* (14.0). DM yields at 27% daylight were highest for *D. intortum* (9.0) and lowest for *S. guyanensis* (2.2) and *M. atropurpureum* (2.6). Percentage nitrogen (N) was not affected by shading and was highest for *L. leucocephala* and *C. pubescens*. Total yields were 314-751 kg/ha/yr in full daylight and 80-285 kg/ha/yr at 27% daylight. Acetylene reduction by soil cores was highly correlated both with light intensity ($r=0.92-0.995$), except for centro which was 0.71, and with DM yields at the different light intensities ($r=0.80-0.996$). Apparent N-fixation rates in kg/ha/yr in full daylight (N-yield of legume less average N-yield of adjacent grasses grown without N) were: *L. leucocephala*, 656; *D. intortum*, 445; *C. pubescens*, 366; *S. guyanensis*, 364; *M. atropurpureum*, 267; and *D. canum*, 266.

Levels of P, K, Ca, Mg, Si, S, Cu and Zn differed among species ($P < .01$), but not between seasons or among light regimes (except the most intense shade). Plant height increased with shading.

The forage grasses evaluated were: *Brachiaria brizantha*, *B. miliiformis*, *Digitaria decumbens*, *Panicum maximum*, *Pennisetum clandestinum*, and *P. purpureum*. DM yields of N-fertilized grasses (365 kg/ha/yr) were highest at 100 and 70% daylight (16-40 T/ha/yr) with *P. maximum* and *P. purpureum* highest. Under 27% daylight, yields were 8-15 tons with *P. maximum*, *B. brizantha*, *B. miliiformis* highest yielding. When no nitrogen was added maximum yields in T/ha/yr were: *B. miliiformis*, 9.2 at 27% daylight; *D. decumbens*, *P. maximum* and *B. brizantha*, 13.5-15.0 at 45% daylight; *P. clandestinum*, 9.2 at 70% daylight and *P. purpureum*, 30 tons at full daylight. Percentage of DM in the forage decreased with shading and N-fertilization. Percent N increased with decreasing light intensity (from 1.0 to 1.6% in minus-N and from 1.2 to 1.9% in the plus-N treatments). Slight acetylene reduction was found in soil cores beneath all species, except *B. brizantha*. Sward height increased significantly with decreasing light intensity and with N-fertilization. With some exceptions P, K, Ca, Mg, S, Cu and Zn tended to be higher in shaded forage, higher in N-fertilized forage (except for P and Zn) and generally higher during the cool-season.

In a pot experiment, *P. maximum*, *B. miliiformis*, and *C. pubescens* were evaluated under 100, 70, 45 and 13% daylight using lath vs. net shading, with similar results as reported in the field experiment.

Grain yields of *Glycine max* and *Vigna unguiculata* also were evaluated at the four light levels. Yields decreased significantly

as light intensity decreased, and this was related to reduced pod numbers per plant at the lower light intensities. Grain yield of *Phaseolus vulgaris* was low at full daylight due to small seed size and was highest at 70 and 45% daylight. Yields during November-February were \approx 50% of April-July yields for *G. max*. Plants were sampled each week from 4 weeks after planting until harvest. Data recorded were acetylene reduction, nodule number, plant height and weights of nodules, stems, leaves, pods and seeds. Acetylene reduction by *P. vulgaris* was very low and was very transient (significant for weeks 4-7 only). This indicates that during pod filling *P. vulgaris* was therefore entirely dependant upon soil N. Acetylene reduction by *G. max* and *V. unguiculata* was high during most of the growth period, with a peak at 8-10 weeks after planting. Acetylene reduction by *G. max* was similar at 100, 70, 45% daylight but was lower at 27% daylight, whereas *V. unguiculata* showed a linear decrease in acetylene reduction with decreasing light intensity.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENT	iii
ABSTRACT	iv
LIST OF TABLES	
LIST OF FIGURES	
CHAPTER I. INTRODUCTION	1
CHAPTER II. REVIEW OF LITERATURE	2
Introduction	3
Measurement of light	4
Effect of light on leaf and plant morphology	5
Light and photosynthesis	7
Light and yield	11
Light and mineral content	15
Some factors affecting N-fixation	15
N-fixation by legumes and grasses	17
CHAPTER III. EFFECTS OF FOUR LIGHT INTENSITY LEVELS USING LATH VS. NET SHADING ON THE PERFORMANCE OF <i>PANICUM</i> <i>MAXIMUM</i> JACQ., <i>BRACHIARIA MILIIFORMIS</i> (PRESL.) A. CHASE. AND <i>CENTROSEMA PUBESCENS</i> BENTH	23
Introduction	23
Materials and methods	25
Results and discussion	27
Forage production and root development	27
Dry matter content	35
Plant height, tiller formation and flowering	37
Mineral content	42
Summary and conclusion	46
CHAPTER IV. THE EFFECT OF LIGHT INTENSITIES AND N-FERTILIZER ON MORPHOLOGY, YIELD, MINERAL CONTENT AND ACETYLENE REDUCTION OF SIX TROPICAL FORAGE GRASSES	49
Introduction	49
Materials and methods	51
Results and discussion	53

TABLE OF CONTENTS (continued)

Page

Dry matter yields	55
Plant morphology	67
Nitrogen percentage and yield	67
Nitrogenase activity in soil core samples	74
Mineral composition	75
Summary and conclusion	80
CHAPTER V. THE EFFECT OF LIGHT INTENSITIES ON MORPHOLOGY, YIELD, MINERAL CONTENT AND ACETYLENE REDUCTION OF SIX TROPICAL FORAGE LEGUMES	83
Introduction	83
Materials and methods	85
Results and discussion	87
Dry matter production	89
Dry matter content	96
Plant height	97
Nitrogen percentage, nitrogen yield and apparent N-fixation	97
Acetylene reduction	101
Mineral composition	104
Summary and conclusion	106
CHAPTER VI. THE EFFECT OF DIFFERENT LIGHT INTENSITIES ON ACETYLENE REDUCTION, DRY MATTER ACCUMULATION AND GRAIN YIELD OF SOYBEAN, COWPEA, BUSHBEAN, AND PIGEON PEA	109
Introduction	109
Materials and methods	111
Light intensity experiment	111
Nitrogen fertilizer experiment on bushbean	114
Results and discussion	115
Soybean	115
Plant growth characteristics	115
Nodulation and N-fixation	115
Dry matter and N accumulation	125
Grain yield	129
Cowpea	134
Plant growth characteristics	134
Nodulation and N-fixation	136
Dry matter and N accumulation	146
Grain yield performance	148

TABLE OF CONTENTS (continued)

Page

Bushbean	152
Plant growth characteristics	152
Nodulation and N-fixation	155
Dry matter and N accumulation	162
Grain yield	167
Nitrogen fertilizer experiment on bushbean	170
Pigeon pea	177
Summary and conclusion	180
APPENDIX TABLES	184
APPENDIX FIGURES	195
LITERATURE CITED	198

LIST OF TABLES

Table		Page
1	Flowering behaviour of guineagrass and corigrass and seed pod production by centro grown in full daylight and under two shading systems	42
2	The mineral content of guineagrass under different light regimes at two seasons; and the relationship between plant height (light-intensity indicator) and mineral content of guineagrass and corigrass under similar conditions	43
3	The mineral content of centro under different light regimes at two seasons; and the relationship between plant dry matter yield and mineral content.	44
4	Effect of reduced light intensity (13% of full daylight) on growth and mineral analysis of two tropical grasses and one tropical legume	47
5	The effect of shading on the dry matter content of forage grasses. Average of three replications (except as noted) and seven harvests	66
6	The effect of shading on leaf-plus-stem area:weight ratio, and leaf-plus-stem area index (LSAI) for three forage grasses at two nitrogen levels. Average of three replications	70
7	The effect of shading on leaf-plus-stem area:weight ratio, and leaf-plus-stem area index (LSAI) for three forage grasses at two nitrogen levels. Unreplicated	71
8	The effect of shading on the nitrogen fertilizer recovery of forage grasses	72
9	The effect of shading on the acetylene reduction of six forage grasses	74
10	The effect of shading on plant height of six forage legumes	98
11	The effect of shading on the annual nitrogen yield and apparent nitrogen fixation (legume N-yield less average N-yield of adjacent minus-N grasses) of six forage legumes	100

LIST OF TABLES (continued)

Table		Page
12	The effect of shading on the acetylene reduction of tropical forage legumes. Average of six harvests during the period August 16, 1976 to February 9, 1977	102
13	The effect of shading on the mineral content of six forage legumes at two seasons. (sun = full daylight; shade = 27% daylight)	105
14	The effect of shading on the number of nodules, nodule dry weight and acetylene reduction per plant, and the specific nodule activity and nodule size of Kahala soybean grown during the summer	119
15	The effect of shading on the number of nodules, nodule dry weight and acetylene reduction per plant, and specific nodule activity and nodule size of Kahala soybean grown during the cool season	121
16	The effect of shading on nitrogen percentage and nitrogen yield of total plant of Kahala soybean grown during two seasons	130
17	The effect of shading of soybean on the top/root ratio	131
18	The effect of shading on the performance of Kahala soybean. Plant density of 365,000 per ha. Average of three replications	132
19	The effect of shading on the number of nodules, nodule dry weight and acetylene reduction per plant, and specific nodule activity and nodule size of cowpea TVu 1190 grown during the summer	139
20	The effect of shading on the number of nodules, nodule dry weight, and acetylene reduction per plant, and specific nodule activity and nodule size of cowpea TVu 4557 grown during the cool season	140
21	The effect of shading on nitrogen percentage and nitrogen yield of total plant of cowpea TVu 1190 (summer season) and cowpea TVu 4557 (cool season)	149
22	The effect of shading on the top/root ratio of cowpea	150
23	The effect of shading on the performance of cowpea TVu 4557 during the cool season. Plant density of 130,400 per ha. Average of three replications	151

LIST OF TABLES (continued)

Table	Page	
24	The effect of shading on the number of nodules, nodule dry weight and acetylene reduction per plant, and specific nodule activity and nodule size of bushbean grown during the summer	157
25	The effect of shading on the number of nodules, nodule dry weight and acetylene reduction per plant, and specific nodule activity and nodule size of bushbean grown during the cool season	158
26	The effect of total plant shading on nitrogen percentage and nitrogen yield of bushbean grown during two seasons	166
27	The effect of shading on the top/root ratio of bushbean	168
28	The effect of shading on the performance of Burpee tenderpod bushbean	169
29	The effect of shading and nitrogen fertilizer on the number of nodules, nodule dry weight and acetylene reduction per plant, and specific nodule activity and nodule size of bushbean	172
30	The effect of shading and nitrogen fertilizer on dry matter yield, N percentage, N yield and top/root ratio of bushbean	173
31	The effect of shading and nitrogen fertilizer on green bean yield and pod number per plant of bushbean. Plant density of 260,000 per ha. Average of three replications	175
32	The effect of shading and nitrogen fertilizer on the performance of bushbean. Plant density of 260,000 per ha. Average of three replications	176
33	The effect of shading and levels of nitrogen fertilizer on the specific leaf weight, leaf area index and leaf area ratio of 4 weeks old bushbean	178
34	The effect of shading on the yield, seed size and seed number per pod on Pigeon pea. Unreplicated. Plant population 40,000 per ha	179

LIST OF APPENDIX TABLES

Table		Page
1	The effect of shading on the P content of six tropical grasses	184
2	The effect of shading on the K content of six tropical grasses	185
3	The effect of shading on the Ca content of six tropical grasses	186
4	The effect of shading on the Mg content of six tropical grasses	187
5	The effect of shading on the S content of six tropical grasses	188
6	The effect of shading on the Si content of six tropical grasses	189
7	The effect of shading on the Cu content of six tropical grasses	190
8	The effect of shading on the Zn content of six tropical grasses	191
9	Analysis of variance of Kohala soybean under different light intensities	192
10	Analysis of variance of cowpea TVu 4557 under different light intensities	193
11	Analysis of variance of Burpee tenderpod bushbean under different light intensities	194

LIST OF FIGURES

Figure		Page
1	Dry weight yields of guineagrass, corigrass and centro grown in full daylight and under two shading systems	28
2	Dry weights of roots at the final harvest of centro and of two grasses (guineagrass and corigrass) grown in full daylight and under two shading systems . .	31
3	Total dry matter yield of tops (total of 6 harvests), stubbles and roots after 16 months growth of guineagrass, corigrass and centro grown in full daylight and under two shading systems	33
4	Average dry matter percentage of guineagrass, corigrass and centro grown in full daylight and under two shading systems	36
5	Effect of shading on plant growth of A) guineagrass and B) corigrass (note: "lad" refers to shading by lath strips and "cloth" refers to shading by polypropylene shade cloth)	38
6	Plant height of guineagrass and corigrass after 8 weeks regrowth when grown in full daylight and under two shading systems	39
7	Development of upright and prostrate stems of corigrass grown in full daylight and under two shading systems	40
8	Percent nitrogen of tropical forage grasses grown at four light intensities in relation to solar radiation and soil temperature at 5 cm depth	54
9	The effect of shading on the annual dry matter yield of forage grasses at two nitrogen levels. Average of three replications	56
10	Growth of guineagrass at 100 and 27% daylight	57
11	Growth of Mealani digitgrass at 100 and 27% daylight . .	58
12	Growth of corigrass at 100, 70 and 27% daylight	59
13	The effect of shading on the annual dry matter yield of unreplicated forage grasses at two nitrogen levels. Yields adjusted for replication effects	56

LIST OF FIGURES (continued)

Figure		Page
14	Dry weight yield of guineagrass grown at two nitrogen levels and four light intensities over a 15 month period. Average of three replications	61
15	Dry weight yield of Mealani digitgrass grown at two nitrogen levels and four light intensities over a 15 month period. Average of three replications	62
16	Dry weight yield of corigrass grown at two nitrogen levels and four light intensities over a 15 month period. Average of three replications	63
17	The effect of shading on the root weight of forage grasses grown in the field at two nitrogen levels. Average of three replications	65
18	The effect of shading on height of tropical grasses at two seasons (---- = cool season; ____ = summer season) and two nitrogen levels (-0 = minus-N; Δ = plus-N)	68
19	The effect of shading on the annual nitrogen yield of six forage grasses at two nitrogen levels	73
20	The effect of shading on P, K, Ca and Mg content of three tropical grasses at two seasons (---- = cool season; ____ = summer season) and two nitrogen levels (0 = minus-N; Δ = plus-N). Average of three replications	76
21	The effect of shading on Si, S, Cu and Zn content of three tropical grasses at two seasons (---- = cool season; ____ = summer season) and two nitrogen levels (0 = minus-N; Δ = plus-N). Average of three replications	77
22	Percent nitrogen of greenleaf desmodium, centro and siratro in relation to solar radiation and soil temperature at 5 cm depth	88
23	Dry matter yield of three forage legumes harvested at 8-weeks intervals over a 15 month period. Average of three replications	90
24	The effect of shading on the annual dry matter yield of six forage legumes	92

LIST OF FIGURES (continued)

Figure		Page
25	Growth of a) centro, b) siratro, c) greenleaf desmodium, d) kaimi clover, e) leucaena, and f) stylo under shade	93
26	The effect of shading on plant height of Kahala soybean grown during two seasons	116
27	The effect of shading on growth of soybean during the summer season	117
28	The effect of shading (100% = full daylight) on nodule number and nodule dry weight of Kahala soybean grown during the summer season (bb=beginning bloom)	118
29	The effect of shading on acetylene reduction of Kahala soybean grown during the two seasons. (bb=beginning bloom; pm=physiological maturity)	122
30	Relationship between root and nodule dry weights of soybean over all shading treatments and sampled 4-12 weeks after emergence during the summer season	126
31	The effect of shading on dry matter accumulation of Kahala soybean grown during the summer season	127
32	The effect of shading on dry matter accumulation of Kahala soybean grown during the cool season	128
33	The effect of shading on the seed yield and number of pods per plant of Kahala soybean	133
34	Growth of cowpea TVu 1190 during the summer season at 45% daylight	135
35	The effect of shading on growth of cowpea TVu 1190 during the cool season	135
36	A) Cowpea TVu 1190 with pods hanging to the ground which resulted in heavy loss from rat damage. B) Cowpea TVu 4557 pods held high above the ground, no rat damage	137
37	The effect of shading (100% = full daylight) on nodule number and nodule dry weight of cowpea TVu 1190 grown during the summer season (no flowering)	138

LIST OF FIGURES (continued)

Figure		Page
38	The effect of shading on the acetylene-reduction activity of cowpea TVu 1190 grown during the summer (no flowering) and cowpea TVu 4557 grown during the cool season (flowering). (bb=beginning bloom; pm=physiological maturity)	141
39	Relationship between root and nodule dry weights of cowpea TVu 1190 during the period 3-9 weeks after emergence grown during the summer season	145
40	The effect of shading on the dry matter accumulation of cowpea TVu 4557 grown during the cool season. (bb=beginning bloom; pm=physiological maturity)	147
41	The effect of shading on the seed yield and number of pods per plant of cowpea TVu 4557 grown during the cool season	153
42	The effect of shading on plant height of bushbean grown during the summer season	154
43	The effect of shading (100% = full daylight) on nodule number and nodule dry weight of bushbean grown during the summer season (bb=beginning bloom)	156
44	The effect of shading on the acetylene-reduction activity of bushbean grown during two seasons. (bb=beginning bloom; pm=physiological maturity)	159
45	Relationship between root and nodule dry weights of bushbean four weeks after emergence during the summer season	163
46	The effect of shading on the dry matter accumulation of bushbean grown during the summer season. (bb=beginning bloom; pm=physiological maturity)	164
47	Growth of bushbean 8 weeks after seeding at A) 100% daylight and B) 45% daylight during the summer season	165
48	The effect of shading on the seed yield and number of pods per plant of bushbean grown during two seasons.	171

LIST OF APPENDIX FIGURES

Figure		Page
1	General view of the A) forage grass and legume plots and the B) grain legume plots	195
2	Plot field layout showing the arrangement of treatments, plot dimensions and plot yield area. Also shown is the set up of the shaded area	196
3	Growth of 8 weeks old Kahala soybean at 70% daylight during the summer season	197

THE EFFECT OF SHADING ON MORPHOLOGY, YIELD AND
NITROGENASE-ACTIVITY OF GRAIN LEGUMES AND
TROPICAL FORAGE GRASSES AND LEGUMES

CHAPTER I

INTRODUCTION

In the tropics levels of radiation are usually high and are often the least variable component of the climate from year to year. However, solar radiation at different locations and at different seasons may vary greatly depending on cloud cover. In Hawaii solar radiation in different areas varies from 429 to 704 cal sq cm⁻² day⁻¹ in June and from 241 to 426 cal cm⁻² day⁻¹ in December (Yoshihara and Ekern, 1977).

In many parts of the tropics and sub-tropics multiple cropping systems are used. When crops are grown together, competition for light will occur, especially if one crop is much taller than the other crops. Often crops are grown together with trees to keep down the weeds, improve the soil fertility by using legumes or to provide an extra source of income from cash crops or from grazed grasses or grass-legume mixtures. The use of legumes in particular has become more attractive due to the high cost and low availability of mineral nitrogen fertilizer within the last few years.

Certain legumes and grasses are more shade tolerant than others. It is of great importance to know which legumes and grasses are shade tolerant, to obtain the best possible yield and quality under different light regimes.

The present studies represent an attempt to evaluate the effect

of four different light regimes on the yield, morphology, chemical composition and nitrogenase activity of a) tropical forage grasses and legumes and b) grain legumes.

CHAPTER II

LITERATURE REVIEW

Introduction. The crop community is basically a converter of solar energy into chemical energy. The quantity of solar energy converted and, therefore, the amount of dry matter (DM) produced depends on the percent intercepted and the efficiency of utilization of the intercepted energy. Utilization of solar energy by plants is conditioned by the distribution of solar radiation over the leaf surfaces of the plant community and by the levels of a number of other environmental factors. The distribution of solar radiation is of significance because individual leaves do not respond equally to all levels of irradiance. The spatial separation and orientation of the leaves within the crop canopy have been suggested as factors influencing the distribution of solar radiation over the leaf surfaces of a community (Donald, 1962).

The irradiance above and within the upper surface of a plant canopy can be split into three components: 1) the direct solar radiation penetrating without appreciable attenuation through the gaps in the foliage in the form of bright sun flecks, 2) the diffuse skylight penetrating through the gaps in the foliage, and 3) the complementary radiation field, consisting of radiation scattered by the foliage and by the ground (Monteith, 1969; Nilisk et al., 1970).

Features of solar radiation relevant to crop ecology are: the angle of incidence of the sun's rays (usually specified by the solar elevation), the spectral composition of the radiation (usually defined by the waveband 400 to 700 nm, i.e., the photosynthetically active radiation), the relative intensity of diffuse radiation from the blue

sky, haze and clouds, and of direct radiation from the solar beam.

The effects of radiation on crop ecology are especially complex in pasture situations because the swards usually consist of several species having different morphology and present in varying proportions. Also the structure is subject to frequent change due to such factors such as seasonal growth fluctuations, fertilizer application, grazing, mowing, trampling, or invasion by other species which may alter the light climate within a pasture.

Measurement of light. Green plants have the greatest absorption in the shorter wavelengths around 470 nm and 680 nm. Sensors for measuring solar radiation above or within a canopy must therefore measure only the radiation which is photosynthetically active and must measure uniformly over the entire range of PAR.

Many different photo-electric cells and chemical cells have been developed for measuring light. Photo-voltaic cells are preferable to other types because they are small and have a high output per unit area (Stern, 1962; Anderson, 1964).

Chemical light meters, which integrate the light received over an interval of time, are cheaper than photo-voltaic cells, but the rate of photooxidation with increasing light should be calibrated against a standardized light meter. Dore (1958) described a method using anthracene and Friend (1961) developed a method using ozalid paper. The method of Friend was later modified by Francis (1970) and Kanemasu (1971).

Measurements of gap frequency at all angles above the horizon can be done by using a camera with a fish eye lens. This method measures canopy density, frequency and size of gaps permitting estimates of

penetration. The method is especially useful for studies of light penetration through the canopies of forest, coconut palms, or other trees where other plants are growing underneath the trees (Anderson, 1971).

Effect of light on leaf and plant morphology. Variation in light intensity causes many changes to take place in the leaves and the whole plants of both legumes and grasses. Maize plants become taller and thinner at low light intensities. Early *et al.*, (1966) found that maize plants increased in height from 1.85 m at full daylight to 2.55 m at 30% daylight, and at the same time the dry weight of stover decreased from 259 gm to 130 gm per plant. A much more rapid elongation was found on new growth of alfalfa (*Medicago sativa* L.) plants, when the mature and fully expanded leaves were grown in 18% light as compared to the new growth of plants in full light (Straley and Cooper, 1972). The shade treatments also altered the quality of incident light. This in turn could alter the plants hormonal balance, thereby causing increases in plant height. When soybean plants were grown under 100, 68, 37, 31, and 18% of full light (39000 lux) the plant heights were 19, 19, 23, 28 and 29 cm, respectively (Yoshida, 1973).

Specific leaf weight (SLW, mg cm^{-2}) is readily affected by environmental changes. It has even been shown that the SLW of leaves of sainfoin (*Onobrychis viciifolia* Scop.) formed in full daylight at the top of plants with mature lower leaves shaded (3.6 mg cm^{-2}), was significantly lower than the SLW of leaves formed at the top of plants in full daylight without mature leaves shaded (4.7 mg cm^{-2}) (Straley and Cooper, 1972). Similar differences were found when a dense and a widely spaced stand of sainfoin plants were compared (Straley, *et al.*,

1972). Shading of lower leaves by upper leaves of alfalfa in dense natural canopies caused the SLW of fully expanded bottom leaves to decline sharply. The effect of shade on the SLW was shown by shading the plant with shade cloth. Intensities of 27 and 45% daylight for 8 days caused the SLW of fully expanded bottom leaves to decline sharply and remain low during the next 10 days. Conversely, with 100 and 70% daylight the SLW value increased during 18 days exposure. After 18 days the SLW for 27% daylight was 3.2 mg cm^{-2} compared to 5.0 mg cm^{-2} for normal daylight (Wolf and Blaser, 1972). When green-gram (*Vigna radiata* (L.) Wilczek) plants were grown under light intensities varying from 20 to 100% daylight the SLW increased linearly from 1.4 mg cm^{-2} to 3.3 mg cm^{-2} (Nomoto *et al.*, 1961).

Morphological differences in sun and shade leaves of alfalfa were described by Cooper and Qualls (1967). The thickness of sun leaves compared to shade leaves appeared to be related to both a larger number and a greater size of palisade and mesophyll cells. The palisade layer of sun leaves was more clearly differentiated than in shade leaves.

Grass leaves (*Lolium perenne* L.) grown under low light intensities were thinner and wider than leaves grown under higher light intensities (Silsbury, 1970).

The decrease in the SLW with shading may represent an adaptive mechanism, since for each unit weight of dry matter partitioned into leaves, a greater amount of area is exposed to available light. Salisbury and Ross (1969) showed that shading of plants increased the leaf area ratio (LAR), which is the ratio of leaf area to plant weight.

The effect of shading upon the SLW, stomata number, and chlorophyll

content was examined in an experiment with "Vernal" alfalfa and "Tana birdsfoot trefoil (*Lotus corniculatus* L.) grown in full daylight and 8% daylight (Cooper and Qualls, 1967). Both species had lower SLW when shaded. The number of stomata per mm^2 were highest for the leaves grown in the sun, while shaded plants of both species contained significantly more chlorophyll per unit of leaf weight but less chlorophyll per unit of leaf area than sun plants.

Light and photosynthesis. Studies on the influence of different light intensities on the rate of growth of plants started at the beginning of this century.

The first studies were concerned with the inhibition of photosynthesis upon exposure to high light intensities rather than with an influence of light intensity on the photosynthetic capacity (Harder, 1930).

In 1929 the first comparisons were made between shade and sun leaves of *Fagus silvatica* L. (Boysen-Jensen and Muller, 1929). As in earlier comparisons between sun and shade plants of different species, they found a higher maximum rate of photosynthesis, a higher saturation light intensity and a higher light compensation point for the sun leaves.

Experiments with plants exposed to artificial light of different intensities during growth while keeping other external factors constant as much as possible, were reported by Flackman *et al.*, (1946). Since then additional data have demonstrated conclusively that most plants are able to develop a higher photosynthetic capacity when grown under high light intensity. Some shade plants, however, suffer damage to the chloroplasts under high light intensities.

Bjorkman (1970) compared the rate of photosynthesis at different light intensities of some plant species from shaded and from sunny habitats. The plants from the shaded habitat were able to utilize very low light intensities and reached their maximum rate of photosynthesis at about 0.2×10^4 erg cm^{-2} sec. The plants from the sunny habitat had a higher light compensation point and photosynthesis rates increased with increasing irradiance even at 30×10^4 erg cm^{-2} sec. Similar results were shown for several other species grown under different light intensities by Black (1963), King and Evans (1967), Beuerlein and Pendleton (1971), Groen (1973), and Singh *et al.* (1974). Differences in photosynthetic characteristics of sun and shade species of higher plants have been reviewed by Boardman (1977).

Groen (1973) grew the shade plant *Impatiens parviflora* at 100, 75, 37 and 12% daylight. From zero to 5×10^4 erg cm^{-2} sec⁻¹ the plants had a higher rate of photosynthesis when grown under 12% daylight, than under higher light intensities, while plants grown under full daylight had the highest rate of photosynthesis when the light was above 10^5 erg cm^{-2} sec⁻¹.

When different grasses and legumes having the C₃ or C₄ photosynthetic pathway (Salisbury and Ross, 1969) hereafter referred to as C₃ or C₄ plants, were grown under different light regimes, it was found that the photosynthesis rates generally were highest in plants grown under full daylight (Bowes, 1972; Singh *et al.*, 1974).

Great variations in the efficiency of photosynthesis have been found for C₃ and C₄ plants grown under different light intensities. In order of increasing photosynthetic efficiency, they are C₃ grasses < C₃ dicots < C₄ aspartate formers < C₄ malate formers (Singh *et al.*,

1974). The increased efficiency of C_4 species, compared to C_3 species, can be explained by the proposed CO_2 concentrating function of phosphopyruvate carboxylase in the C_4 species. Increased CO_2 at the site of RuDP (ribulose diphosphopyruvate) carboxylase stimulates photosynthesis and inhibits photorespiration in C_4 species (Singh *et al.*, 1974).

The CO_2 compensation concentration of soybean leaves, the CO_2 concentration at which the rate of photosynthesis equals the rate of photorespiration, was not affected by the light intensity received during growth. The constant nature of the compensation concentration in soybean was taken to indicate that the dark reaction limiting photosynthetic rate also limits the rate of photorespiration (Dornhoff and Shibles, 1970; Bowes *et al.*, 1972).

The relationship between net photosynthesis, respiration and leaf area index (LAI) at three different light intensities were studied for wheat, lucerne and subterranean clover (King and Evans, 1967). Net crop photosynthesis rose rapidly with increasing LAI. In wheat the increase was very rapid to an LAI of about four and then slowly increased with increasing LAI to 10.6. For the low light intensities (1100 f.c.) no increase in net photosynthesis was observed after LAI of about three. For all three species there was no obvious decline in net photosynthetic rate per unit ground surface at high LAI values. The dark respiration rate per unit ground surface of the community did not increase linearly with increase in LAI, but rather approached an asymptote at LAI values above five. This implies very low respiration rates in lower older leaves. Similar data was earlier obtained for subterranean clover in Australia (Black, 1963).

The RuDP carboxylase activity in green leaves generally is highly and positively correlated to photosynthesis rate (Bjorkman, 1970; Bowes *et al.*, 1972; Singh *et al.*, 1974). In wheat and soybean, the extractable carboxylase activity was greater than the photosynthesis rate when both quantities were expressed on a per unit leaf area basis, whereas photosynthesis exceeded extractable carboxylase activity in the C₄ species maize and sorghum. The CO₂ concentrating function of phosphopyruvate carboxylase presumably allows these species to photosynthesize at higher rates with less RuDP carboxylase activity than is needed by the C₃ species (Singh, *et al.*, 1974). The activity of RuDP in sun species was found to be from 2 to 5 times higher than in shade species (Bjorkman, 1970).

The photosynthetic rate was shown to be proportional to chlorophyll content only at low light levels and the concentration was optimum at 3 to 5 mg chlorophyll (a and b) dm⁻² (Cooper and Qualls, 1967). An increase in chlorophyll content beyond this limit does not affect photosynthesis (Gabrielsen, 1948; Cooper and Qualls, 1967).

Khein and others (1971) found that changing the light regime from high to low intensity raised the rate of cyclic photophosphorylation and a reverse affect occurred with a reversed regime of illumination. Within a few days or less the chloroplasts were able to acquire characteristics typical of plants which normally grow at high or low light intensities. Thus changing the light regime could alter the properties of the photosynthetic apparatus of plants.

Because of absorption of PAR by leaves, light transmitted by a leaf is of a lower quality for photosynthesis than direct daylight. In an experiment where the plant *Pittosporum* was grown under *Colocasia*

leaves and under natural day light at the same light intensity (15 klux), the photosynthetic rate of the leaf grown under the *Colocasia* leaf decreased to about 70% of the rate for the leaf grown in daylight. The transmissibility of foliage leaves was measured to be 5-10% for herbs, grasses and climbing plants. The transmissibility of young leaves was 20% or higher than that of matured leaves. Transmissibility generally diminished with chlorophyll content, following the light extinction law of Beer-Lambert (Kasanaga and Monsi, 1954).

Light and yield. Some grasses and legumes are more shade tolerant than others, which means that their yield is not depressed as much as other grasses and legumes at a given degree of shade (Myhr and Saebø, 1969). It is of importance to know how tolerant the different species are to shade if the grasses or legumes are to be grown under trees or other plants, or even in areas where clouds are common. In Sri Lanka it was found that *Brachiaria miliiformis* (Presl.) A. Chase was much more shade tolerant than *Brachiaria brizantha* Hochst. ex. Chiov. when compared under full and one fourth daylight (Santhirasegaram and Fernandez, 1967). Richards and Bevedge (1969) found that silverleaf desmodium (*Desmodium uncinatum* (Jacq) D.C.) was more shade tolerant than *Lotononis bainesii* Bak under native conifers in Southern Queensland. When siratro (*Macroptilium atropurpureum* (D.C.) Urb.), centro (*Centrosema pubescens* Benth.), greenleaf desmodium (*Desmodium intortum* (Mill.) Urb.), Tinaroo glycine (*Glycine wightii* (R. Grah. ex. Wight and Arn.) Verdc.) and stylo (*Stylosanthes guyanensis* Swartz) were grown under 100, 70, 50 and 30% daylight it was found that the yield of all four species was highest at 70% daylight. Centro and greenleaf

desmodium were found to be the most shade tolerant of the five species (Ranacou, 1972).

Grasses and legumes are often used as cover crops under tree crops such as rubber and coconuts. As the trees grow taller the cover crop gets less daylight, and the more shade tolerant species become dominant. In Malaysian rubber plantations it is normal estate practice to establish cover plants, either natural or introduced, between the rows of trees at planting time. A combination of several legumes are established to provide a good cover and eliminate weeds. The more shade persistent legumes used in Malaysia include the bush *Flemingia congesta* Roxb. and the viny centro (Watson, 1963).

Early *et al.* (1966) measured the effect of shade on the growth and grain production of three corn hybrids. The different percentages of light were obtained by covering 30, 60, 70, 80 and 90 percent of the area of both sides and tops of thin wooden frames with strips of 26 gauge galvanized sheet metal. With decreasing light intensity there was a significant decrease in grain, stover, kernels/plant and stalk area. Days from planting to emergence of tassel, anther and silk were increased with decreasing light intensity. A canopy analysis of the top, middle and bottom portions of a maize plant showed that the top five leaves contributed 26% of leaf and 40% of productivity, the middle four leaves contributed 42% of leaf and 35-50% of productivity and the bottom six leaves contributed 32% of leaf and 5-25% of productivity. The lower leaves were less productive due primarily to shading by the upper leaves (Allison and Watson, 1966).

Low light intensity (40% of full daylight) prior to clipping increased the number of tillers on reed canary grass (*Phalaris*

arundinacea L.) and climax timothy (*Phleum pratense* L.) (Horricks and Washko, 1971). However Mitchell (1953) reported the opposite for ryegrass (*Lolium* spp.). Possible reasons for this variance are different photoperiods, species and temperature conditions. Although the number of tillers in canarygrass and timothy increased under the 40% light intensity treatment, the total dry matter production was lower for the shaded grass.

High nitrogen fertilization for grasses grown under low light intensity is not advisable. Experiments done with Coastal bermuda grass (*Cynodon dactylon* (L.) Pers.) in 1956 and 1957 in Georgia, showed that the efficiency of bermuda grass in converting solar energy into dry matter was reduced by heavy nitrogen fertilization. When 220 kg N ha⁻¹ was applied the relative dry matter yields for 100, 64, 43 and 29% light were 100, 91, 67 and 53, compared to relative yields of 100, 68, 42 and 29 when 1800 kg N ha⁻¹ yr⁻¹ was applied. Under heavy shade, the heavily fertilized grass contained 26% more crude protein and 30% less available carbohydrates. Apparently proteins were formed at the expense of carbohydrates, perhaps as a mechanism to keep nitrate and ammonia nitrogen from building up within the plant to toxic levels. It seems possible that the available carbohydrates left after protein synthesis (6.4%) were inadequate to support a rate of growth as high as that measured at the low nitrogen level (9.1% available carbohydrates) (Burton *et al.*, 1959). Later work by Deinum (1966), and Myhr and Saebo (1969) confirmed that shaded grasses had lower dry matter and much higher crude protein than grasses grown in full daylight.

Under low light intensities the energy available for synthesizing carbon compounds in the plant is limited. Consequently nitrate-nitrogen

accumulates, and concentrations of total water-soluble carbohydrates or other carbohydrate fractions in shaded grass may be only half the concentration found in unshaded grass (Deinum, 1966; Hight *et al.*, 1968; Paulsen and Smith, 1969). In the late thirties Blackman and Templeman (1938) worked on the interaction of light intensity and nitrogen supply on the leaf production of clover (*Trifolium repens* L.). They found that the addition of either ammonium sulfate or calcium nitrate increased growth significantly. When the light level was 61 and 44% of daylight the yield decreased at the same rate with and without fertilizer. Data from Japan (Nomoto, 1961) showed that the total plant weight of mung bean (*Vigna radiata*) grown in 75% light followed closely that of plants grown in full light, but total plant weight was depressed markedly by heavy shading (30 and 20% of full daylight).

It is possible to increase the yield of some crops by increasing light intensity to higher than normal levels. Schou *et al.* (1974) measured the effect of light enrichment at different stages of plant development on yield of soybean. Aluminum light reflectors were placed between soybean rows for two weeks at various stages of development. The best results were obtained when light enrichment was imposed at the early pod formation stage. The yield was increased by 57% and the total weight of the seeds increased by 26, 28 and 195% for the upper, middle and lower positions of the plant.

Shading affects the nutritive value of grasses. Deinum *et al.* (1968) found that when ryegrass (*Lolium perenne* L.) was grown under shade (30% of full daylight) at various temperature and nitrogen levels, the digestibility was slightly decreased. The chemical composition

of the grass was changed considerably more than the digestibility. Hight *et al.* (1968) found that the *in vivo* digestibility coefficients of several temperate grasses were not significantly different between shaded and unshaded grass, but the daily gain of the animals fed grass which had been shaded was lower due to much lower daily forage intake.

Light and mineral content. When temperate grasses were grown under shady conditions the ash content sometimes increased to levels twice that of unshaded plants because of higher concentrations of Ca, Mg, K and P. The average content of K, Ca, Mg and P for seven grasses grown in Norway under natural light were 1.50, 0.34, 0.15 and 0.26% and under shade 3.80, 0.55, 0.30 and 0.50% (Myhr and Saebo, 1969). Mayland and Grunes (1974) reported that the elements P, K, Ca, Mg, Na and Cl in *Agropyron desertorum* (Fisch.) Schult. and *Elymus cinereus* Scribn. and Merr. were significantly higher in grasses grown under 25% daylight than under full daylight, except for the P content in *Agropyron desertorum*.

Cunningham and Nielsen (1965) reported greater cation concentrations in plants grown during cloudy weather than in plants grown during sunny weather.

Some factors affecting N-fixation. The importance of inoculation with appropriate rhizobia was shown for four forage legumes grown in pots in different Hawaiian soils. In most cases inoculation doubled the N yield of the legumes (Rotar *et al.*, 1967). In field trials from Hawaii *Desmodium canum* (Gmel.) Schintz and Thellung benefited from inoculation whereas *Desmodium intortum* did not (Whitney and Green, 1969). Many tropical legumes require specific *Rhizobium* strains for

efficient N-fixation. t'Mannetje (1969) found differences among 21 *Stylosanthes* accessions regarding their affinities to 25 *Rhizobium* strains, the differences being related to morphological differences among the legumes. Chomchalow (1971) obtained a range of 59-141 mg N per peanut plant in sterile culture, depending on the strain of *Rhizobium*.

Shade affected the nitrogen fixation rates of soybean (*Glycine max* L.) (Sampaio and Döbereiner, 1968; Yoshida 1973). When soybean plants were grown under 100, 64, 37, 31 and 18% of full light intensity (39000 lux) the nitrogen fixed (mg per 20 plants) were 62, 70, 78, 17 and 19 respectively, the number of nodules per 20 plants were 1208, 1008, 950, 796 and 650 while the number of nodules per g of roots were 27, 23, 26 and 31 (Yoshida, 1973).

Soil temperature also can limit nodulation and N-fixation rates. The optimum root temperature for nodulation of *Glycine wightii*, *Desmodium uncinatum*, *Desmodium intortum*, *Stylosanthes humilis* H.B.K. and *Macroptilium atropurpureum* was 30 C. Thus decreases in the soil temperature caused by shade by trees or clouds might effect legume nodulation. N-fixation appears less sensitive to temperature than nodulation. Thus Dart and Day (1971) demonstrated considerable fixation at 35 C in soybean and cowpea. Guss and Döbereiner (1972) showed some restriction in N-fixation of beans, and Souto and Döbereiner (1970) in some pasture spp. when temperatures were about 33 C.

Sprent (1971, 1972) reported drastically decreased nitrogenase-activity when legumes were under water stress.

The influences of nutrient supply on symbiotic N-fixation have been reviewed by Munns (1975). Elements which commonly are deficient

in the host plant for efficient N-fixation include P, K, Ca, and S. The elements P, Ca, and Mo are most often limiting factors for nodulation and N-fixation by *Rhizobium*. Nitrogen fertilization of soybean was found to reduce nodulation (Abu-Shadra and Bassiri, 1971; Abu-Shadra, 1975) and the N-fixation rate (Lawn and Brun, 1974; Bezdicek, 1974). Other work indicates that small amounts of N fertilizers stimulate nodule formation (Perkins, 1924; Richardson *et al.*, 1957).

The optimum pH for the availability of plant nutrients falls in the range of 5.5 to 5.8 for organic soils, 5.0 for sphagnum peats, and 1 to 1.5 units higher for mineral soils (Lucas and Davis, 1961). The critical pH for survival of root nodule bacteria in soil is between 4.3 and 4.9 (Norris, 1959). When 18 tropical and temperate legumes were grown on a high manganese Typic Torrox (pH 4.7) in Hawaii, the lime requirement for 90% of maximum yield ranged from 0.1-16.0 T/ha (Munns and Fox, 1975). This suggests that different legumes respond very differently to a high level of soil Mn and a low level of soil Ca.

N-fixation by legumes and grasses. Cultivated plants vary in their requirements for nitrogen (Date, 1973). Two processes- nitrogen fertilization and biological nitrogen fixation - are significant in meeting these requirements. Free living soil organisms such as *Clostridium* and *Azotobacter* fix relatively little nitrogen (Delwiche and Wijler, 1956) though there is now steadily accumulating evidence of significant fixation in some rhizosphere associations (Döbereiner *et al.*, 1973; Yoshida and Ancajas, 1973). Harris and Dart (1973)

reported that $55 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ was fixed in the rhizosphere compared to only $5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in nonrhizosphere soil. Rhizosphere associations of *Azotobacter paspali*-*Paspalum notatum* Flugge (bahiagrass) and other grasses in tropical areas fixed up to $90 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Döbereiner *et al.*, 1972). Significant C_2H_2 -reduction rates have been found in washed roots of pangola (*Digitaria decumbens* Stent) and *Paspalum notatum* (Döbereiner and Day, 1974). Also Döbereiner and Day (1974) showed that instead of loose rhizosphere associations in *Digitaria decumbens* cv. Transvala and possibly by several other tropical grasses, a primitive kind of intracellular root symbiosis exists. In general, maximal N-fixing rates in rhizospheres occur when the soil is waterlogged, sunlight is prevalent, and the root system is releasing large amounts of exudates (Domergues *et al.*, 1973).

The legume - *Rhizobium* symbiosis is probably the major source of fixed nitrogen in agriculture. Date (1973) suggests an average fixation rate of between 100 and $200 \text{ kg ha}^{-1} \text{ yr}^{-1}$. This would be equivalent to applying more than $500 \text{ kg (NH}_4\text{)}_2\text{SO}_4 \text{ ha}^{-1} \text{ yr}^{-1}$, and N utilization undoubtedly would be more efficient.

The symbiotic association of the bacteria and the legume shows great complexity in the infection process, nodulation development, and host-bacterial specificities that determine the N-fixing capacity in nodules. Symbiosis ultimately depends on the formation of nitrogenase (the N-fixing enzyme) in the *Rhizobium* bacteroids within the nodule. The actual rate of N-fixation can be estimated by either direct or indirect methods.

N-fixation is often estimated by the Kjeldahl method, but the disadvantages of this method include lack of sensitivity and rapidity,

destruction of the sample, and lack of ability to distinguish N from endogenous sources prior to the digestion. Two recent innovations, the ^{15}N method and the acetylene reduction method, provide sensitive and direct assays of nitrogenase activity.

The ^{15}N method provides positive evidence of N-fixation. The method is 100 times more sensitive than the Kjeldahl method. Its disadvantages include the use of costly ^{15}N and an even more costly mass spectrometer, and the requirement for more chemical manipulations than are required for the Kjeldahl method (Burris and Wilson, 1957).

The acetylene reduction method is simple, rapid, relatively inexpensive, and about 1000 times more sensitive than the ^{15}N method (Hardy *et al.*, 1968). Nitrogenase catalyzes acetylene reduction to ethylene as well as N_2 reduction to NH_3 (Dilworth, 1966; Schollhorn and Burris, 1967). The procedure involves the addition of acetylene to an N-fixing system, incubation, removal of the gas sample, separation of acetylene and ethylene by gas liquid chromatography, and quantitative detection of ethylene by an H_2 flame ionization detector. Gas mixtures can be handled in the field and gas samples to be analyzed can be stored in gastight containers for weeks before analysis in the laboratory. Acetylene reduction has been used to detect N-fixation in intact nodules (Koch and Evans, 1966; Sloger, 1969; Bergersen, 1970), in cell free extracts prepared from nodules (Koch *et al.*, 1967) and in the field (Stewart *et al.*, 1967; Hardy *et al.*, 1968; Mague and Burris, 1971).

Mague and Burris (1971) found that the relative rates of nitrogen fixation for intact soybean plants, nodulated roots and detached nodules were approximately 100/46/23. The soybean plants exhibited

a diurnal cycle of acetylene reduction depending upon light intensity and air temperature. In the experiment, Mague and Burris (1971) observed that the C_2H_2 ratio = 2 rather than the assumed value of 3.0 based on a six-electron transfer for the reduction of N_2 to $2NH_3$ verses two electrons for reduction of C_2H_2 to C_2H_4 (Hardy *et al.*, 1968 b; Silver and Mague, 1970). Mague and Burris (1971) and Sprent (1971) found a marked decrease in acetylene-reduction when nodules were soaked in water.

Hardy *et al.*, (1971 b) suggested four parameters to be used to evaluate symbiotic N-fixation of plants with the acetylene reduction method: 1) time to reach a specific low initial N-fixing activity, 2) rate of increase during the logarithmic phase, 3) age of termination of the logarithmic phase, and 4) total N fixed.

Symbiotic N-fixation is an important source of N for legumes during reproductive growth while reduction of nitrate from the soil via the enzyme nitrate reductase is most important during vegetative growth (Harper and Hageman, 1972). Symbiotic N-fixation by soybean is enhanced by efficient soybean-*Rhizobium* strain associations (Sloger, 1969; Weber *et al.*, 1971; Mague and Burris, 1972; Hittle, 1975), CO_2 enrichment (Hardy and Havelka, 1973), proper amounts of water (Sprent, 1971, 1972), and sunlight (Mague and Burris, 1972).

In Hawaii it has been shown that forage legumes such as *Desmodium* spp. and *Centrosema pubescens* grown alone or together with grasses were able to fix between 47 and 407 kg of N $ha^{-1} yr^{-1}$ (Whitney *et al.*, 1967; Whitney and Green, 1969; Whitney, 1970). The nitrogen fixation rate for *Trifolium subterraneum* L., *Stylosanthes guyanensis* and *Medicago sativa* L., varied between 90 and 220 kg N fixed per ha

(Erdman, 1959; Bell and Nutman, 1970).

Nitrogen fixation rates above 600 kg N/ha per year for temperate and tropical forage legumes under very good growth condition, have been reported by Melville and Sears (1953), Henzell and Norris (1962), Rotar *et al.* (1976), and Brewbaker *et al.* (1972).

Tropical tree legumes like *Leucaena leucocephala* (Lam) de Wit have a high potential for N fixation. In Hawaii the estimated N recovery from several selected varieties varied from 483-905 kg N per ha (Brewbaker *et al.*, 1972).

Harvest frequency has been shown to affect N-fixation rates. The nitrogen fixation rate for greenleaf desmodium (*Desmodium intortum*) grown together with pangolagrass (*Digitaria decumbens* Stent) and kikuyugrass (*Pennisetum clandestinum* Hochst. ex. Chiov.) was twice as high when the plants were cut every 10 weeks compared to cutting every 5 weeks (Whitney, 1970).

Significant amounts of N are also fixed by legumes grown for seed production. Stewart (1966) stated in a review that the average amount of nitrogen fixed by soybeans for a growing season was 94 kg per ha. The contribution of fixed nitrogen to the growth and yield of soybean varies. In low nitrogen soils, nodulated legumes are almost entirely dependent upon fixed nitrogen. Weber (1966) showed that the quantity of fixed nitrogen and the ratio of fixed nitrogen to total nitrogen nearly doubled when soil nitrogen was immobilized by corncobs, but the yield remained the same. By integrating the acetylene reduction activity of nodulated plants over a growing season, it was estimated that between 80 and 163 kg per ha of N was fixed or between 25 and 50% of the total nitrogen requirements of the mature

plant were supplied by N-fixation (Hardy *et al.*, 1968; Hardy *et al.*, 1971 a and b; Weber *et al.*, 1971). Hardy *et al.* (1968 and 1971 b) showed that for soybeans a linear relationship existed between time and the logarithm of the amount of nitrogen fixed. The logarithmic phase extended from 30 to 85 days after planting. During this period the total nitrogen fixed doubled every 6 to 10 days. More than 80% of the nitrogen was fixed between flowering and early greenbean stages according to estimates made from acetylene reduction data by Weber *et al.* (1971).

In view of the recent drastic price increases in nitrogen fertilizer and the predicted shortages of oil before the year 2000, the importance of legumes which have the ability to fix large quantities of nitrogen will undoubtedly become greater. Also land will have to be used more intensively in order to provide for increase in population, especially in the tropical countries. Intercropping of legumes with taller growing cereal crops or underneath the canopies of e.g. oil-or coconut palms or other crops will become more important. Our knowledge of different tropical legumes ability to fix nitrogen at different light intensities is very limited and much additional work is needed in this area.

CHAPTER III

EFFECTS OF FOUR LIGHT INTENSITY LEVELS USING LATH VS. NET SHADING ON THE PERFORMANCE OF *PANICUM MAXIMUM* JACQ., *BRACHIARIA MILIIFORMIS* (PRESL.) A. CHASE. AND *CENTROSEMA PUBESCENS* BENTH.

INTRODUCTION

In many parts of the tropics multiple cropping systems are commonly practiced. When crops are grown together, competition for light will occur, especially if one crop is much taller than the others. Often crops are grown together with trees, such as rubber or coconut trees, in order to suppress weeds, improve soil fertility or as an extra source of income (Javier, 1974; Mac Evoy, 1974; Nitis, 1976). Plants grown under the trees usually receive direct sunlight and shade simultaneously depending on the canopy patterns. Reduced light intensity also occurs in many areas of the tropics due to cloudy weather. Under these conditions the whole plant is shaded. (Grime, 1966; Hughes, 1966; Loach, 1970; Ludlow *et al.*, 1974). In Hawaii the total solar radiation at different locations varies from 429 to 704 cal sq. cm⁻² day⁻¹ in summer time (June-July) and from 241 to 426 cal sq. cm⁻² day⁻¹ in winter time (Dec.-Jan.) due to differences in cloud cover (Yoshihara and Ekern, 1977).

Most plants have the ability to adjust to changes in light regimes through both morphological and physiological changes. Shading generally causes elongated growth, reduced specific leaf weights (SLW), and increased shoot/root ratio of legume (Cooper and Qualls, 1967;

Bowes *et al.*, 1972; Straley and Cooper, 1972; Wolf and Blaser, 1972; Singh *et al.*, 1974; Ludlow *et al.*, 1974) and grasses (Early *et al.*, 1966; Paulsen and Smith, 1969; Silsbury, 1970; Woledge, 1971; Ludlow *et al.*, 1974).

Shading also reduced the number of tillers or runners of forage grasses and legumes (Mitchell, 1953; Alberda, 1957; Langer, 1963; Cooper and Tainton 1968; Ludlow *et al.*, 1974). However, the number of tillers or runners is determined by the overall growth of the plant rather than the direct effect of light intensity (Ludlow *et al.*, 1974). de Guzman (1974) in his review article discusses the adaptability of some tropical grasses and legumes to shady conditions.

Under low light intensities the energy available for photosynthesis is limited. Consequently if soil nitrate is adequate, nitrate can accumulate in the plant with the result that shaded grasses have much higher apparent crude protein (total N) content and lower concentrations of total soluble carbohydrates than grasses grown in full daylight. This can present serious problems in forage quality when high rates of nitrogen fertilizer are used under low light conditions (Bathurst and Mitchell, 1958; Deinum, 1966; Hight *et al.*, 1968; Myhr and Saebo, 1969; Paulsen and Smith, 1969; Mayland and Grunes, 1974).

Shading decreased percent dry matter without affecting the total crude protein content in a New Zealand study (Bathurst and Mitchell, 1958). Temperate grasses grown under shady conditions and a higher mineral content in several experiments: Cunningham and Nielsen, 1965; Myhr and Saebo, 1969; Mayland and Grunes, 1974. Cunningham and Nielsen (1965) reported that total cations were positively correlated

with N content, and at equal nitrogen percentage more total cations entered the grass in a dull than a sunny year, or a cloudy than in clear weather.

Some grasses and legumes are more shade tolerant than others (Blackman and Templeman, 1938; Santhirasegaram and Fernandez, 1967; Richards and Bevedge 1969; Ranacou, 1972; Eriksen, 1974). Ranacou (1972) found centro (*Centrosema pubescens* Benth.) and greenleaf desmodium (*Desmodium intortum* (Mill.) Urb.) to be more shade tolerant than siratro (*Macroptilium atropurpureum* (D.C.) Urb.) Tinaroo glycine (*Glycine wightii* (R. Graham. ex Wight & Arn.) Verdc.) or stylo (*Stylosanthes guyanensis* (Aubl.) Scv.) when grown under 100, 70 50 and 30% of daylight. *Brachiaria miliiformis* (Presl.) A. Chase was found to be more shade tolerant than *B. brizantha* Hochst. ex. Chiov. when growth was compared under 100 and 25% daylight (Santhirasegaram and Fernandez, 1967).

The experiment reported here was conducted to more fully define the effects of shading on two forage grasses and one forage legume grown in pots and subjected to various proportions of daylight.

MATERIALS AND METHODS

A pot experiment was conducted at the Mauka Campus Facility of the College of Tropical Agriculture (21° 05' N and 156° 22' W, air temperature range 20-27 C) to compare the plant growth and morphology of the climbing legume centro (*Centrosema pubescens* Benth.) the bunch grass guineagrass (*Panicum maximum* Jacq.) and the stoloniferous grass corigrass (*Brachiaria miliiformis* (Presl. A. Chase) when different light regimes were provided using polypropylene shade cloth (70, 45 and

13% of full daylight), compared with lath shades which intercepted the same proportions of light as the propylene materials. Seventy and 45% of daylight were provided by stretching polypropylene shade cloth over the tops and sides of wooden frames; 13% daylight was provided by covering the frames with 2 layers of shade cloth, and rated at 27% and the other at 45% light interception. Wooden laths 3.8 cm x 0.6 cm thick were applied to similar frames at varying intervals to provide 70 and 45% daylight, and 20 cm wide x 0.3 cm thick plywood strips were used for providing 13% daylight. The experiment was laid out as a completely randomized 2 x 3 factorial design (2 shade materials; 3 light intensities) with 4 replications and full daylight as a check. Data from each of the 3 plant species were statistically analyzed separately.

The plants were grown in plastic pots, (23 cm diameter x 30 cm high) filled with Makiki stoney clay loam. At the time of establishment the equivalent of 100 kg/ha of P as treble super-phosphate and 100 kg/ha of K as muriate of potash were applied, and 50 kg/ha of P and 50 kg/ha of K were applied every 6 months subsequently. Nitrogen was applied to the grasses at a rate of 100 kg/ha of N as ammonium sulphate at time of establishment and 80 kg/ha after each cutting. The plants were watered twice daily using an overhead sprinkler system.

Prior to planting, centro seeds were scarified in concentrated H_2SO_4 for 5 min., inoculated using a commercial peat culture, and coated with rock phosphate. Guineagrass was established from seeds, and corigrass was established from three 15 cm cuttings per pot. Three weeks after establishment (October 20, 1974) centro and guineagrass were thinned to 3 plants per pot. A wire trellis (90 cm diameter x

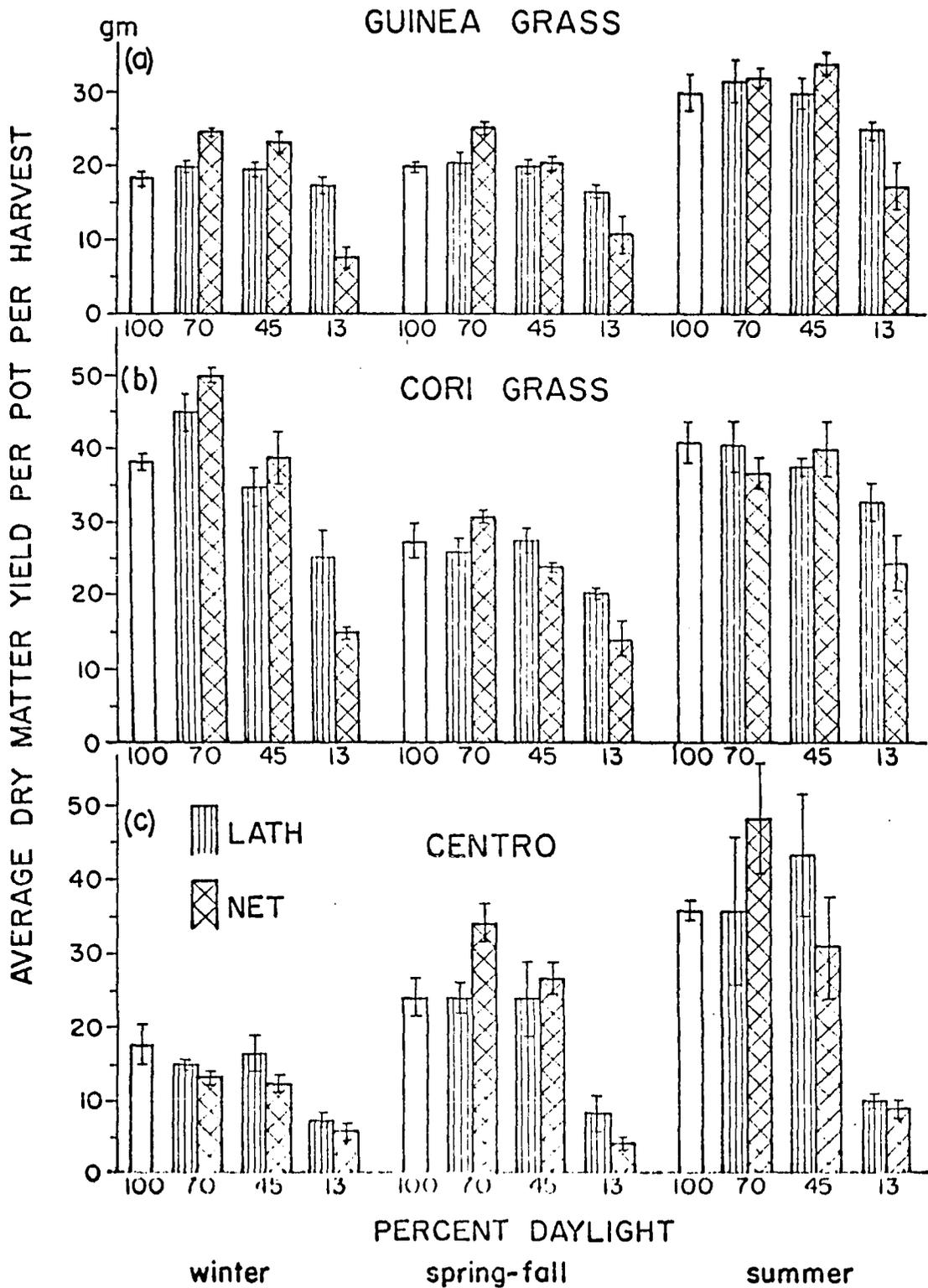
100 cm high) was placed above the centro pots to support the vines. The plants were harvested every 8 weeks over the period February 1975 to February 1976.

Measurements taken included: 1) green weight; 2) dry weight measured by drying the samples at 55C to constant weight; 3) nitrogen content of the dried and ground samples by Kjeldahl digestion (0.5g. sample, with CuSO_4 and Selenized Hengar granule catalysts) followed by determination of NH_4 by Nesslerization using an automatic analyzer; 4) mineral content (Ca, K, P, Mg, Si, S, Al, Mn, Fe, Cu, Zn) for the August 1975 and February 1976 harvests by X-ray fluorescence quantometer; 5) plant height for the August, December and February harvests; 6) number of flowering panicles for the grasses prior to harvesting for the August, October, December and February harvests; 7) number of centro pods/pot for the December harvest; 8) number of upright and horizontal tillers on corigrass, and number of tillers (all upright) on guineagrass for the August, December and February harvests; and 9) dry weights of root and stubble at time of completion of the experiment.

RESULTS AND DISCUSSION

Forage production and root development. Dry matter (DM) yields of 8 weeks harvests of centro, guineagrass and corigrass were grouped according to season on the basis of similar light intensity responses: winter (7 December and 2 February), spring/fall (22 April and 13 October), and summer (16 June and 16 August). The effect of light regimes on DM yields was significant for all three species at all three seasons (Figure 1) with the greatest yield reduction under the most intense shade (13% of daylight). There was very little

Figure 1. Dry weight yields of guineagrass, corigrass
and centro grown in full daylight and
under two shading systems.



effect of shade on DM yields at 70 and 45% of daylight except for the winter crop of corigrass, where the yield at 70% daylight was about 20% higher than at 100 or 45% daylight. There was no statistical difference between the two shade systems, except at 13% daylight where netting reduced yields more than lath. The light intensity underneath the netting was probably below the light compensation point most of the day, whereas the plants underneath the lath received full daylight on a portion of their foliage most of the day.

Root dry weights at the final harvest 16 months after establishment were drastically reduced as light intensity decreased (Figure 2). The effects of shade materials on centro root weights were not significant but the decrease in grass root weights was significantly greater under netting than under lath, with the difference being most pronounced under the most intense shade (13% of daylight). The depressing effect of shade on root weights significantly exceeded the effect of shade on top weights at all seasons and on all three forages, except for centro at 70% daylight. This had the effect of widening the top/root ratios of the shaded plants, as reported by Ludlow *et al.* (1974) for ruzi grass (*Brachiaria ruziziensis* Germain *et* Everard), siratro (*Macroptilium atropurpureum*), and calopo (*Calopogonium mucunoides* Desv.).

Burton *et al.* (1959) used the green weight of new growth of coastal bermudagrass (*Cynodon dactylon* (L.) Pers.) as an index of the reserves left below ground at the end of one season by growing field plugs (6" diameter x 6" deep) in tin cans under a greenhouse bench for 33 days. The yield from the plugs grown in the field at 43% and 29% daylight only yielded 28% and 5% respectively of the yield recorded from plugs grown at full daylight.

Figure 2. Dry weights of roots at the final harvest of centro and of two grasses (guineagrass and corigrass) grown in full daylight and under two shading systems.

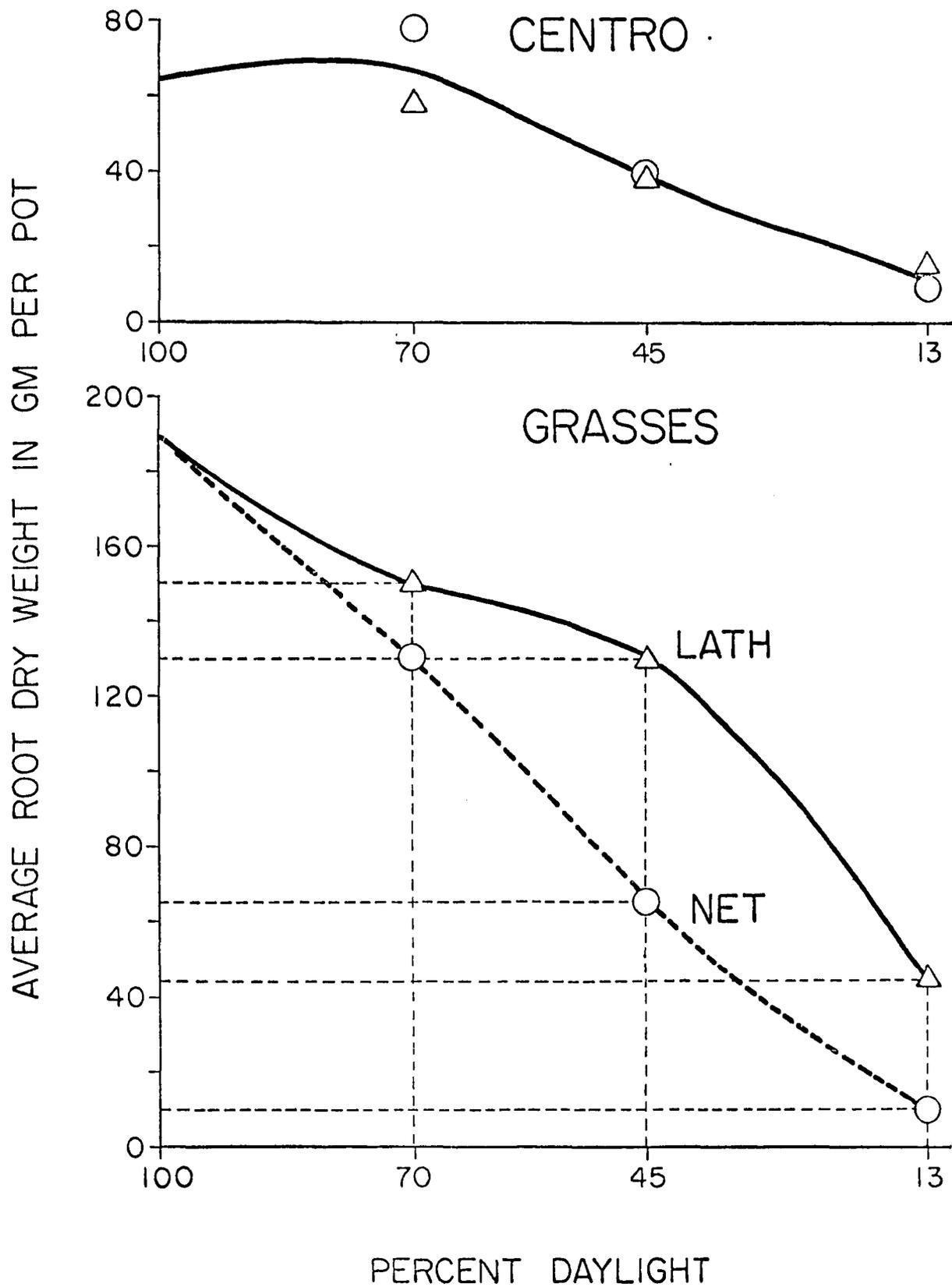
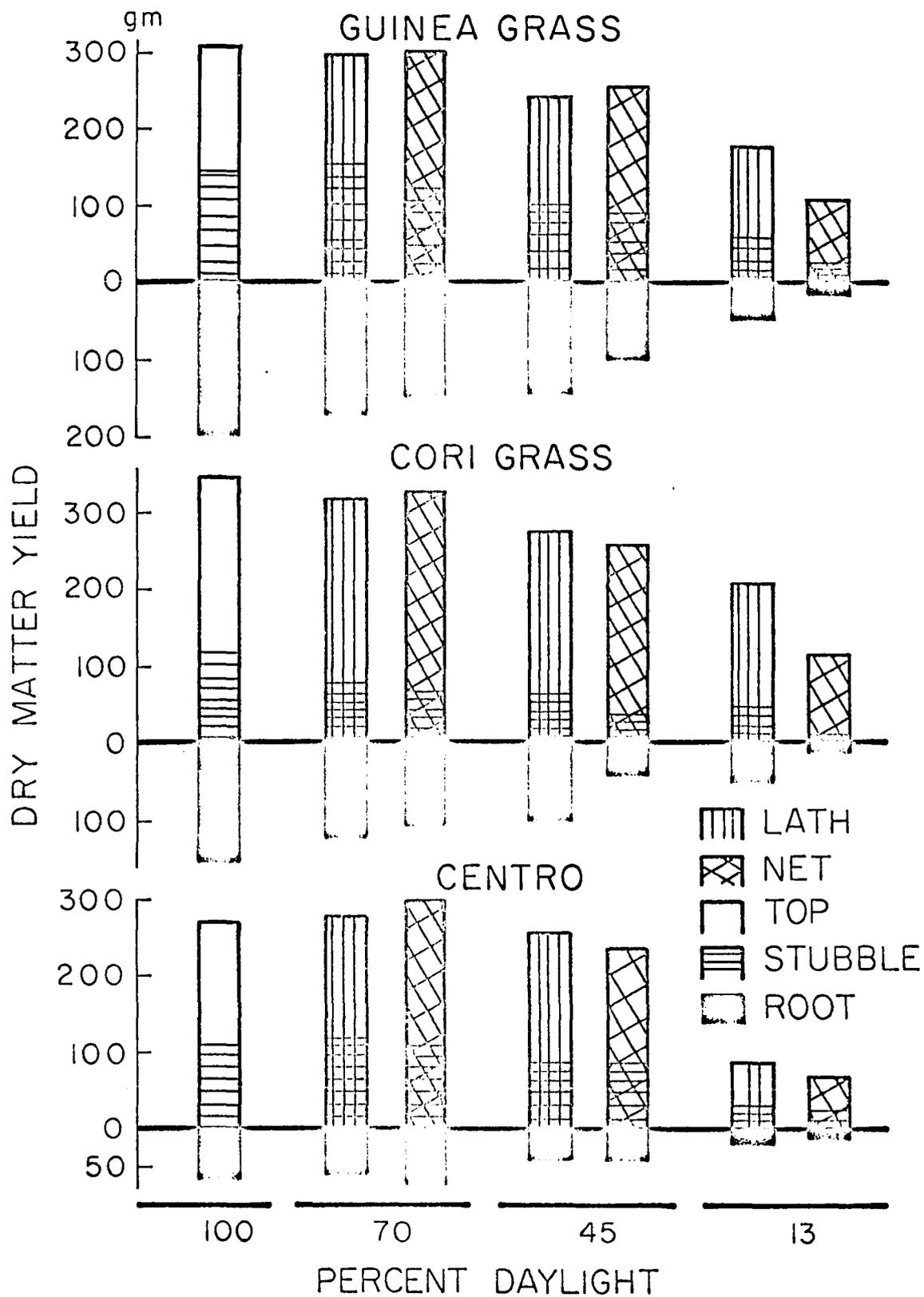


Figure 3. Total dry matter yield of tops (total of 6 harvests),
stubbles and roots after 16 months growth of guineagrass,
corigrass and centro grown in full daylight and
under two shading systems.



The total DM yields of forage for 6 harvests plus stubble and root weights at the final harvest are shown in Figure 3. As mentioned earlier there was little difference in the harvested DM yields of the grasses at 100, 70 and 45% daylight. However when the yields of tops, stubble, and roots over the 16 months period were combined, the total DM yield decreased significantly with decreasing light intensity. As reported by Deinum (1966), the plants adapted to the lower light intensities by translocating a lower proportion of the assimilates to the roots. Because of the lower carbohydrate reserves under shaded conditions, a slower regrowth after grazing would be expected. Therefore heavy grazing of shaded pastures should be avoided, and the intervals between grazings should be longer than for pastures grown under full daylight.

Dry matter content. Percentage DM decreased with decreasing light intensity for all species (Figure 4), and the decrease was significantly greater under netting than under lath. Plants grown under 45% daylight (netting) had only 78-80% as much DM per unit of fresh forage as plants grown under full daylight (or 70% daylight - lath) and those under 13% daylight (netting) had only 60 - 69% as much DM. This has important implications for cattle production since ruminants can only consume a fixed volume of fresh forage per day, and would not obtain adequate nutrients from forage too high in moisture. It is a general observation that during the rainy season, which is characterized by heavy cloud cover, animal growth declines even though forage is abundant. Since shading by lath reduced DM content less than shading by netting, the data suggest that animal gains on pastures beneath plantation trees, such as coconuts (40 - 80% daylight) would be less

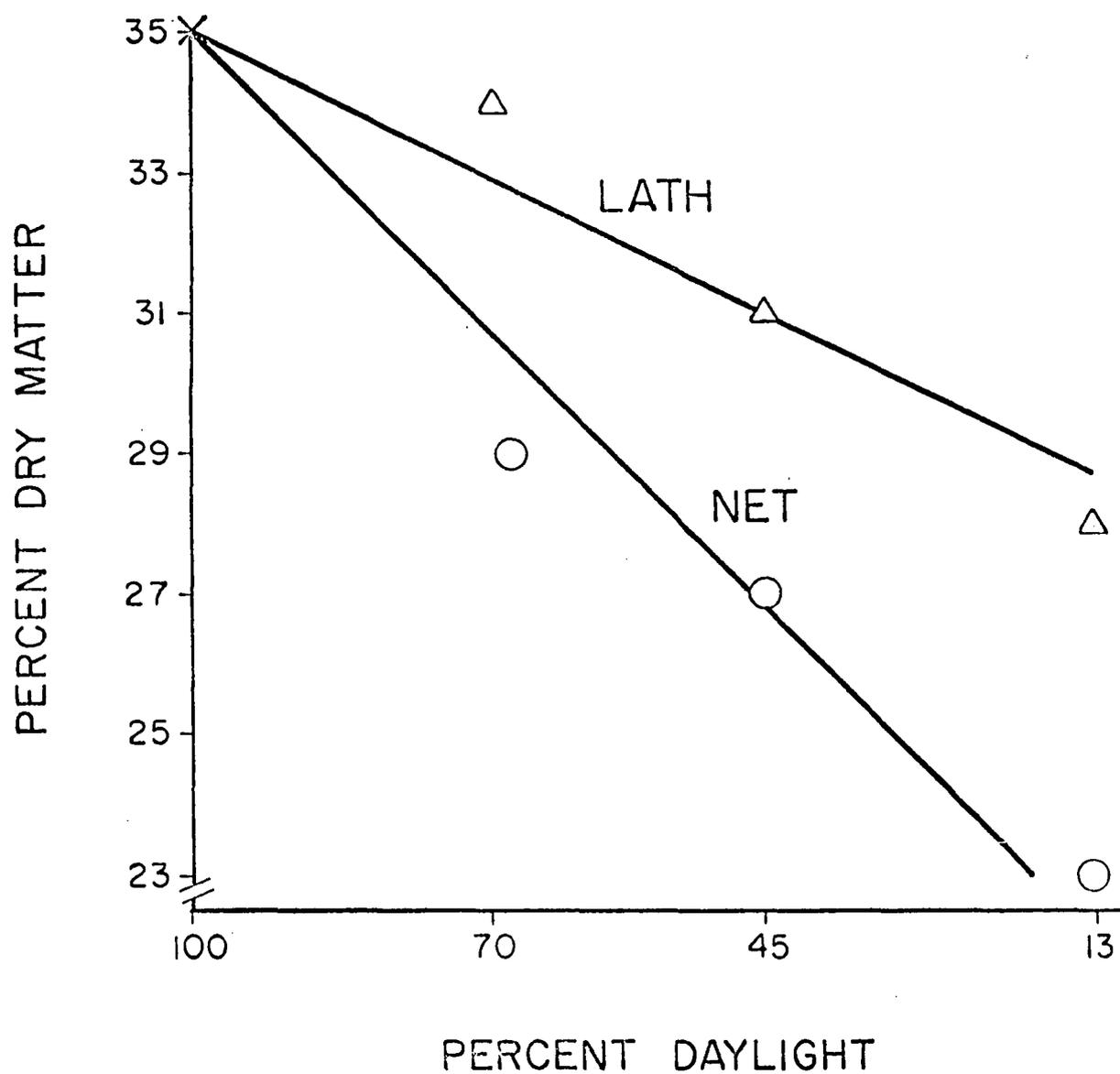


Figure 4. Average dry matter percentage of guineagrass, corigrass and centro grown in full daylight and under two shading systems.

affected than by the same levels of shading caused by heavy cloud cover.

Plant height, tiller formation and flowering. Plant height of guineagrass and corigrass increased significantly with decreasing light intensity (Figure 5) at all three seasons measured (Figure 6). Corigrass grown under 13% daylight was four times as tall as when grown without shading and guineagrass was twice as tall. Both grasses were significantly taller by 5-23 cm when grown under netting than when grown under lath. Both grasses were tallest at the August harvest probably due to more vigorous growth under the warmer air temperatures. Elongated growth of grasses grown under low light intensity has also been reported by several others, e.g. Early *et al.* (1966), Paulsen and Smith (1969), and Pyon (1976). Shading of corigrass caused tillers to grow upright rather than prostrate. Number of upright and prostrate tillers of corigrass grown in full daylight and under the two shading systems for the August, December and February harvest were not significantly different and the averages are presented in Figure 7. Shading by netting caused the greatest change under all shade levels, with 70, 45 and 13% daylight (as netting) having 45, 12 and 1% prostrate tillers, compared to 93, 23 and 6% prostrate tillers when shaded by lath. These results indicate that the quality of the light is more important for the control of stem elongation and tiller morphology than the total amount of light received.

Shading also affected tiller number in guineagrass, but the effect was significant only under 13% daylight; tillers per pot were 60-70 under full daylight and moderate shading, 41 for 13% lath and 32 for 13% netting. Tiller formation in cori grass was highest under 45% netting (152 tillers) and 13% lath (143 tillers). The other

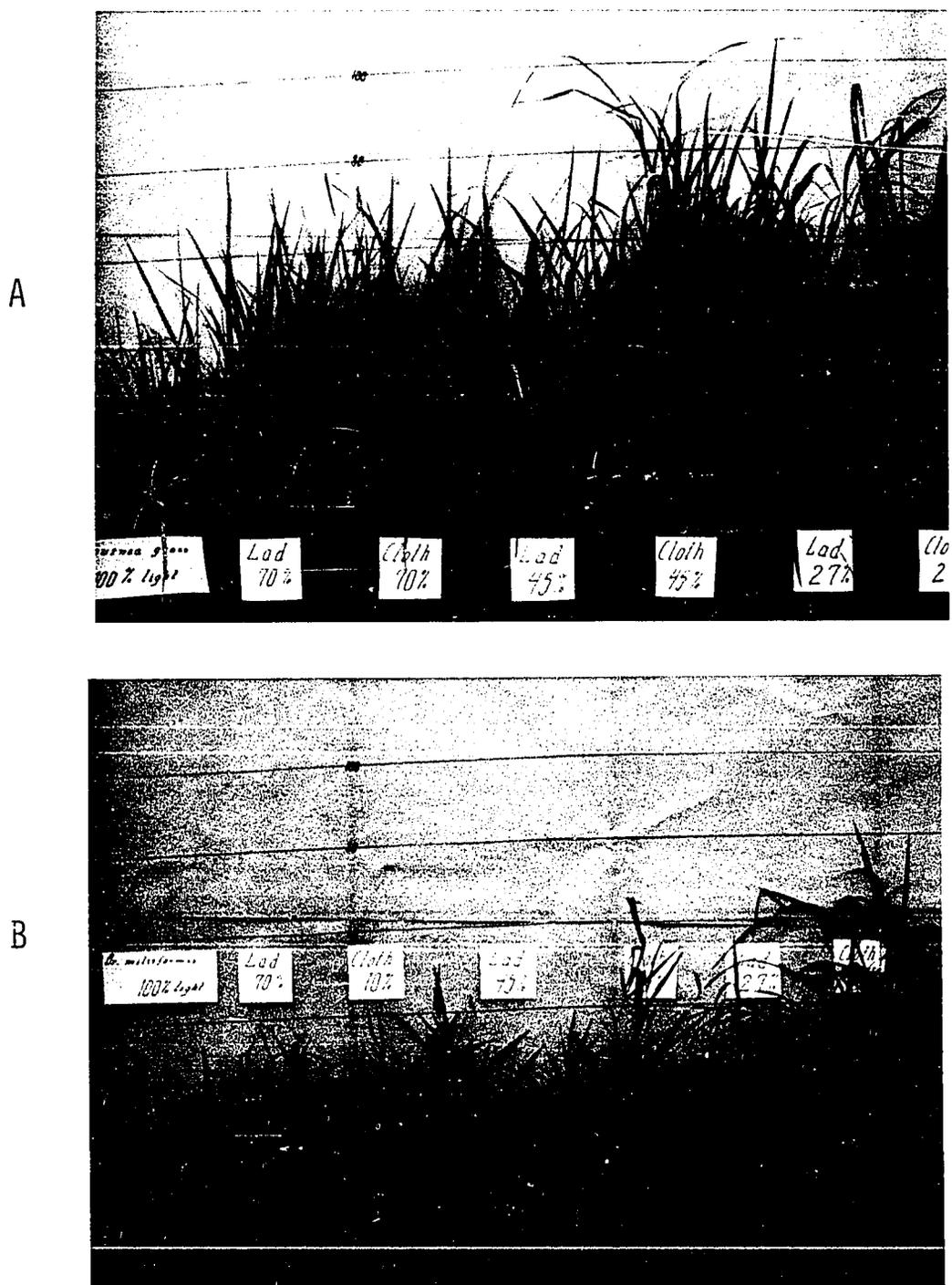


Figure 5. Effect of shading on plant growth of A) guineagrass and B) corigrass (note: "lad" refers to shading by lath strips and "cloth" refers to shading by polypropylene shade cloth).

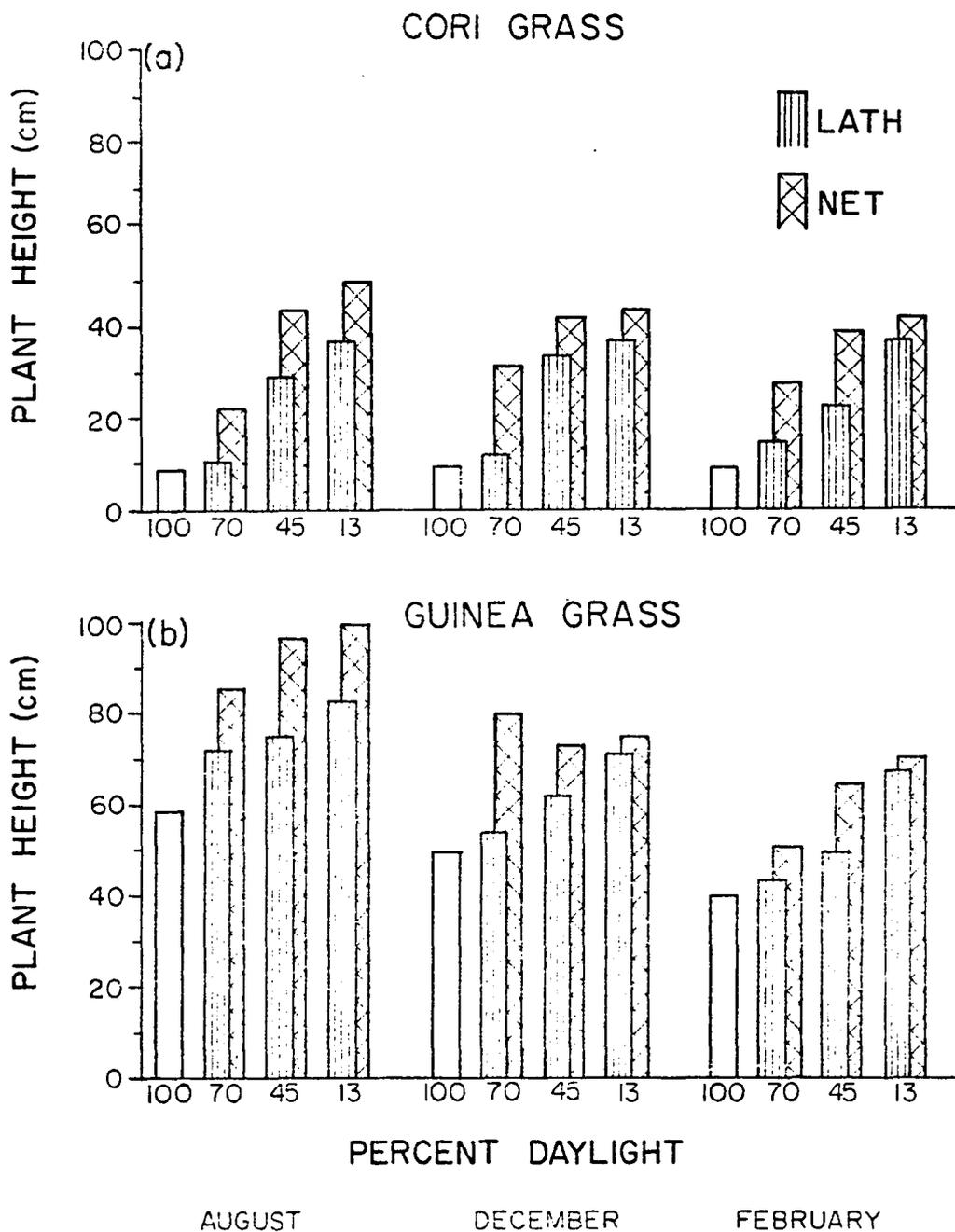


Figure 6. Plant height of guineagrass and corigrass after 8 weeks regrowth when grown in full daylight and under two shading systems.

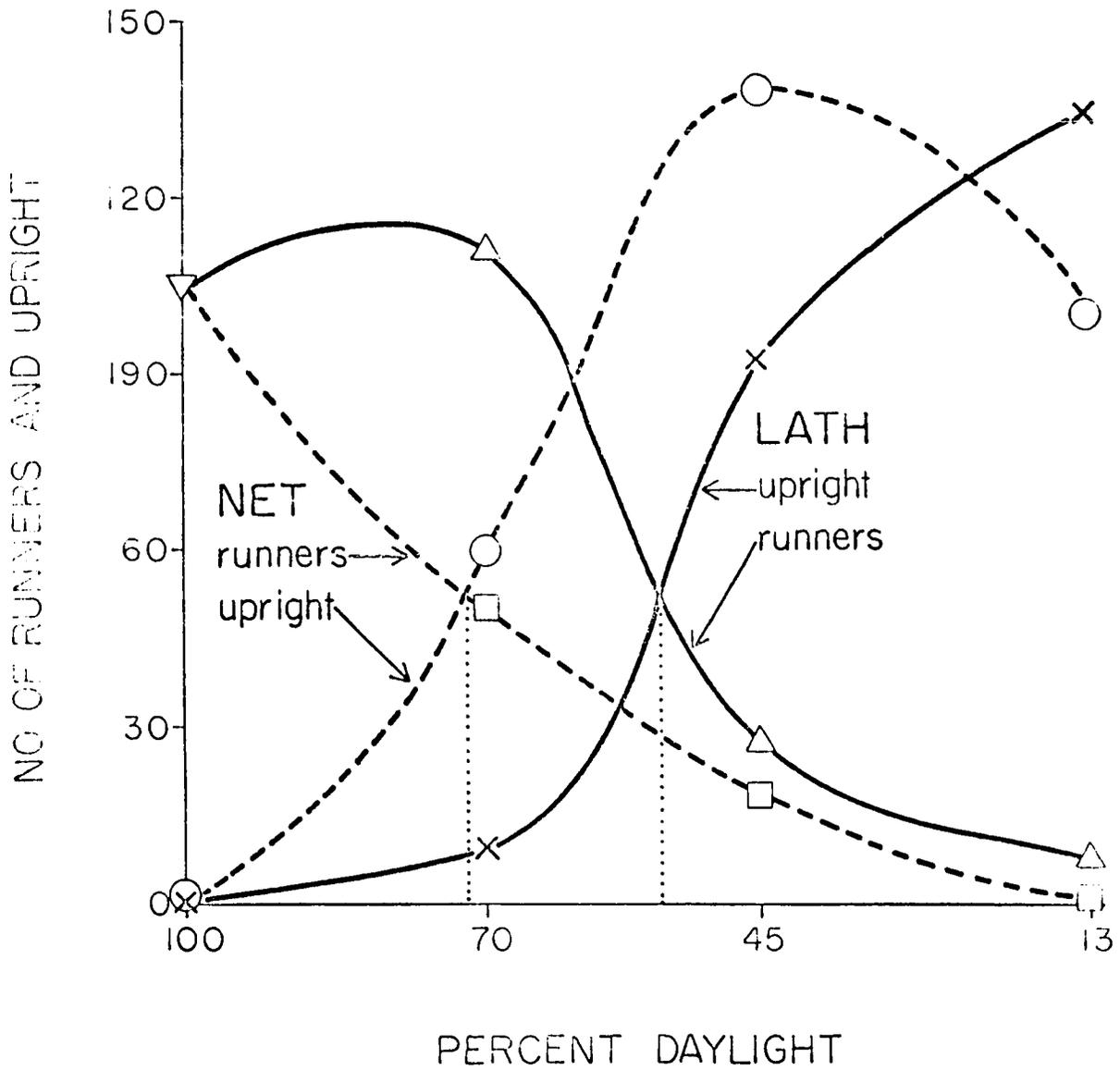


Figure 7. Development of upright and prostrate stems of corigrass grown in full daylight and under two shading systems.

treatments all had between 105-120 tillers per pot. The weight per tiller did not differ significantly between light regimes in guinea-grass, but corigrass tiller weights were significantly lower under 13% daylight (both netting and lath) and under 45% netting. Differences among species with respect to light intensity effects on tiller weight and number have been reported by others. For example, Horricks and Washko (1971) observed more but lighter tillers when reed canarygrass (*Phalaris arundinacea* L.) and "Climax" timothy (*Phleum pratense* L.) were grown under 40% daylight. However other authors have reported that shading decreased tiller number in temperate grasses (Alberda, 1957; Mitchell, 1957; Ryle, 1961). Shading was also reported to decrease tiller number in the tropical grasses ruzigrass (*Brachiaria ruziziensis*) and green panic (*Panicum maximum* var. *trichoglume* Eyles, (Ludlow *et al.*, 1974). Tiller weight of ruzigrass was not affected by shading, but shading drastically decreased tiller weights of green panic.

Flower and seed development were suppressed by decreasing light intensity (Table 1). Guinea-grass had few or no flowering tillers during the six month period August to February. Corigrass had no flowering tillers in August or October and only 2 to 3 tillers per pot in February. However in December corigrass had 45-61 flowering tillers/pot at 100 and 70% daylight, but only 5 or less at 45 and 13% daylight.

Shading significantly reduced pod number of centro with the greatest effect occurring under the netting at the 45 and 13% levels. Plants shaded by lath had four times as many pods as plants shaded by netting.

Table 1. Flowering behaviour of guineagrass and corigrass and seed pod production by centro grown in full daylight and under two shading systems.

Light regime	Avg. no. of flowering tillers/pot					Avg. no. of pods/pot
	guineagrass			corigrass		centro
	Aug.	Oct.	Dec.	Dec.	Feb.	Dec.
100	3	2	1	61	3	68
70 lath	5	2	1	45	2	41
70 net	1	1	0	58	3	23
45 lath	2	0	0	5	0	17
45 net	0	0	0	5	0	4
13 lath	0	0	0	5	0	9
13 net	0	0	0	1	0	2

Mineral content. Shading affected the content of various mineral nutrients both in the grasses (Table 2) and in centro (Table 3). Grasses grown under shade contained higher concentrations of the micro-nutrients N, P, K, Ca, Mg, S and Si and the micro-nutrient Fe at both seasons than did grasses grown in full daylight. The concentration of Zn did not vary significantly between treatments. The highest concentrations of all minerals (except K and Si) were found during the cool season. There were no apparent shading effects on the plant levels of Al, Mn and Cu (not shown). Concentration of Al varied between 54-190 ppm for both grasses. Cu content was much lower in guineagrass (1-2 ppm) than corigrass (3-6 ppm) at both seasons. Similarly, Mn concentration was lower in guineagrass (about 10 ppm both seasons) than in corigrass (16 ppm summer, 24 ppm cool season). Nitrogen concentration of both grasses increased with decreasing light intensity at both seasons. These results are similar to those reported

Table 2. The mineral content of guineagrass under different light regimes at two seasons; and the relationship between plant height (light intensity indicator) and mineral content of guinea-grass and corigrass under similar conditions.

Element	Season	Mineral content of guineagrass at light regime						Correlation between plant height (x) and mineral content (y)						
		100	70		45		13		guineagrass			corigrass		
			lath	net	lath	net	lath	net	slope	intc.	r	slope	intc.	r
N (%)	summer	0.55	0.59	0.63	0.63	0.63	0.66	1.08	0.0069	0.12	0.53	0.0117	0.24	0.58
	winter	0.76	0.96	1.01	1.01	1.10	1.62	1.85	0.0269	-0.30	0.84	0.0242	0.29	0.72
P (%)	summer	0.13	0.13	0.15	0.15	0.16	0.16	0.22	0.0012	0.06	0.58	0.0014	0.13	0.53
	winter	0.26	0.26	0.27	0.26	0.30	0.27	0.25	0.0001	0.26	0.18	0.0012	0.21	0.40
K (%)	summer	0.68	0.81	1.05	0.90	1.33	1.22	1.83	0.0201	-0.56	0.65	0.0233	0.69	0.70
	winter	0.57	0.74	0.91	0.78	1.21	1.30	1.75	0.0304	-0.64	0.92	0.0278	0.32	0.73
Ca (%)	summer	0.38	0.40	0.43	0.43	0.50	0.45	0.71	0.0045	0.09	0.74	0.0018	0.31	0.36
	winter	0.58	0.58	0.65	0.62	0.60	0.73	0.84	0.0066	0.30	0.72	0.0005	0.43	0.08
Mg (%)	summer	0.24	0.25	0.27	0.29	0.31	0.27	0.39	0.0027	0.07	0.82	0.0055	0.15	0.61
	winter	0.50	0.48	0.56	0.51	0.53	0.55	0.54	0.0016	0.43	0.38	0.0054	0.33	0.59
S (%)	summer	0.02	0.03	0.04	0.03	0.05	0.04	0.09	0.0009	-0.03	0.78	0.0019	0.04	0.66
	winter	0.05	0.06	0.06	0.06	0.06	0.09	0.10	0.0011	0.01	0.70	0.0028	0.05	0.64
Si (%)	summer	2.06	2.69	2.29	3.16	3.10	3.40	3.58	0.0086	2.38	0.39	0.0033	1.12	0.69
	winter	3.36	3.03	3.10	3.24	3.41	3.59	3.55	0.0115	2.69	0.53	0.0128	1.85	0.39
Fe (ppm)	summer	62	73	79	74	84	88	130	0.11	-4.4	0.77	1.69	58	0.55
	winter	90	99	111	93	98	97	150	0.91	58	0.47	-0.38	136	-0.12
Zn (ppm)	summer	20	14	15	15	16	12	18	-0.03	18	-0.07	0.11	19	0.24
	winter	33	34	26	33	34	42	53	0.46	11	0.56	0.76	29	0.58

t-test for significance of r (df = 26): P = 0.05, r>0.38; P = 0.01, r>0.47

Table 3. The mineral content of centro under different light regimes at two seasons; and the relationship between plant dry matter yield and mineral content.

Element	Season	Mineral content of centro at light regime								Correlation between dry matter yield (x) and element (y)		
		100	70		45		13		slope	intercept	r	
			lath	net	lath	net	lath	net				
N (%)	summer	2.34	2.24	2.50	2.28	2.63	2.45	2.77	-0.0013	2.49	-0.08	
	winter	2.30	2.55	2.61	2.65	2.67	2.90	3.12	-0.0011	2.98	-0.83	
P (%)	summer	0.20	0.19	0.19	0.18	0.21	0.22	0.23	-0.0006	0.22	-0.50	
	winter	0.24	0.25	0.28	0.24	0.26	0.24	0.25	-0.0001	0.25	-0.05	
K (%)	summer	1.06	1.10	1.26	1.15	1.39	1.52	1.45	-0.0024	1.34	-0.29	
	winter	0.84	1.00	1.11	0.80	1.33	0.90	1.22	-0.0075	1.22	-0.31	
Ca (%)	summer	0.97	0.91	0.94	1.04	1.02	1.04	1.08	0.0000	1.00	0.00	
	winter	0.85	0.80	0.86	0.95	0.82	1.00	1.19	-0.0063	1.09	-0.39	
Mg (%)	summer	0.43	0.40	0.40	0.44	0.40	0.34	0.38	0.0007	0.37	0.41	
	winter	0.37	0.31	0.34	0.37	0.31	0.36	0.36	0.0009	0.32	0.20	
S (%)	summer	0.15	0.15	0.16	0.17	0.18	0.19	0.23	-0.0006	0.19	-0.39	
	winter	0.14	0.15	0.16	0.18	0.16	0.19	0.21	-0.0015	0.20	-0.46	
Si (%)	summer	0.69	0.60	0.73	0.81	0.67	0.63	0.79	0.0002	0.69	0.04	
	winter	0.67	0.71	0.64	1.02	0.51	0.95	1.04	-0.0070	0.95	-0.25	
Fe (ppm)	summer	236	235	242	255	255	279	295	-0.013	281	-0.37	
	winter	154	167	177	205	201	190	259	-0.842	214	-0.18	
Zn (ppm)	summer	42	40	41	44	40	36	40	0.142	35	0.48	
	winter	53	53	57	68	57	67	71	-0.310	68	-0.22	

t-test for significance of r (df=26): P = 0.05, r>0.38; P = 0.01 r>0.47

for temperate grasses and legumes by Bathurst and Mitchell (1958) and for coastal bermudagrass (*Cynodon dactylon*) by Burton *et al.* (1959). Shading of centro by netting or lath had little or no effect on the concentration of nitrogen or other nutrients in the harvested portion. Cunningham *et al.* (1965) found that total cation content was positively correlated with N percentage. Since centro maintained constant N concentration under shading, cation concentrations were also not affected. Mineral levels of centro forage also were similar at the summer and cool season harvests (except Zn and Fe) in contrast to the grasses where the mineral content was higher during the cool season. The overall average concentrations of Al, Mn and Cu in centro varied between 70-170 ppm for Al, 20-26 ppm for Mn, and 16-21 ppm for Cu (not shown). Nitrogen content was determined for each harvest and was lowest in August and highest in February.

Grass tetany, a magnesium (Mg) deficiency in grazing ruminants occasionally occurs during periods of reduced radiation levels and is related to the ratio of K to the sum of Ca + Mg with a ratio greater than 2.2:1 being critical (Grunes *et al.*, 1970; Mayland and Grunes, 1974). However, the ratio of K/(Ca+Mg) in the species tested never exceeded 2.2, even at the lowest light intensities. However the ratio did increase with decreasing light intensity.

Plant height was chosen as a plant indicator of light intensity since it integrated the effects of both shade materials and percent transmission of light. This parameter was then correlated with the mineral levels found in the various treatments. In the grasses, the mineral contents of N, K, Mg, S and Si were all significantly correlated to plant height at both seasons, P levels in corigrass

and guineagrass (summer season only), while the micro-nutrients Zn and Fe were significantly correlated (one season only) for both grasses (Table 2). The correlation between calcium and plant height was highly significant for guineagrass but not for corigrass. The correlations between dry weight yield of centro and mineral content were very low for most of the elements. Only nitrogen for the winter harvest was highly correlated with yield, with 69% of the variation in yield accounted for by the variation in N percentage, but r^2 levels were less than 35% for the other minerals at both harvests.

The effects of shading on guineagrass, corigrass, and centro are summarized in Table 4. In general the data indicate that shading of forage grasses and legumes decreased DM yield, root weight and flowering, but increased mineral content on a dry weight basis, especially in the grasses. Plant height of the grasses was also increased with shading. The effect of shading on tiller weight and number was found to vary between grass species.

SUMMARY AND CONCLUSION

A pot experiment was conducted in Hawaii over a 16 month period to compare the plant growth and morphology of the climbing legume *Centrosema pubescens*, the bunch grass *Panicum maximum* and the stoloniferous grass *Brachiaria miliiformis* when different light regimes were provided using polypropylene shade cloth (70, 45 and 13% daylight), compared with laths intercepting the same proportions of light as the rated interception of the polypropylene materials.

Dry matter (DM) yields of the harvested portion at 100, 70 and 45% daylight were similar, while DM yields at 13% daylight was

Table 4. Effect of reduced light intensity (13% of full daylight) on growth and mineral analyses of two tropical grasses and one tropical legume.

Growth factor	Reduction (-) or increase (+) associated with reduced light*		
	guineagrass	corigrass	centro
DM yield	--	--	---
root dry weight	---	---	---
height	++	+++	N/A
tiller no.	--	+	N/A
tiller weight	0	--	N/A
flowering/pod no.	---	---	---
N concentration	++	++	+
P "	+	+	0
K "	+++	+++	+
Ca "	++	+	+
Mg "	+	++	0
S "	+++	++	+
Si "	++	++	+
Fe "	+	0	+
Zn "	0	0	0

*Key: N/A = not applicable, +++ = strong effect (> 100%), ++ = mod. effect (40-100%), + = slight effect (15-40%), 0 = \pm 15%, - = slight negative effect (15-40%), -- = mod. negative effect (40-100%), --- = strong negative effect (> 100%).

significantly lower ($P < .01$) than any other treatment. Root weights and stubble weights at the final harvest were drastically reduced as light intensity decreased, resulting in a significant decreased total dry matter production (top & stubble root weights) with decreasing light intensity. There was no statistical difference between shade materials, except at 13% daylight where netting reduced yields more than lath. Percentage DM decreased with decreasing light intensity, with a significantly greater decrease under netting than under lath for the grasses.

Plant height increased significantly with decreasing light intensity. Both grasses were significantly taller by 5-23 cm when grown under netting than when grown under lath. Shading of *B. miliiformis* caused a morphological change in tiller growth from prostrate to upright. Weight per tiller did not differ between light regimes in *P. maximum*, but was lower at moderate to heavy shading in *B. miliiformis*. Flower and pod development was suppressed by decreasing light intensity especially under netting.

Shaded grasses contained higher concentrations of the macro-nutrients N, P, K, Ca, Mg, S and Si and the micro-nutrient Fe than unshaded grasses. Mineral levels were generally highest during the cool-season. There was no apparent shading effect on the plant levels of Al, Mn and Cu. Shading of centro had little or no effect on the concentration of nitrogen or other nutrients in the harvested portion.

CHAPTER IV

THE EFFECT OF LIGHT INTENSITIES AND N-FERTILIZER ON MORPHOLOGY, YIELD, MINERAL CONTENT AND ACETYLENE REDUCTION OF SIX TROPICAL FORAGE GRASSES

INTRODUCTION

Decreased dry-matter (DM) production under reduced light intensity has been found with many grass and legume species (Blackman and Templeman, 1938; Alberda, 1957; Burton *et al.*, 1959; Deinum, 1966; Santhirasegaram *et al.*, 1966; Ludlow *et al.*, 1974), but the magnitude of the effect on the growth will depend on the stage of growth and on concurrent temperature, moisture and nutrient (especially nitrogen) stresses.

Positive interactions between light intensity and nitrogen application have been reported for several temperate grasses (Blackman and Templeman, 1938; Burton *et al.*, 1959; Deinum, 1966). For example, Blackman and Templeman (1938) reported that shading to 61 and 44% of daylight did not effect the yield of *Agrostis tenuis* Sibth. and *Festuca rubra* L. at low nitrogen fertilization. When nitrogen fertilizer was added the yield increased drastically in normal daylight, but not in the shade. *Trifolium repens* L. yields were highest in normal daylight with little response to nitrogen fertilization, due to *T. repens* ability to fix its own nitrogen. Deinum (1966) reported

that DM and nitrogen yields were higher at reduced light intensities ($100 \text{ cal cm}^{-2} \text{ day}^{-1}$) when nitrogen was deficient. However when the yields of stubble and roots were included, total yields were equal at all light intensities, since the plants adapted to the lower light intensity by translocating a lower proportion of the assimilates to the roots. Increased shoot:root ratios under low light intensity have also been reported for both tropical and temperate grasses and legumes by others (Burton *et al.*, 1959; Ludlow *et al.*, 1974).

Shading of grasses and legumes generally causes elongated growth, reduced specific leaf weight (SLW) and increased leaf area ratio (LAR) of legumes (Cooper and Qualls, 1967; Straley and Cooper, 1972; Wolf and Blaser, 1972; Ludlow *et al.*, 1974; Singh *et al.*, 1974) and grasses (Early *et al.*, 1966; Paulsen and Smith, 1969; Woledge, 1971; Ludlow *et al.*, 1974; Pyon, 1976).

The nitrogen and mineral contents (dry weight basis) of grasses usually increase with shading, but nitrogen and mineral contents of legumes are not greatly affected by shading (Bathurst and Mitchell, 1959; Burton *et al.*, 1959; Gordon, 1962). Cunningham and Nielsen (1965) reported that total cations were positively correlated with N-content. Myhr and Saebo (1969) and Mayland and Grunes, (1974) report similar results.

Plants grown in the shade are more succulent, resulting in a lower DM percentage in shaded plants, (Gordon *et al.*, 1962).

Little work has been done on the effect of shading on tropical forage grasses and legumes. However such studies could be very useful since there are extensive areas in the tropics where grazing could be profitably carried out under coconut palms (Hugh, 1972; Javier, 1974;

Mac Evoy, 1974) and other plantation crops. Also total solar radiation at different locations and at different seasons varies greatly depending on cloud cover. In Hawaii solar radiation in different areas varies from 429 to 704 cal sq cm⁻² day⁻¹ in summer time and from 241 to 426 cal sq cm⁻² day⁻¹ in winter time (Yoshihara and Ekern, 1977).

The experiment reported here were therefore carried out in order to assess the effect of shading on the performance of six tropical grasses fertilized with N (365 kg N, ha⁻¹ yr⁻¹) or given no N fertilizer.

MATERIALS AND METHODS

Six grasses were grown on an Oxic Haplustoll near Paia, Hawaii (20°55'N and 156°22'W, 100 meters above sea level) during the period July 1975 to February 1977. Grasses which were replicated three times included: corigrass (*Brachiaria miliiformis* (Presl.) A. Chase), Mealani hybrid digitgrass (*digitaria decumbens* Stent.), and guineagrass (*Panicum maximum* Jacq.). Grasses which were not replicated included: signalgrass (*Brachiaria brizantha* Hochst. ex. A. Rich.), kikuyugrass (*Pennisetum clandestinum* Hochst. ex. Chiov.) and napiergrass 3418 (*Pennisetum purpureum* Schumach.). Each species was grown under two nitrogen levels: without N ("minus-N"), and with 365 kg N ha⁻¹ yr⁻¹ as urea broadcast after each cutting ("plus-N"). The plants were grown under four different light regimes: 100, 70, 45 and 27% of full daylight, by shading with three densities of polypropylene screening. The screening was stretched over the plots 1.9 m above the ground, to allow air circulation and easy passage underneath. The sides facing East and West slanted down at a 45° angle to 1 m above the ground, to shade the plants from morning and evening sun. Each shaded block measured

12.2 x 13.4 m (Appendix Figure 1).

Before planting, phosphate and potash were applied at a rate of 150 kg/ha of P as treble superphosphate and 180 kg/ha of K as muriate of potash. Lime was applied at a rate of 3400 kg/ha to increase the pH to about 6.3. An additional 80 kg/ha of P was applied one year later and an additional 90 kg/ha of K was applied at 6 months and 12 months after establishment.

Watering was by subsurface drip irrigation using polyethylene tubes (13 mm inside diameter) buried 15 cm deep and spaced at 90 cm intervals. Emitter spacing was varied so that treatments receiving 100, 70, 45 and 27% daylight received water in proportions of 100, 89, 72 and 50.

Three replications of a split-split plot arrangement were used, with light regimes as whole plots, species as sub-plots, and grass N-levels as sub-sub-plots. Each sub-sub-plot measured 2.0 x 2.6 m. The total area harvested for yield determination per plot was 2.7 m² (Appendix Figure 2).

Guineagrass was established from seeds and the other grasses were established by vegetative propagation. The experiment was established on July 27-29, 1975, shaded 2 month later, and the species harvested every 8 weeks during the period November 1975 to February 1977. All species were cut at 4-7 cm above the ground using a small sickle-bar mower, except for guineagrass (cut at 15 cm) and napiergrass (30 cm).

Measurements taken included: 1) green weight; 2) dry weight measured by drying the samples at 55 C to constant weight; 3) nitrogen content of the dried and ground samples by Kjeldahl digestion (0.5 gm sample) with CuSO₄ and selenized Hengar granule catalysts followed by

determination of NH_4 using an automatic analyzer; 4) mineral content (P, K, Ca, Mg, Si, S, Cu, Zn) for the March 9, and August 25 harvests by X-ray fluorescence quantometer; 5) sward height measured after 8 weeks regrowth on March 5 and August 24, 1976; 6) area:dry weight ratio of the foliage (leaves plus stem) and leaf-plus stem area index at the August 29, 1976 and February 9, 1977 harvests based on the projected area of three weighed subsamples of chopped fresh forage per plot using an optical planimeter (Davis *et al.*, 1966. Modified); 7) nitrogenase activity (measured as acetylene reduction) of undisturbed soil cores (17 cm diameter x 20 cm depth) incubated for 24 hours with 5% acetylene (95% air) and subsequently measured for ethylene production by gas chromatography; 8) root dry weights based on a sampled soil volume of 30 x 30 cm in each plot at completion of the experiment.

Results were analyzed statistically using split-split plot analysis of variance and the Bayes LSD. The results from the non-replicated species were adjusted using the procedures for augmented designs described by Federer (1956).

RESULTS AND DISCUSSION

The solar radiation in full daylight and the average daily temperature under a grass sward at 5 cm depth at noon for 100 and 27% daylight during the experimental period is shown in Figure 8. The soil temperature under 27% daylight was between 0.8 C (cool season) and 2.0 C (summer) lower than full daylight, with 45 and 70% daylight in-between.

During summer (June-August) the shade treatments resulted in average levels of radiation (in $\text{cal cm}^{-2} \text{ day}^{-1}$) of about 660 (100% day-

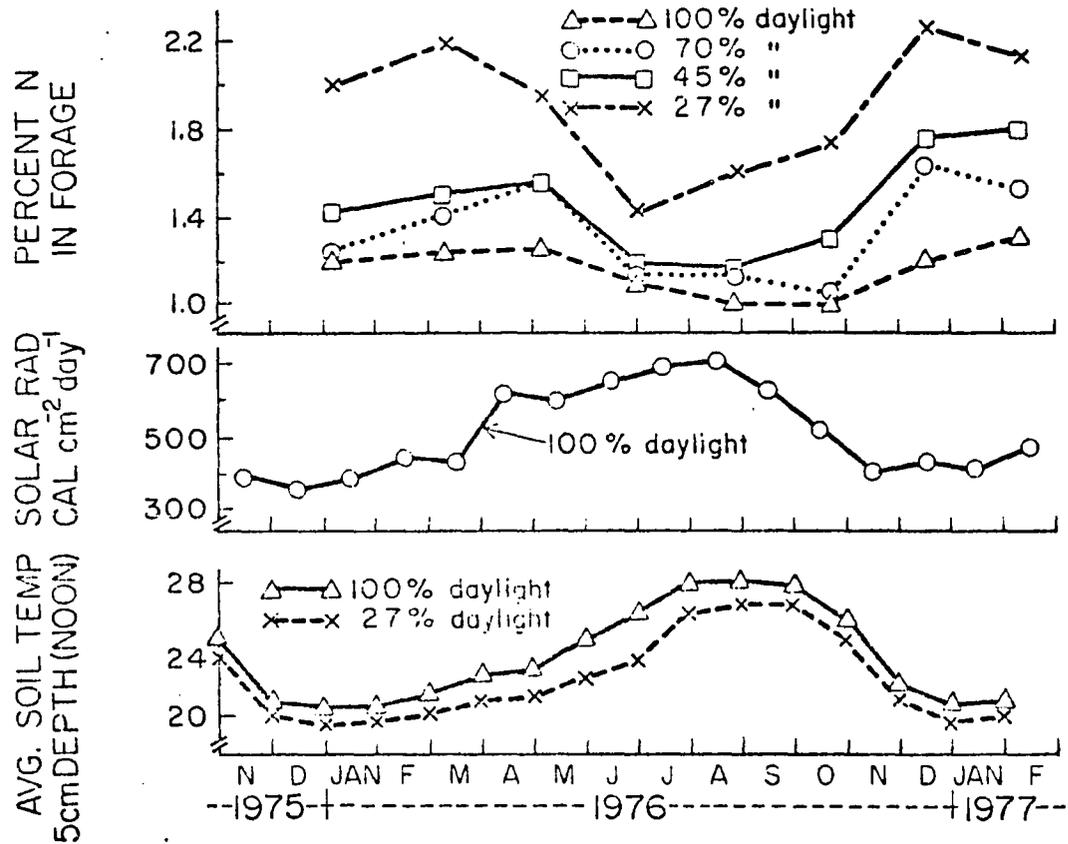


Figure 8. Percent nitrogen of tropical forage grasses grown at four light intensities in relation to solar radiation and soil temperature at 5 cm depth.

light), 462 (70% daylight), 297 (45% daylight), and 178 (27% daylight). During the cool season (December-February) these values were, respectively: 380, 266, 171, and 103.

Conditions were therefore generally suitable for growth of the species tested, although there were some seasonal variations in growth as noted in the following sections.

Dry matter yields. The three replicated grasses (guineagrass, Mealani digitgrass, and corigrass) all responded markedly to application of N when grown at 100 or 70% daylight. Annual dry matter (DM) yields of the plus-N treatments at 100 and 70% daylight were 2.5 to 3.5 times higher than comparable minus-N plots (Figure 9). At 27% daylight, however, the plus-N plots yielded only 1.4 times the yield of the minus-N plots (also see photographs Figure 10, 11 and 12). Yields of the minus-N treatments were highest at 45% daylight for guineagrass and Mealani digitgrass while the yield of corigrass was highest at 27% daylight. Thus in the absence of N fertilization, nitrogen rather than light was the limiting growth factor for grass growth. It may therefore be concluded that the light x N-level interactions shown by these tropical grasses are similar to the temperate grasses studied earlier by Blackman and Templeman (1938) and Deinum (1966).

Yields were adjusted according to Federer (1956) for replication effects of the unreplicated grasses. The results showed strong species interaction with light intensity (Figure 13). Napiergrass was very high yielding, except under the 27% daylight treatment; signalgrass yields were moderately high and were not significantly affected by shading; and kikuyugrass yielded poorly at all light intensities and

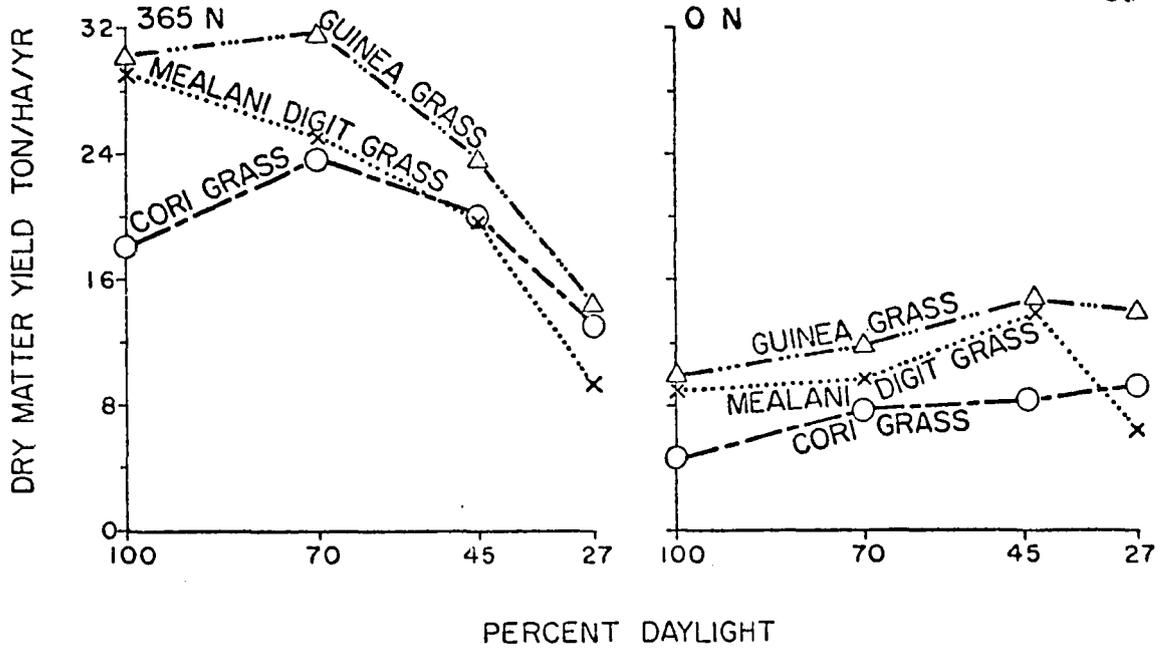


Figure 9. The effect of shading on the annual dry matter yield of forage grasses at two nitrogen levels. Average of three replications.

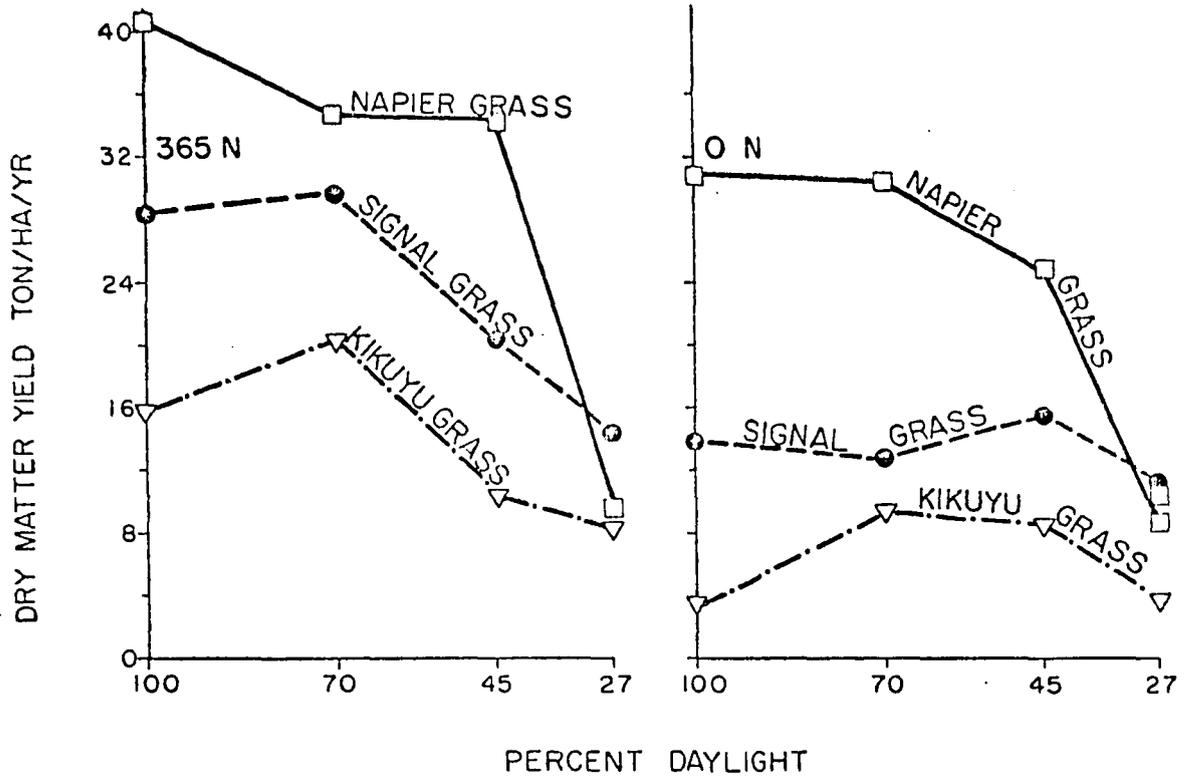


Figure 13. The effect of shading on the annual dry matter yield of unreplicated forage grasses at two nitrogen levels. Yields adjusted for replication effects.



Figure 10. Growth of guineagrass at 100 and 27% daylight.

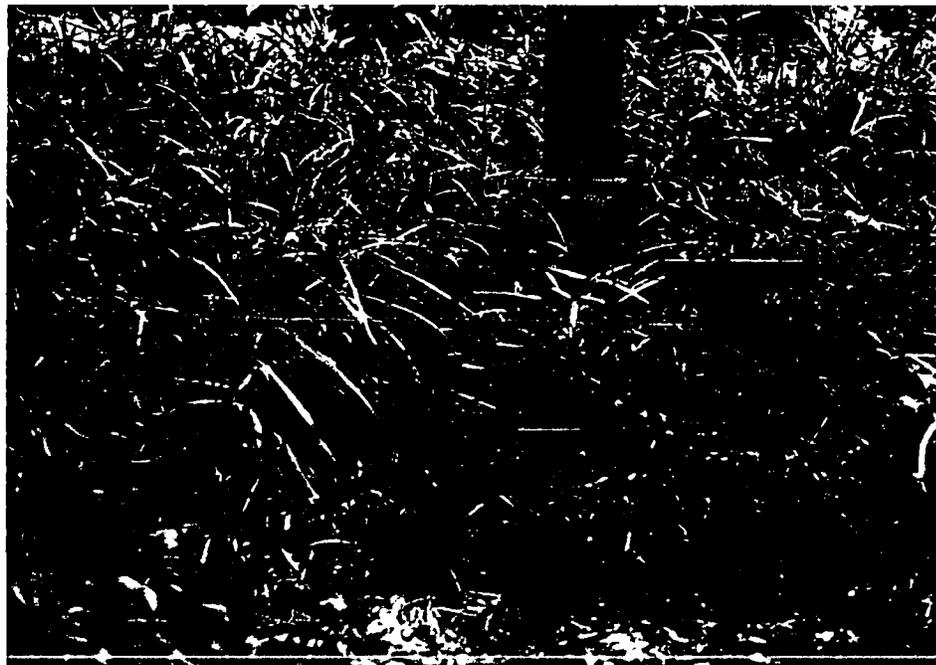
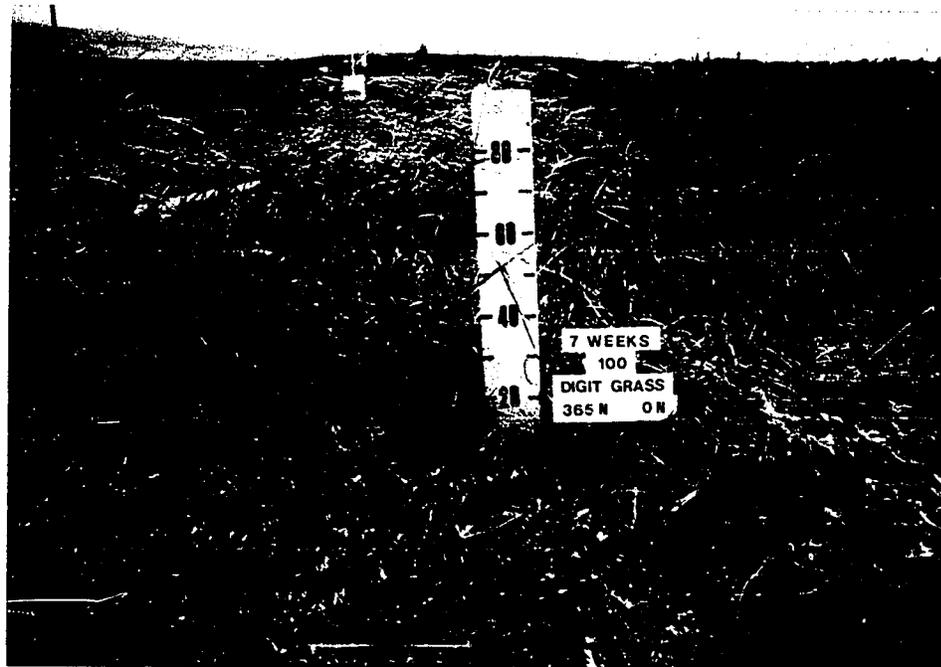


Figure 11. Growth of Mealani digitgrass at 100 and 27% daylight.

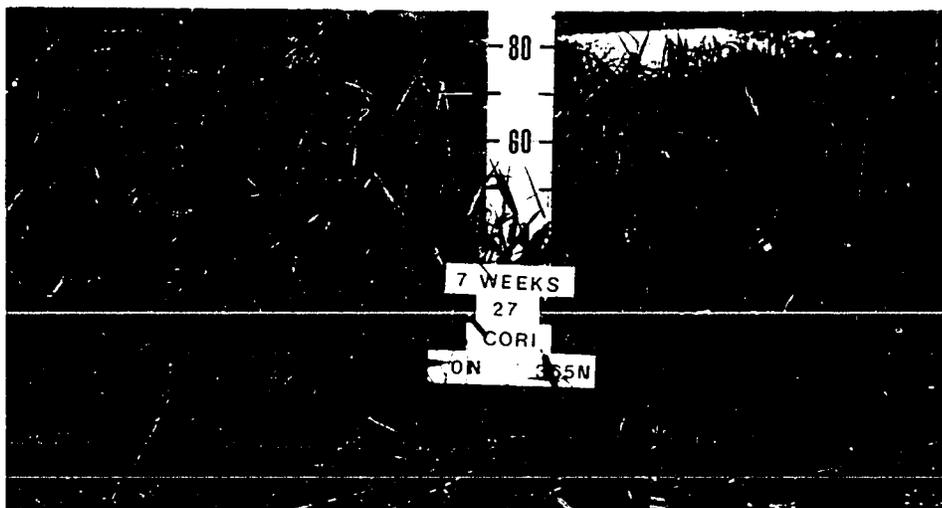
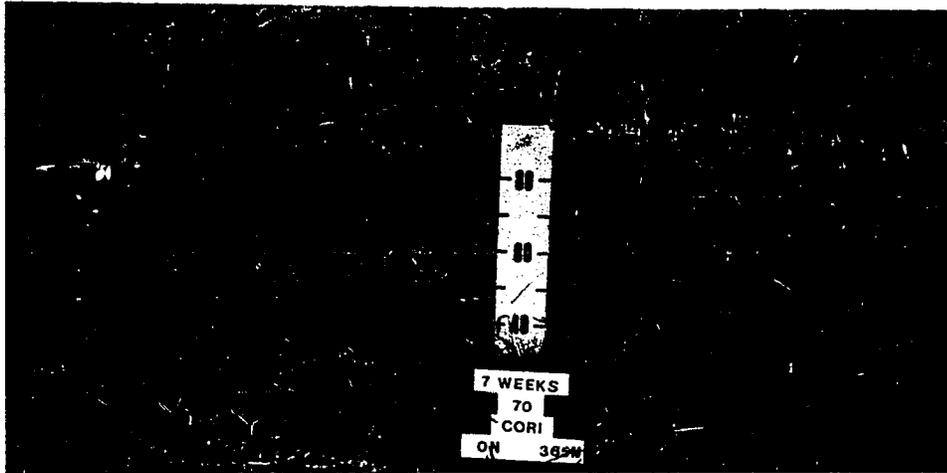
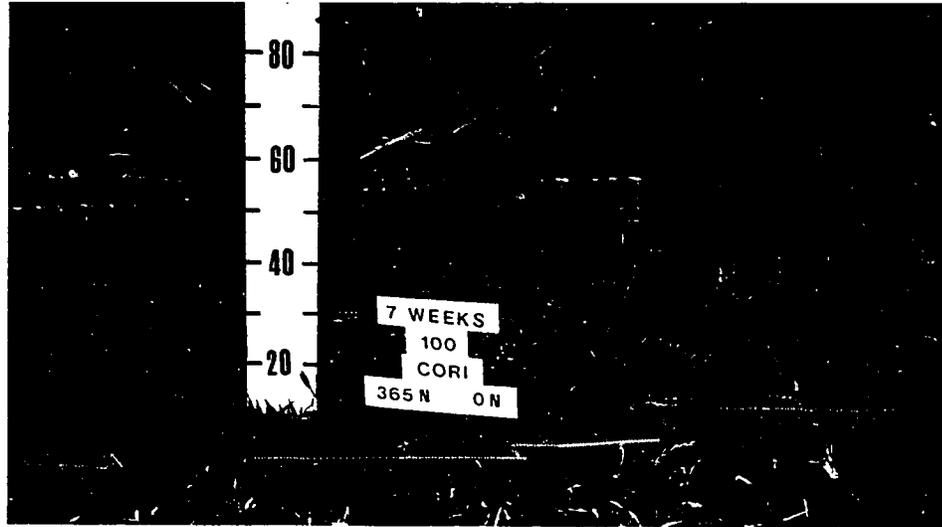


Figure 12. Growth of corigrass at 100, 70 and 27% daylight.

under both levels of nitrogen. In general, yield levels in full daylight were similar to those reported elsewhere for tropical grasses, (Younge and Ripperton, 1960; Tamimi *et al.*, 1968; Campbell *et al.*, 1970; Grof and Harding, 1970; Whitney, 1970, 1974; Olsen, 1972; Ng, 1972; Ng and Wong, 1976).

The growth of the different species varied greatly with season (Figures 14, 15 and 16). Guineagrass was the highest yielding of the three replicated species at all harvests, except the July harvest, when Mealani digitgrass excelled. The yields of minus-N guineagrass and corigrass under full daylight were very low during the summer months. These yield reductions may be due to the destruction of chlorophyll by sunlight at a rate faster than it could be replenished by the nitrogen-stressed plants (Friend, D.T.C. Personal communication.) although chlorophyll contents were not measured, this hypothesis is supported by visual observations that the leaves of the minus-N grasses grown in full daylight were very yellow.

Stomatal resistance measurements were made on guineagrass (minus-N treatments) at midday, but there were no significant differences among light intensities. This would seem to exclude stomatal closure (with consequent reduction in CO₂ uptake) during the hot part of the day as a factor in the lower yields in full sunlight compared to shade. Since soils in the tropics are often low in soil nitrogen and N-fertilizer is often in short supply or very expensive there may be a significant advantage for producing grass forage under shade (e.g. under coconuts or other tree crops).

The three unreplicated grasses responded quite differently to season: kikuyugrass was unaffected; signalgrass yields were slightly

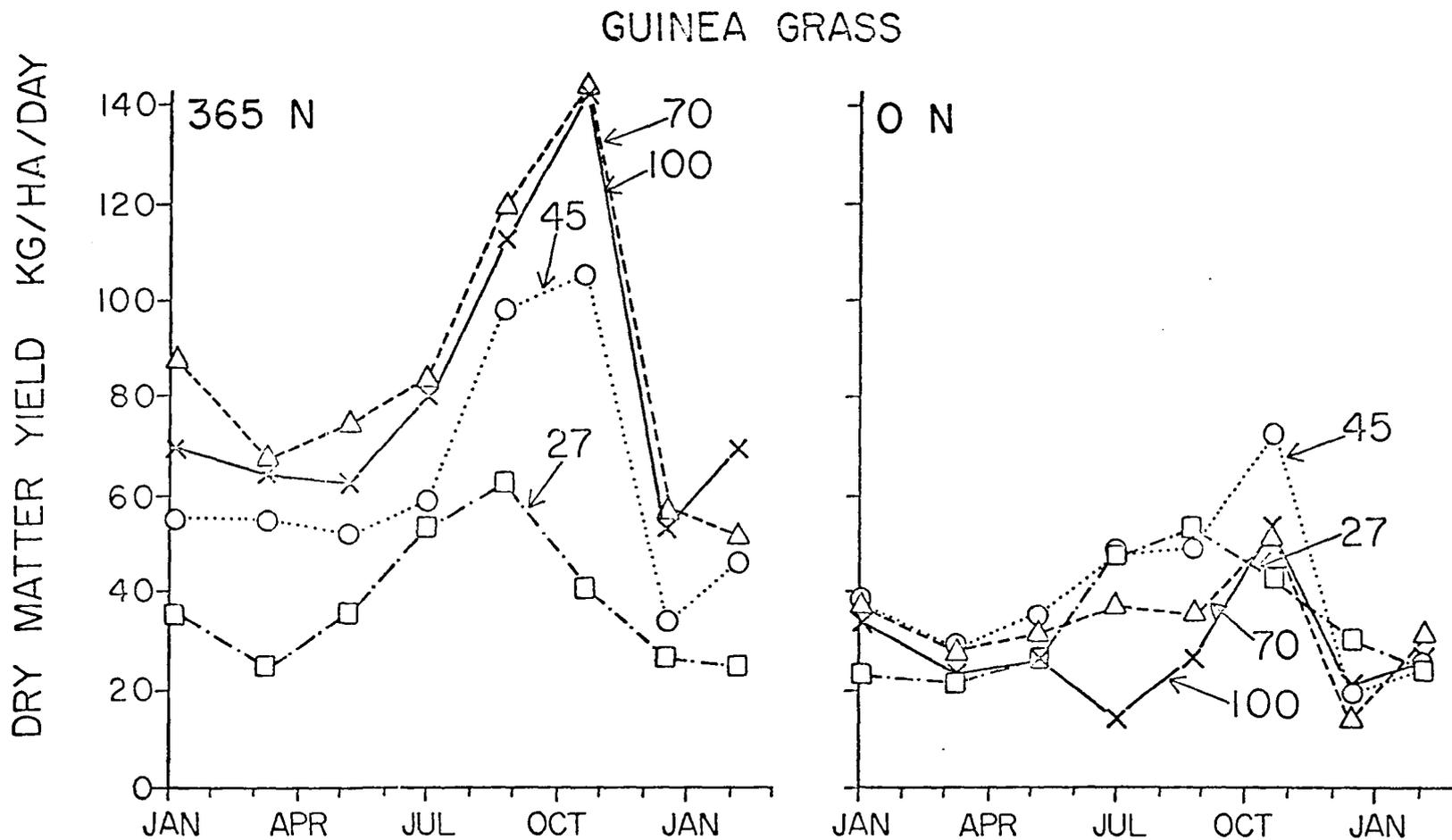


Figure 14. Dry weight yield of guineagrass grown at two nitrogen levels and four light intensities over a 15 month period. Average of three replications.

MEALANI DIGIT GRASS

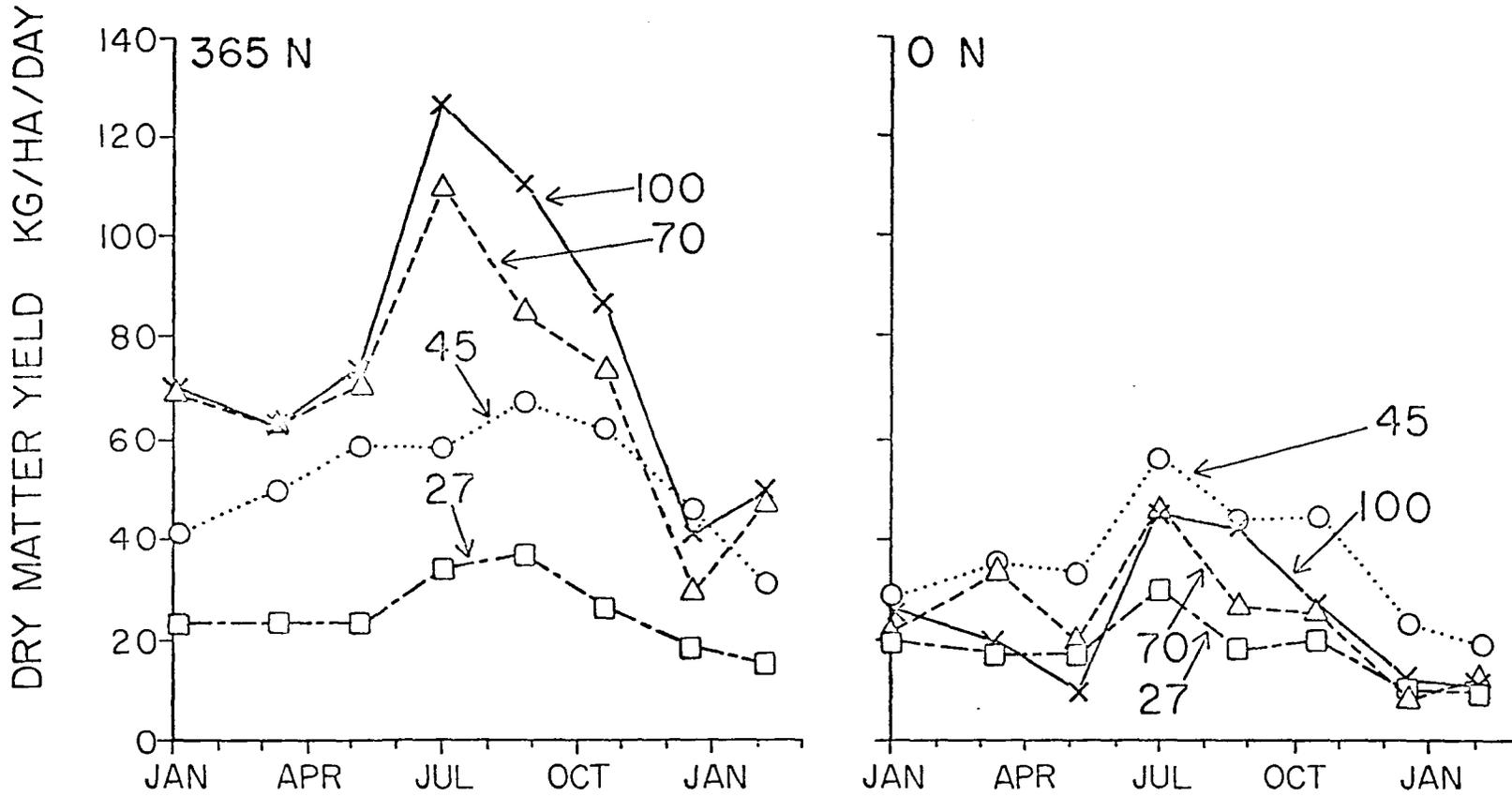


Figure 15. Dry weight yield of Mealani digitgrass grown at two nitrogen levels and four light intensities over a 15 month period. Average of three replications.

CORI GRASS

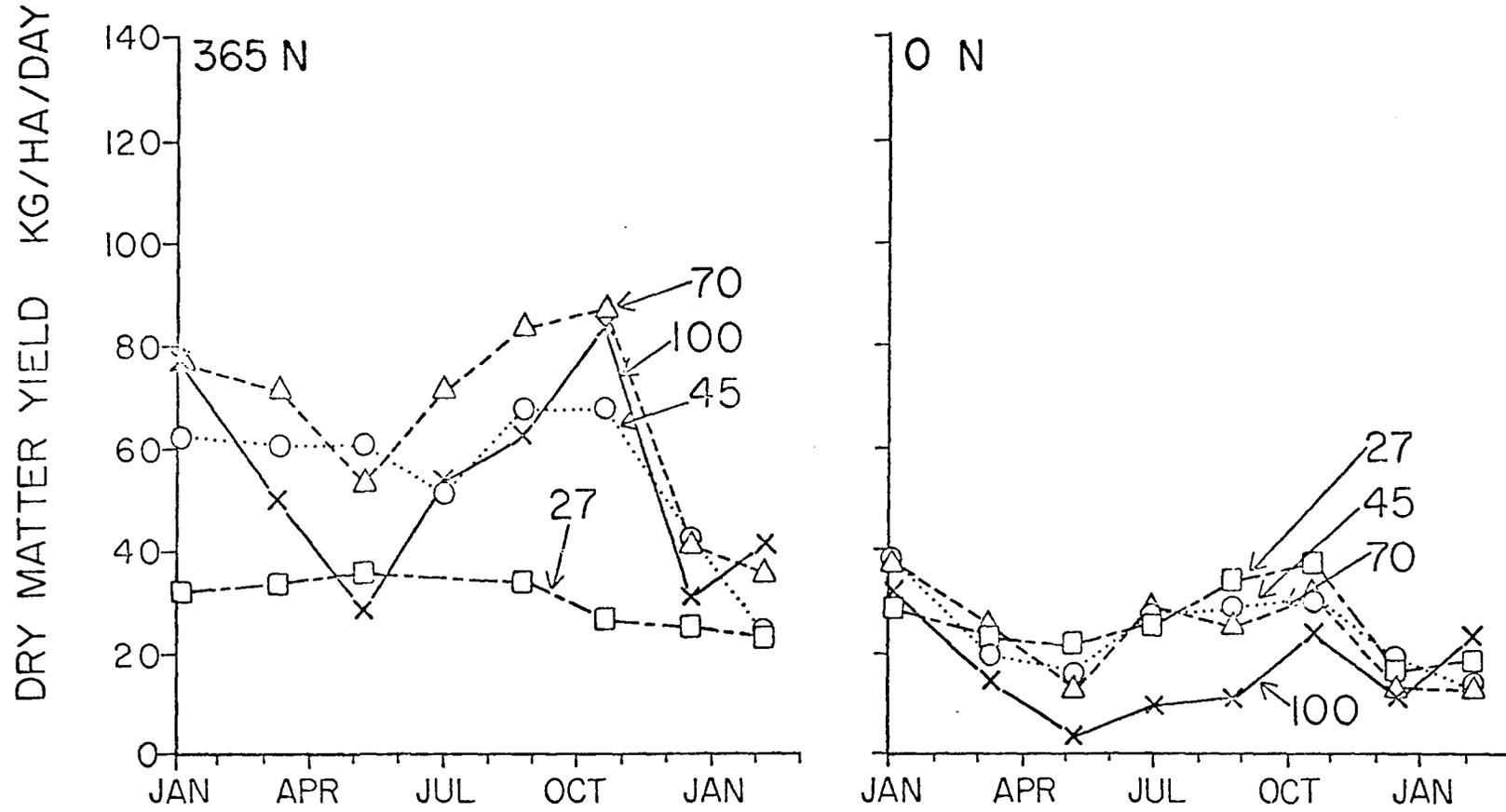


Figure 16. Dry weight yield of cori grass grown at two nitrogen levels and four light intensities over a 15 month period. Average of three replications.

depressed during the cool season; and napiergrass yields were reduced by 50% during the cool season.

Root weights were significantly reduced by shading at both N-levels (Figure 17), resulting in a much greater shoot:root ratio under shading. These grasses thus respond similarly to the tropical and temperate grasses studied by Burton *et al.* (1959), Deinum (1966), and Ludlow *et al.* (1974). The proportional root weights at 100, 70, 45 and 27% daylight were 100%, 40%, 26% and 9% for the fertilized and 100%, 48%, 21% and 10% for the unfertilized grasses, respectively. If root weights are added to the annual DM yields of tops, the total DM yields are similar under all four light intensities. Regrowth after harvesting was observed to be slower in the shaded plots undoubtedly because of reduced carbohydrate reserves in the roots and stubble. Such results have been reported for other forage species (Burton *et al.*, 1959). We conclude that close cutting or heavy grazing of shaded pastures should be avoided, and the intervals between cutting or grazing should be longer than for pastures grown under normal daylight.

Percentages of DM in the forage of all six grasses were significantly reduced by decreasing light intensity and by N-fertilization ($P < .01$) (Table 5). These results agree well with the results reported for orchardgrass (*Dactylis glomerata*) (Gordon, 1962) and for guinea-grass and corigrass in the pot experiment described earlier. Percentage DM recorded in Table 5 are averages for 7 harvest dates since there was no significant difference in DM percentage between seasons. The depressing affects of shading and N-fertilization on DM percentage has important implications for cattle production. Ruminants can only consume a fixed volume of fresh forage per day, and thus would not

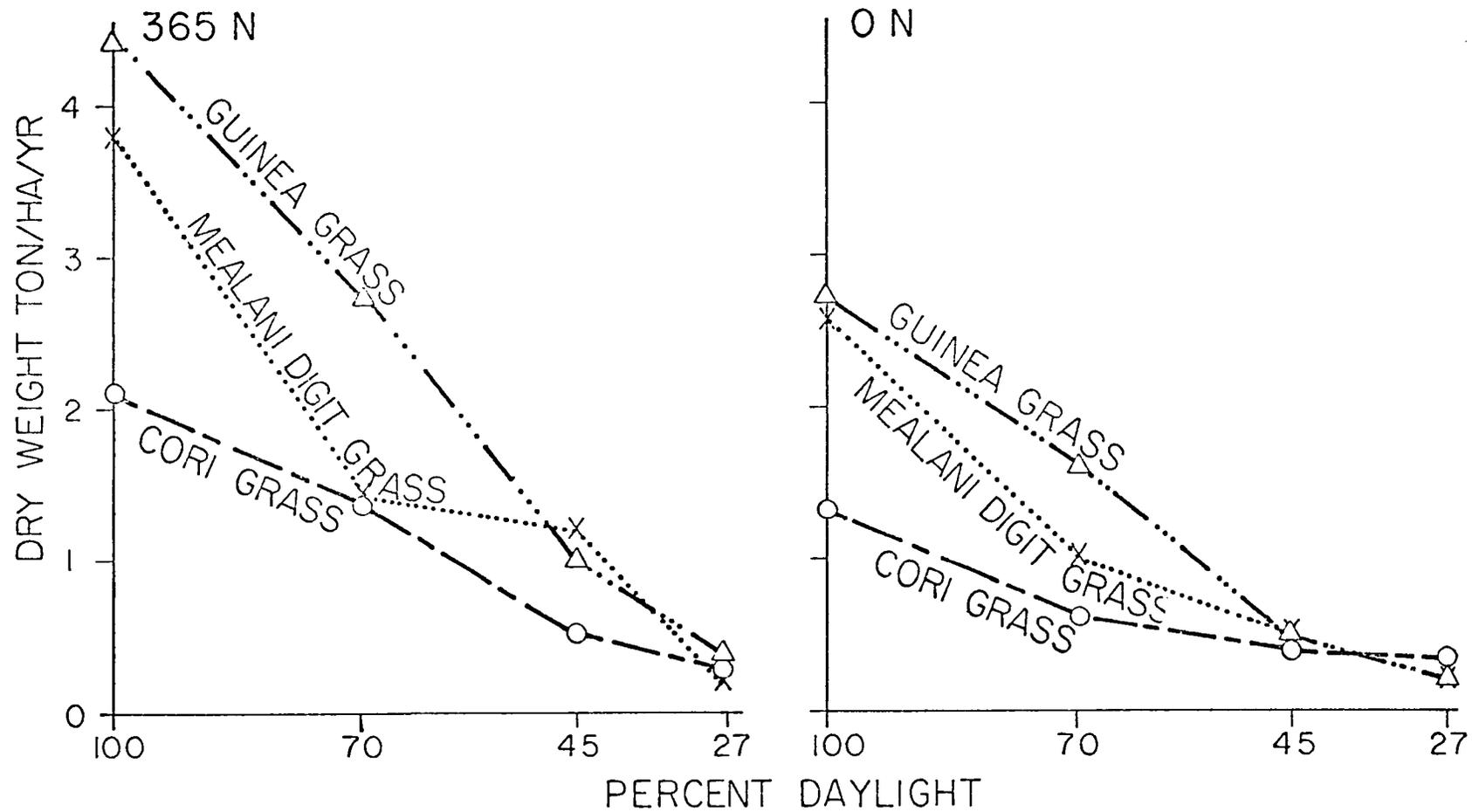


Figure 17. The effect of shading on the root weight of forage grasses grown in the field at two nitrogen levels. Average of three replications.

Table 5. The effect of shading on the dry matter content of forage grasses. Average of three replications (except as noted) and seven harvests.

Grass Species	N- levels	Percent dry matter at light intensity			
		100	70	45	27
Mealani digitgrass	-N	23	20	18	16
	+N	22	19	17	15
guineagrass	-N	28	25	20	20
	+N	25	22	19	18
corigrass	-N	27	23	18	16
	+N	21	18	16	14
kikuyugrass*	-N	25	21	21	15
	+N	22	21	18	15
signalgrass*	-N	26	22	18	17
	+N	25	18	18	15
napiergrass*	-N	19	17	16	14
	+N	18	15	16	14

*unreplicated; data corrected for replication effects.

obtain adequate nutrients from forage too high in moisture, unless digestibility was also enhanced sufficiently to significantly increase the rate of passage through the digestive tract.

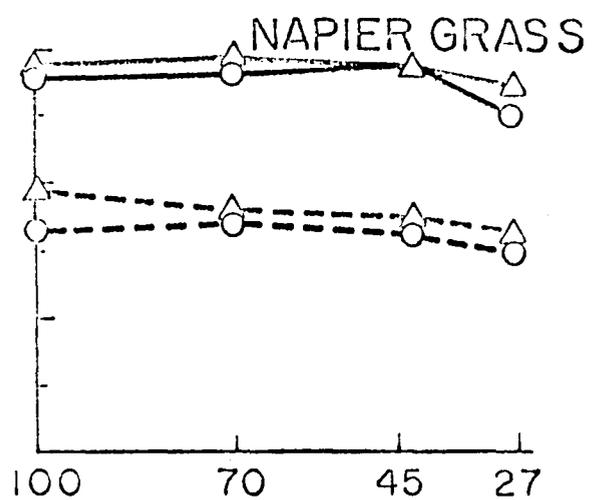
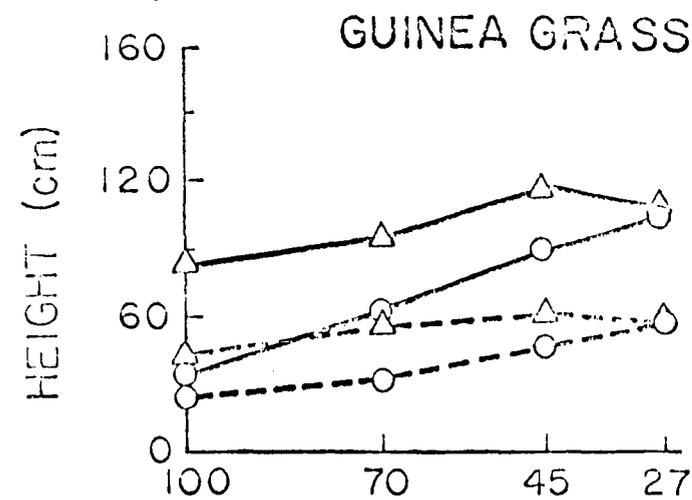
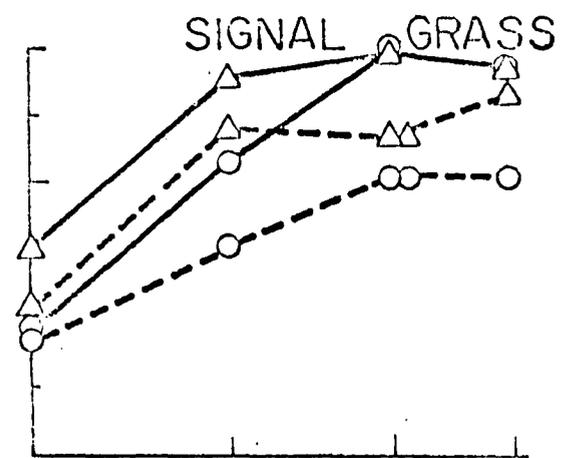
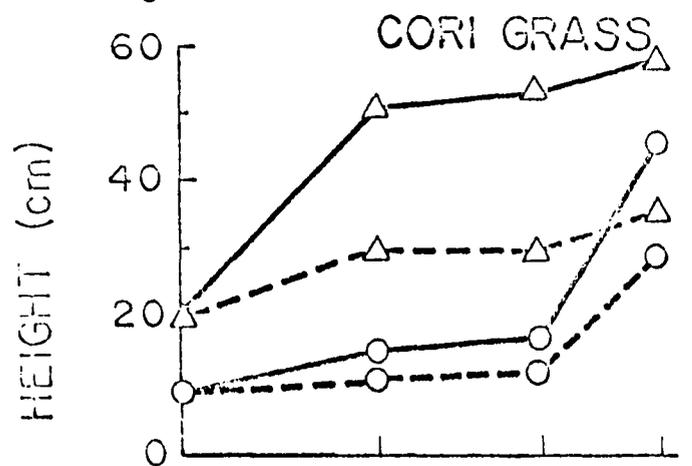
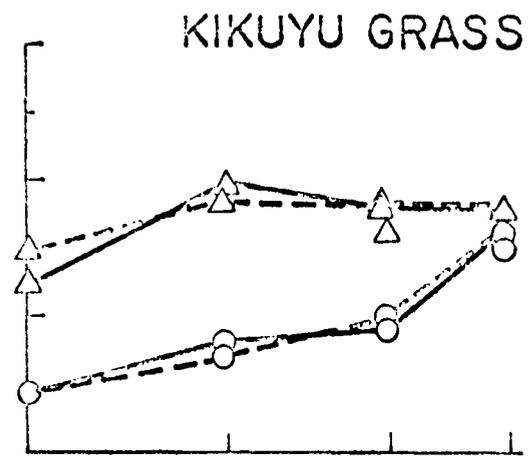
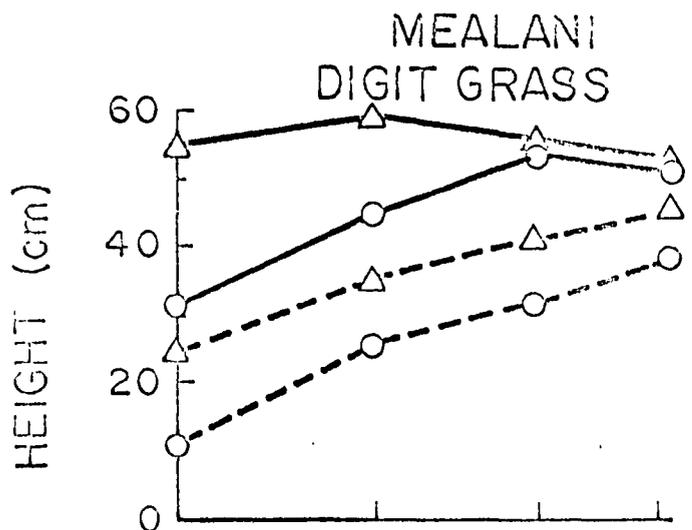
Plant Morphology. Plant height of most species increased significantly with decreasing light intensity (Figure 18) as was reported for the pot experiment. Within each light intensity, average plant height of each grass was highly correlated with seasonal DM yield (low in the cool season etc.).

The ratio of foliage area (leaves plus stems) to plant weight provided an indirect measure of leafiness. Nitrogen level had no significant effect on leafiness, but the leafiness index (area:weight ratio) generally increased ($P < .01$) with decreasing light intensity (Table 6 and 7). The leafiness index was also slightly higher during the cool season. The values of about $100 \text{ cm}^2/\text{g}$ measured in full daylight are in accord with data from previous experiments with kikuyugrass in Hawaii (Whitney, 1974). Leaf-plus-stem area index values at each light intensity were closely related to DM yields.

Nitrogen percentage and yield. The percentages of nitrogen in the dried forages of guineagrass, corigrass and Mealani digitgrass varied inversely with yield and temperature (and hence with daylength or radiation) and were higher at reduced light intensities (Figure 8). Forage N levels were significantly higher ($P < .01$) at 27% daylight than under more intense light at all harvest dates.

Percent N was also significantly higher (by about 0.10-0.46 percentage units) in the nitrogen fertilized treatments at all harvest dates. The N-percentage of Mealani digitgrass was higher during the

Figure 18. The effect of shading on height of tropical grasses at two seasons (---- = cool season; _____ - summer season) and two nitrogen levels (0 = minus-N; Δ = plus-N).



PERCENT DAYLIGHT

PERCENT DAYLIGHT

Table 6. The effect of shading on leaf-plus-stem area:weight ratio, and leaf-plus-stem area index (LSAI) for three forage grasses at two nitrogen levels. Average of three replications.

Light intensity	Mealani digitgrass		guineagrass		corigrass	
	-N	+N	-N	+N	-N	+N
<u>a) Leaf-plus-stem area:weight ratio (cm² g⁻¹DW).</u>						
August 25 harvest.						
100	92	87	101	111	101	120
70	100	113	130	166	118	130
45	129	136	144	121	140	149
27	141	138	162	140	177	169
February 10 harvest.						
100	119	134	102	99	72	147
70	153	141	104	137	102	145
45	166	185	137	148	127	162
27	180	184	139	165	190	198
<u>b) Leaf-plus-stem area index (LSAI).</u>						
August 25 harvest.						
100	2.13	5.44	1.54	5.89	0.59	4.17
70	1.59	5.40	2.63	9.50	1.65	6.13
45	3.13	5.14	4.03	6.64	2.85	5.69
27	1.41	2.85	4.82	4.86	3.26	3.00
February 10 harvest.						
100	0.64	3.70	1.55	3.91	0.62	3.41
70	1.12	3.71	1.84	3.99	0.78	2.99
45	1.75	3.23	1.90	3.83	0.84	2.04
27	0.90	1.55	1.88	2.31	1.84	2.65

Table 7. The effect of shading on leaf-plus-stem area:weight ratio, and leaf-plus-stem area index (LSAI) for three forage grasses at two nitrogen levels. Unreplicated.

Light intensity	napiergrass		kikuyugrass		signalgrass	
	-N	+N	-N	+N	-N	+N
a) Leaf-plus-stem area:weight ratio ($\text{cm}^2 \text{g}^{-1}\text{DW}$).						
August 25 harvest.						
100	96	94	93	133	75	91
70	93	114	138	108	110	119
45	118	98	139	148	106	156
27	135	90	177	142	200	156
February 10 harvest.						
100	150	150	-	122	125	108
70	157	138	-	134	147	137
45	145	156	135	139	153	167
27	159	166	169	183	190	211
b) Leaf-plus-stem area index (LSAI).						
August 25 harvest.						
100	6.23	9.70	0.10	3.02	2.33	3.60
70	5.43	8.50	2.10	4.60	3.37	6.83
45	5.71	7.90	1.85	2.75	3.74	5.62
27	1.89	1.35	2.75	2.87	5.01	4.67
February 10 harvest.						
100	4.73	8.11	-	-	1.68	2.81
70	4.30	8.13	-	-	1.06	4.02
45	4.24	4.98	0.95	2.59	1.54	2.45
27	2.06	1.77	0.81	1.60	1.71	3.29

Table 8. The effect of shading on the nitrogen fertilizer recovery of forage grasses.

Grass species	Percent N-recovery at light intensity**			
	100	70	45	27
Mealani digitgrass	72	73	35	26
guineagrass	69	78	45	9
corigrass	49	62	52	30
napiergrass*	41	39	58	17
kikuyugrass*	51	42	20	27
signalgrass*	42	76	40	23

*unreplicated.

**A-B/C; where A = plus-N and B = minus-N nitrogen yields, and C = kg N applied.

cool season than guineagrass and corigrass, but this was reversed during the summer season, resulting in similar forage N levels for all three species when averaged over the whole year. The N-yields of the minus-N grasses were higher (by 2-3 times) under moderate-to-heavy shade than at full daylight (Figure 19) due in part to higher N percentage in the shaded forage. Nitrogen fertilization increased the N-yield significantly for all species. Nitrogen recoveries of applied N ranged from 39-78% at 100 and 70% daylight, 20-58% at 45% daylight and only 9-30% N-recovery at 27% daylight (Table 8).

The nitrogen recovery of napiergrass at 100 and 70% daylight was lower than the other grasses, and this was related to the very high yields of minus-N napiergrass. The reason for the high yield of minus-N napiergrass is not known, but it is possible that it was able to rob N from adjacent plus-N plots by virtue of its very extensive root system. Some nitrogenase activity was measured in napiergrass

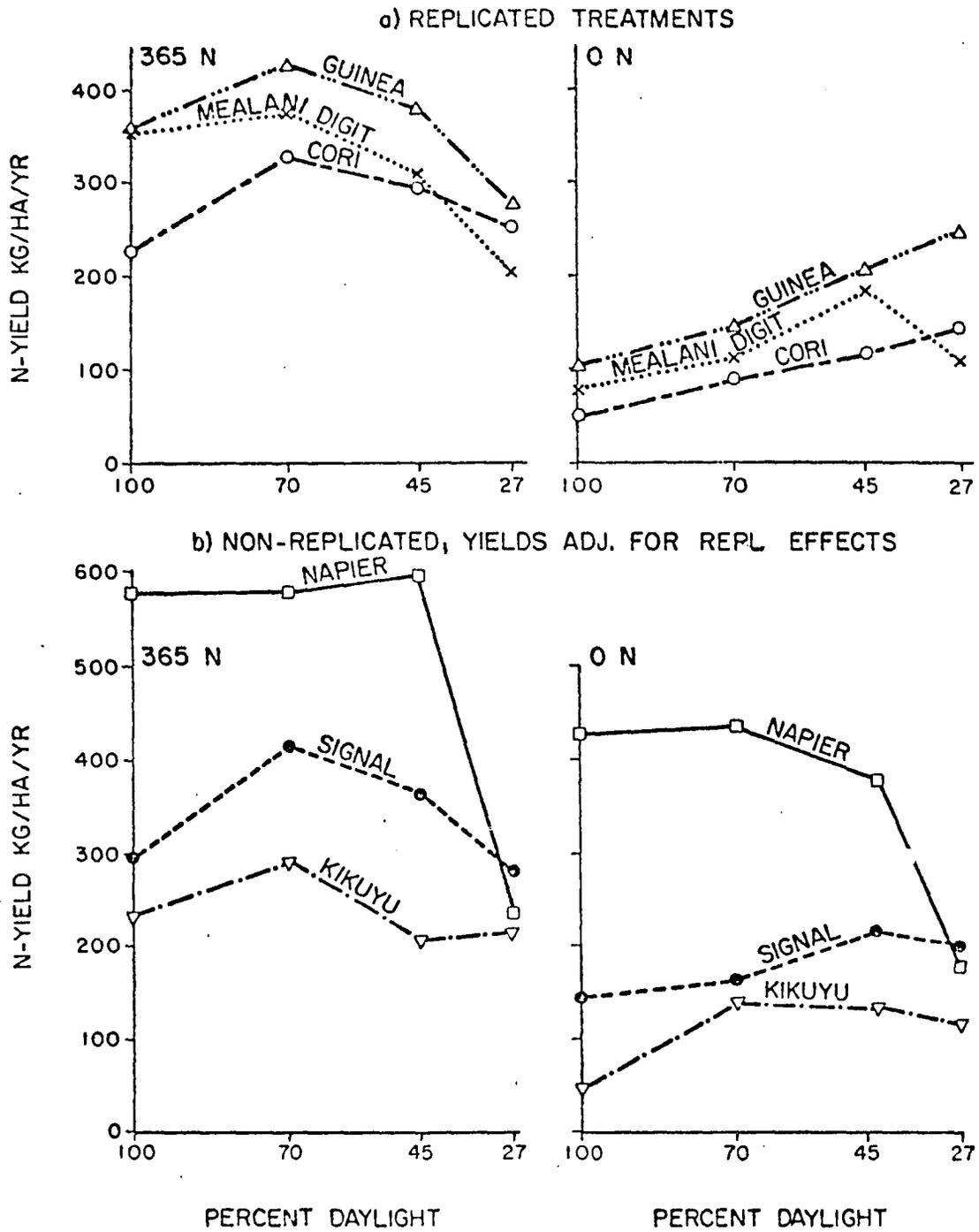


Figure 19. The effect of shading on the annual nitrogen yield of six forage grasses at two nitrogen levels.

Table 9. The effect of shading on the acetylene reduction of six forage grasses.

Grass species	Acetylene reduction at light intensity**			
	100	70	45	27
Mealani digitgrass	++	+++	+	+
guineagrass	++	++	+	0
corigrass	+	+	0	0
kikuyugrass*	++	+++	0	0
signalgrass*	0	0	0	0
napiergrass*	+	+	0	0

*unreplicated:

***+++ = <20 $\mu\text{mol}/\text{m}^2$ per hr.;

+ = detectable activity;

++ = 10-20 $\mu\text{mol}/\text{m}^2$ per hr.;

0 = no detectable activity.

(see next section), but it cannot account for the very high yields of the minus-N plots.

Nitrogenase activity in soil core samples. Nitrogenase activity (estimated by acetylene-reduction assay) (Hardy *et al.*, 1968) has been measured in some rhizosphere associations in recent years (e.g. Döbereiner *et al.*, 1973, 1974; Schank and Day, 1977). In our experiment great variability in nitrogenase activity was measured among both species and light intensities (Table 9).

Nitrogenase activity of core samples during August 1976 was highest in Mealani digitgrass and kikuyugrass at 70% daylight. Slightly lower values were measured at full daylight for the same two species and for guineagrass. Nitrogenase activity was also detected in corigrass and napiergrass at 100 and 70% daylight; only signalgrass showed no sign of activity. Some activity was found at 45 and 27% daylight in Mealani digitgrass and at 45% daylight in guineagrass, with no activity

measured at these low light intensities for any of the other grasses. Schank and Day (1977) also reported great variability in nitrogenase activity among species and even among varieties within species of 30 grasses in Brazil.

Mineral composition. With some exceptions, mineral levels in the three replicated grasses tended to be higher in shaded forage, higher in N-fertilized grasses (except for P, Si, and Zn) and generally higher during the cool season. The following discussion refers to data shown in Figures 20-21 and Appendix Tables 1-8.

Phosphorus. The P values of Mealani digitgrass, and guineagrass increased with decreasing light intensity during the summer season ($P < .01$) but not during the cool season. P values of corigrass increased with decreasing light intensity in both summer and cool season except for the N-fertilized summer harvest, when lower P levels at moderate to heavy shading were recorded.

The P levels in N-fertilized guineagrass and Mealani digitgrass were only 60-80% of the levels measured in the control. Decreased P content with N-fertilization was also reported by Addison (1956), Vicente-Chandler *et al.* (1959) and Plucknett and Fox (1965) in full daylight.

Potassium. Potassium values increased linearly with decreasing light intensity, increasing by as much as 25-100% at heavy shading. This response is in agreement with the responses of temperate grasses reported earlier by Myhr and Saebo (1969), and Mayland and Grunes (1974). Potassium content increased with N fertilization for all six

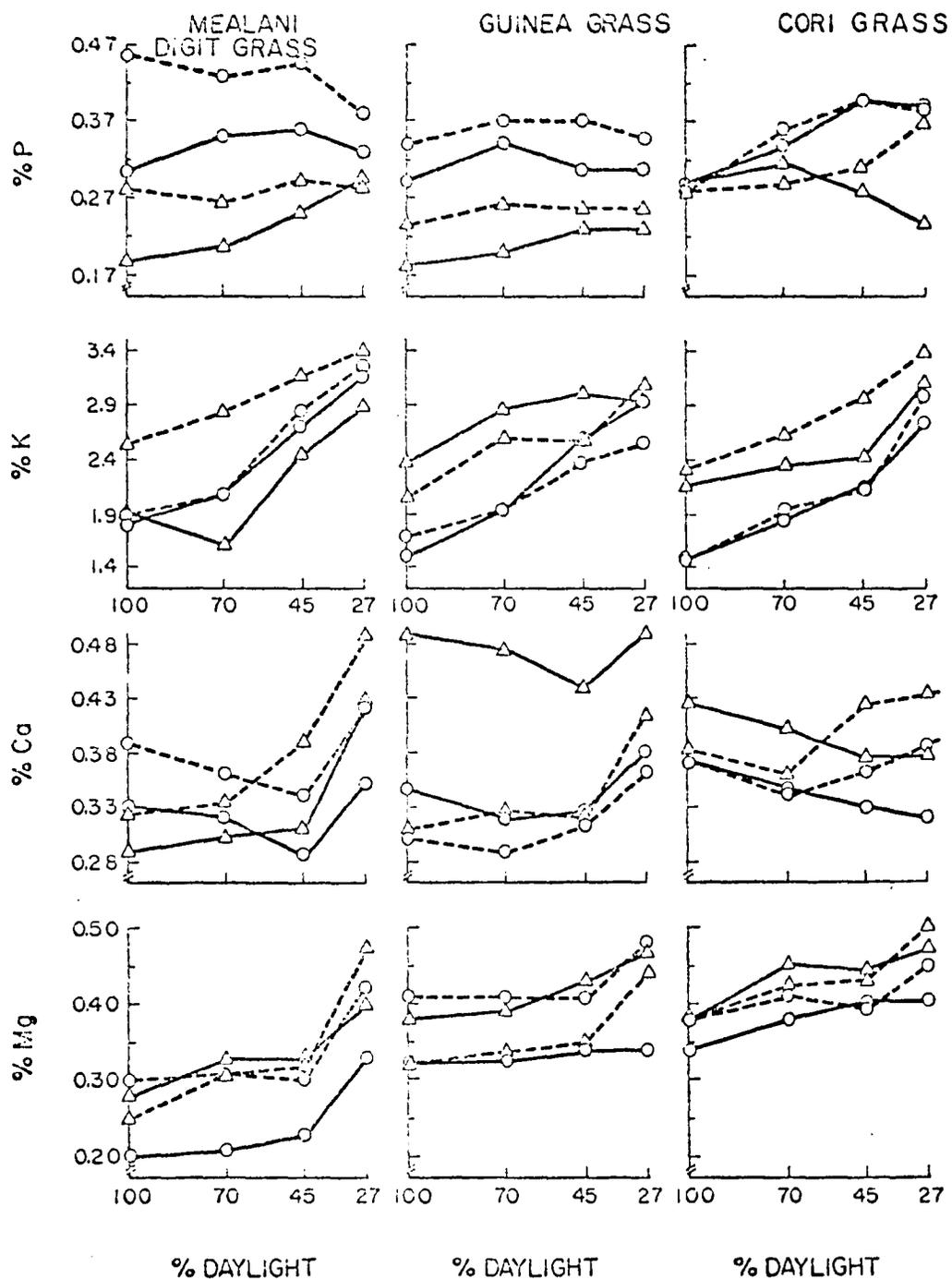


Figure 20. The effect of shading on P, K, Ca and Mg content of three tropical grasses at two seasons (---- = cool season; — = summer season) and two nitrogen levels (0 = minus-N; Δ = plus-N). Average of three replications.

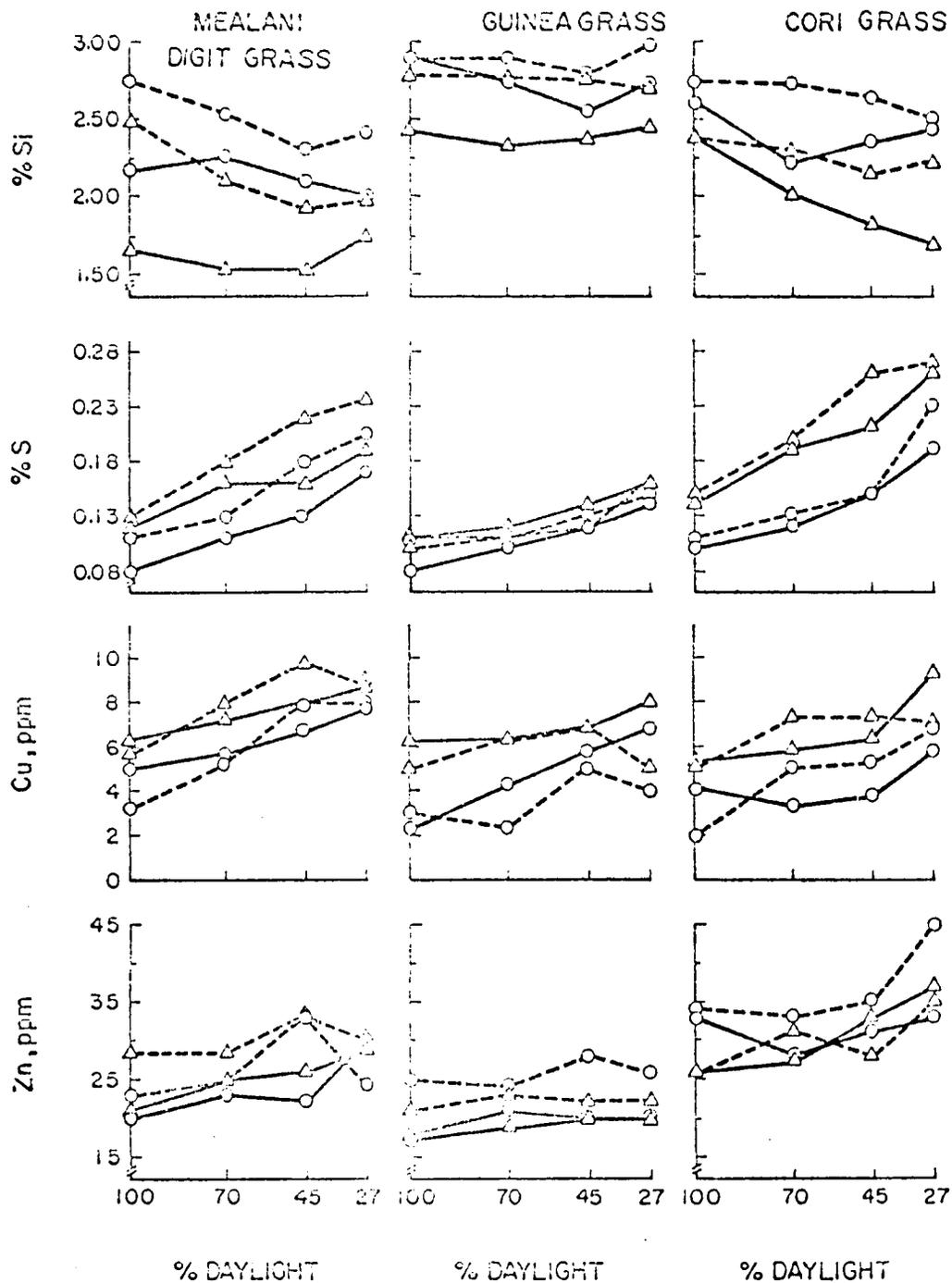


Figure 21. The effect of shading on Si, S, Cu and Zn content of three tropical grasses at two seasons (---- = cool season; — = summer season) and two nitrogen levels (O = minus-N; Δ = plus-N). Average of three replications.

species, except for napiergrass and for shaded Mealani digitgrass at the summer harvest. Reduced K content in N-fertilized napiergrass (in contrast with other tropical grasses) has also been reported by Vicente-Chandler *et al.* (1959). The K content in napiergrass in full daylight was also about double the amount measured in the other grasses. This is in general agreement with the findings by Gomide *et al.* (1969), although the K values found in their study were generally lower than those reported here.

Calcium. The calcium values for guineagrass and Mealani digitgrass were significantly increased under heavy shading at both seasons ($P < .01$), and for corigrass during the cool season. However, the Ca content in corigrass was reduced by shading during the summer season. The Ca content was highest in the N-fertilized forage for all six species except for Mealani digitgrass at 70-100% daylight. The Ca values reported for this investigation are similar to those reported by Vicente-Chandler (1959), Myhr and Saebo (1969), Mayland and Grunes (1974) and Whitney (1974).

Magnesium. In full daylight the Mg content of Mealani digitgrass was much lower (0.26 %) than in guineagrass and corigrass (0.37 %) ($P < .01$), which is in line with the findings by Gomide *et al.* (1969). At heavy shading the difference among the three replicated forages with respect to Mg content was small. Increasing Mg content with shading was also reported by Burton *et al.* (1959) and Mayland and Grunes (1974) on temperate grasses, although their values were lower than ours. The Mg content of napiergrass was lower than the other grasses, reaching values as low as 0.26 % at both seasons.

Silicon. The highest Si content of the replicated forages was measured in guineagrass (2.7 %) and the lowest in Mealani digitgrass (2.1 %).

Shading had a very limited affect on the Si content of guineagrass and Mealani digitgrass at the summer harvest, but decreased the Si content in corigrass and Mealani digitgrass at the cool season harvest. The Si content of the non-replicated N-fertilized kikuyugrass was very low (1.1-1.6 %) at both seasons, compared to napiergrass (2.1-2.7 %) and signalgrass (1.7-2.4 %).

Sulfur. In both Mealani digitgrass and corigrass the S content doubled from 0.1-0.2 % when grown under heavy shade compared to full daylight. The increase was slightly less for guineagrass; also the increase in S content due to N-fertilization was less in guineagrass than in the other grasses. The highest S content was found in kikuyugrass (0.15-0.30 %) and the lowest in napiergrass (0.07-0.16 %) at both seasons.

Copper. During the cool season the Cu content in the N-fertilized grasses was highest at 45% daylight for all six species. The highest Cu content was recorded for N-fertilized Mealani digitgrass (5.7-9.7 ppm). Gomide *et al.* (1969) also found that pangolagrass was high in copper, followed by guineagrass, napiergrass, kikuyugrass, molassesgrass (*Melinis munitiflora* Beauv.) and bermudagrass (*Cynodon dactylon* Pers.). Our rankings were similar, but our values were lower than theirs.

Zinc. The Zn contents tended to be higher in the minus-N forage for all species except Mealani digitgrass. Shading did not change the Zn content in guineagrass. In summer, the Zn content of corigrass and

Mealani digitgrass was highest in heavy shade, while in the cool season, the Zn content of Mealani digitgrass was highest in moderate shade.

The highest Zn content was measured in corigrass and kikuyugrass (26-45 ppm) and the lowest in guineagrass (17-28 ppm) for both seasons.

In general it can be concluded that shading has a decreasing effect on dry matter content, and on dry matter yield if nitrogen is not limiting. If the soil nitrogen level is low increasing yield can be expected with decreasing light intensity. Also mineral content, nitrogen content and plant height generally increased with decreasing light intensity.

SUMMARY AND CONCLUSION

Six tropical forage grasses were evaluated on an Oxic Haplustoll in Hawaii (100 meters above sea level) over a 20-month period under four light regimes (100, 70, 45 and 27% daylight using polypropylene netting) in the field. Guineagrass (*Panicum maximum*) was established from seeds, while Mealani digitgrass (*Digitaria decumbens*), corigrass (*Brachiaria miliiformis*), signalgrass (*Brachiaria brizantha*), kikuyugrass (*Pennisetum clandestinum*) and napiergrass 3418 (*Pennisetum purpureum*) were established from cuttings.

The DM yields of the N-fertilized grasses ($365 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) were highest at 100 and 70% daylight ($16\text{-}40 \text{ tons ha}^{-1} \text{ yr}^{-1}$) with napiergrass and guineagrass proving most productive. Under 27% daylight the yields were between $8\text{-}15 \text{ tons ha}^{-1} \text{ yr}^{-1}$ with guineagrass, signalgrass and corigrass producing the highest yields. When no nitrogen was added maximum yields in $\text{tons ha}^{-1} \text{ yr}^{-1}$ of the various grasses were as follows: corigrass, 9.2 tons at 27% daylight; Mealani digitgrass,

guineagrass and signalgrass, 13.5-15.0 tons at 45% daylight; kikuyugrass, 9.2 tons at 70% daylight; napiergrass, 30 tons at full daylight. Dry matter yields of N-fertilized guineagrass, Mealani digitgrass and napiergrass were reduced by about 50% during the cool season; corigrass and signalgrass were slightly depressed during the cool season; and kikuyugrass was unaffected by seasons. The lowest seasonal fluctuations were recorded under dense shade. Root weights were affected more by shading than top weights, with the average relative root weight of guineagrass, corigrass and Mealani digitgrass at 100, 70, 45 and 27% daylight being 100, 44, 23 and 10 of full daylight for both plus and minus N-fertilizer plots. By comparison relative top weights were 100, 103, 82 and 47 for plus-N plots and 100, 121, 155 and 126 for minus-N plots. Guineagrass and the two *Brachiaria* spp. (corigrass and signalgrass) yielded relatively better than Mealani digitgrass and kikuyugrass at the lower light intensities. Dry matter content decreased with shading and N-fertilization, with no difference between seasons. Highest DM content was measured in guineagrass and lowest in napiergrass.

Average percent N increased from 1.0 to 1.6 with decreasing light intensity in minus-N treatments and from 1.2 to 1.9 in plus-N treatments with little difference between species. Total N-yield averaged 200 to 430 kg ha⁻¹ yr⁻¹ in plus-N forage and 50 to 240 kg ha⁻¹ yr⁻¹ in minus-N forage (excluding napiergrass). In the minus-N treatments the yields at 45% were double the yields in full daylight.

A low level of acetylene reduction was found in 100 and 70% daylight for all species, except signalgrass. Slight activity was also found at 45 and 27% daylight in Mealani digitgrass, and at 45% daylight

in guineagrass.

Sward height increased significantly with decreasing light intensity and with N-fertilization. The ratio of foliage area (leaves plus stem) to plant weight increased significantly with decreasing light intensity, with no difference between N-levels. Leaf-plus-stem area index values at each light intensity were closely related to DM yields.

With some exceptions P, K, Ca, Mg, S, Cu and Zn tended to be higher in shaded forage, higher in N-fertilized forage (except for P and Zn) and generally higher during the cool season. The Si content generally decreased with decreasing light intensity and with N-fertilization.

CHAPTER V

THE EFFECT OF LIGHT INTENSITIES ON MORPHOLOGY, YIELD, MINERAL CONTENT AND ACETYLENE REDUCTION OF SIX TROPICAL FORAGE LEGUMES

INTRODUCTION

In the tropics levels of radiation are usually high and are often the least variable component of the climate from year to year (Coaldrake, 1964). However solar radiation at different locations and at different seasons may vary greatly depending on cloud cover. In a pasture community of grasses and legumes the relative ability of grasses and legumes to compete for light is often an important factor influencing grass-legume balance (Santhirasegaram *et al.*, 1966). In recent years there has been an increased interest in growing improved legumes and grass-legume mixtures under coconut palms and other plantation crops in order to suppress weeds, improve soil fertility or to provide extra income through cattle production (Watson, 1963; Hugh, 1972; Javier, 1974; Mac Evoy, 1974).

According to Ludlow *et al.* (1974) tropical legumes would be relatively more favoured under low radiation than tropical grasses, since shaded tropical legumes showed a smaller reduction in net assimilation rate and greater compensatory increase in leaf area ratio than shaded grasses.

Moderate to heavy shading reduced yield of greenleaf desmodium (*Desmodium intortum* (Mill.) Urb.) and centro (*Centrosema pubescens* Benth.), but the yield reduction was less than that reported for some other legumes such as siratro (*Macroptilium atropurpureum* (D.C.) Urb.) and stylo (*Stylosanthes guyanensis* Swartz) (Ranacou, 1972). Poor growth of siratro at low light intensity has also been reported by Ludlow *et al.* (1974).

In Hawaii greenleaf desmodium produced over 20 ton ha⁻¹ yr⁻¹ of dry matter (DM) in cinder-filled plots (Whitney *et al.*, 1967). Others (Younge *et al.*, 1964; Plucknett and Fox, 1965; Whitney and Green, 1969) have reported yields of 10-21 ton ha⁻¹ yr⁻¹ from trials of legume and grass-legume mixtures in Hawaii. Olsen and Moe (1971) reported over 16 ton DM ha⁻¹ yr⁻¹ for greenleaf desmodium and stylo in Uganda. Slightly lower annual yields were recorded for stylo, centro and siratro grass mixtures from field trials in Malaysia (Ng and Wong, 1976).

Date (1973) estimated that the average amount of N fixed by tropical forage legumes grown in association with grasses is about 100-200 kg N ha⁻¹ yr⁻¹. In Hawaii *Desmodium* spp. grown alone and in combination with grasses were able to fix between 47 and 407 kg ha⁻¹ yr⁻¹ (Whitney *et al.*, 1967; Whitney and Green, 1969; Whitney, 1970). N-fixation rates for centro of 269 kg ha⁻¹ yr⁻¹ were reported in Hawaii (Whitney *et al.*, 1967) and 235 kg ha⁻¹ yr⁻¹ were fixed over a 5 month period in a pot study in Malaysia (Watson, 1957). Even higher N-fixation rates have been reported for the leguminous shrub *Leucaena leucocephala* (Lam.) de Wit. (Hutton and Bonner, 1960; Brewbaker *et al.*, 1972).

Use of the acetylene reduction technique (Hardy *et al.*, 1968)

has proved to be very useful for measuring the responses of temperate pasture legumes to cutting and grazing management or fertilizer treatment (Moustafa *et al.*, 1969; Sinclair, 1973) and water stress (Engine and Sprent, 1972). Chu and Robinson (1974) and Halliday and Pate (1976) have also used this method to study the effects of defoliation on nitrogen fixation activity of temperate legumes. However there is little similar information on the effects of defoliation or shading on nitrogen fixation activity by tropical forage legumes. A shading experiment was therefore conducted in the field at Paia, Hawaii, to determine the effects of defoliation on the performance of six tropical legumes.

MATERIALS AND METHODS

Six forage legumes were grown on an Oxic Haplustoll near Paia, Hawaii (20°55'N and 156°22'W, 100 meters above sea level) during the period July 1975 to February 1977. Legumes which were replicated three times included: centro (*Centrosema pubescens* Benth.), greenleaf desmodium (*Desmodium intortum* (Mill.) Urb.), and siratro (*Macroptilium atropurpureum* (D.C.) Urb.). Legumes which were not replicated included: kaimi clover (*Desmodium canum* (Gmel.) Schintz and Thellung), "Hawaiian Giant" leucaena (*Leucaena leucocephala* (Lam.) de Wit.), and "Schofield" stylo (*Stylosanthes guyanensis* Swartz).

Shade levels, fertilization (except that N was not applied) and watering were as described in chapter IV.

The experiment employed a split-plot design with light regimes as whole plots, species as sub-plots, and three replications. Each sub-plot measured 2.6 x 3.2 m. The total area harvested for yield

determination was 5.0 m² per sub-plot (Appendix Table 2).

Prior to planting, seeds were scarified using concentrated sulphuric-acid treatment for 5 min., and inoculated using commercial peat cultures¹⁾. The experiment was established on July 27, 1975, shaded 2 months later, and the species harvested every 8 weeks over the period November, 1975 to February, 1977. All species were cut at 4-7 cm above the ground using a small sickle-bar mower except for leucaena which was cut by hand at 35 cm height.

The parameters measured were: 1) green weight, 2) dry weight, 3) nitrogen content, 4) mineral content, 5) sward height, and 6) nitrogenase activity as described in Chapter IV. However nitrogenase measurements differed in that they were taken 7 weeks after cutting in August, October, December and February, 1976-1977, and 2 and 4 weeks after cutting in September 1976. Three soil cores per plot, (8 cm diameter by 15 cm deep) were removed by using a soil auger, and transferred into individual 1000 ml plastic bottles. Acetylene was introduced within 5 minutes of sampling (10% by volume) by first taking out air using a syringe and then adding acetylene. After incubation for 2½ hours, 0.5 ml was removed and ethylene production determined following the procedure described in Chapter IV.

Results were analyzed statistically by standard split plot analysis of variance and means were ranked and tested using the Bayes LSD. The results from the unreplicated species were adjusted using the methods for augmented design described by Federer (1956).

¹⁾Supplied by the Nitragin Co., Milwaukee, Wis.
No endorsement is implied.

RESULTS AND DISCUSSION

Solar radiation in full daylight and the average daily noon temperatures under a grass sward at 5 cm depth is shown in Figure 22.

Initial stands of all species, except greenleaf desmodium, were good, and growth was relatively uniform in all plots. Greenleaf desmodium seedlings were killed by chinese rose beetles (*Adoretos sinicus*) while very small, and the greenleaf desmodium plots were re-established and sprayed regularly with insecticide. It was also necessary to treat greenleaf desmodium regrowth with insecticide 1-2 weeks after each harvest (full daylight and 70% daylight treatments only). Growth of siratro was severely restricted under moderate to heavy shading due in part to severe *Anthracnose*, *Rhizoctonia solani* and powdery mildew attacks. It was necessary to spray siratro regularly with fungicides during periods of cool-moist weather to prevent complete loss of the stand.

The soil under greenleaf desmodium was characterized by much better soil structure and increased microbial activity than the soil under the other legumes. This was probably due in large part to the abundant fall of leaves from the densely-shaded lower portion of the canopy to the soil after 6-8 weeks of regrowth. All legumes flowered heavily in full daylight, but flowering and seed set were drastically reduced with decreasing light intensity. Under heavy shading a few flowers were observed in kaimi clover, but none in the other legumes tested.

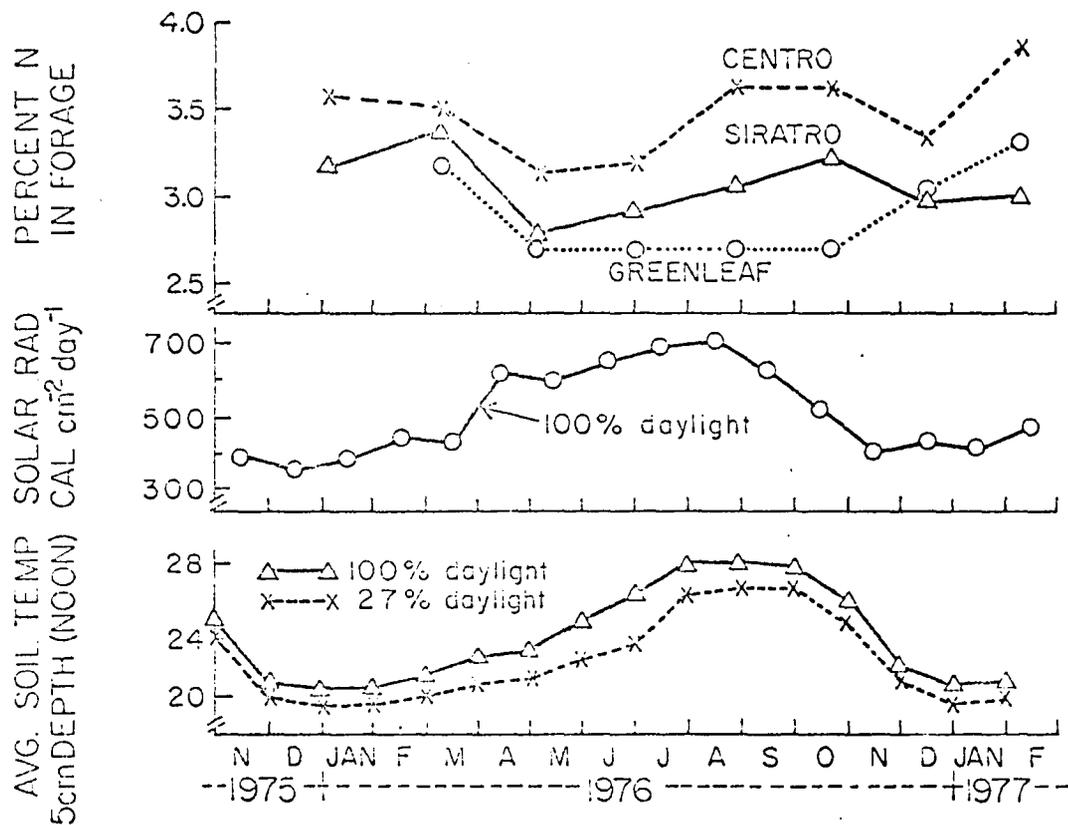


Figure 22. Percent nitrogen of greenleaf desmodium, centro and siratro in relation to solar radiation and soil temperature at 5 cm depth.

Dry matter production. Total daily DM production by greenleaf desmodium was higher at all light intensities and harvest dates than centro or siratro (Figure 23). In full daylight the DM yields of siratro and centro were very similar, while under lower light intensities the DM yield of siratro was lower than centro, indicating that centro is more shade tolerant than siratro.

Daily DM production was 2 to 3 times higher during April-September, than during November-February for all six species. The DM yield of kaimi clover was reduced during the cool season more than the other legumes, but this might be due in part to the effects of a virus disease, which caused bright yellow leaf mottling during the cool season.

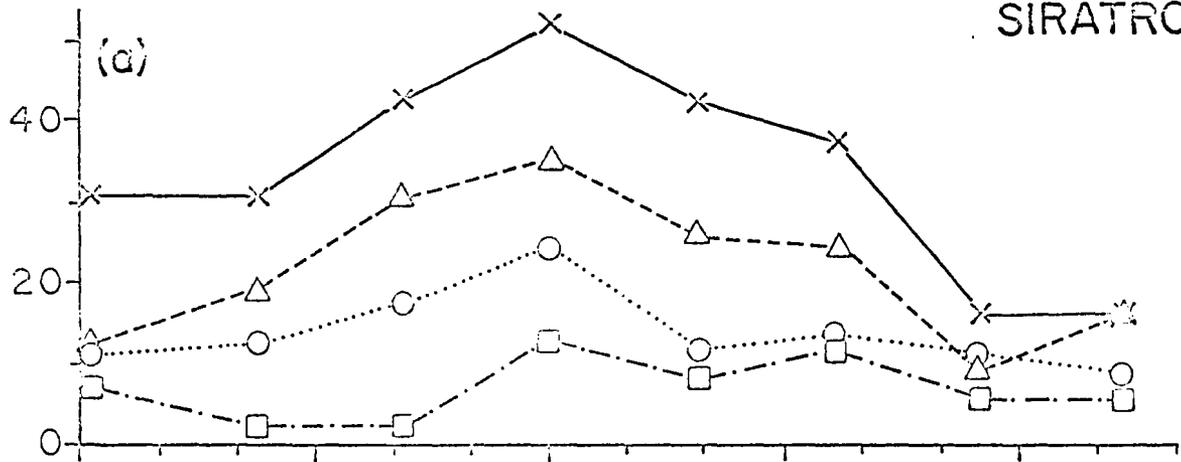
The overall performance of the legumes, expressed as DM production in $\text{ton ha}^{-1} \text{ yr}^{-1}$ is shown in Figure 24 (also see photographs Figure 25). The relative DM production of the replicated legumes at 100, 70, 45 and 27% daylight were 100, 89, 76 and 46 for greenleaf desmodium, 100, 82, 62 and 44 for centro and 100, 69, 41 and 20 for siratro, respectively.

Yields were adjusted according to Federer (1956) for replication effects of the unreplicated legumes. The results showed that the DM yield of stylo was drastically reduced as light intensity decreased, with the yield at 27% daylight being only 12% of the yield at full daylight. Stylo established well, but in the shade treatments, many plants died following every harvest.

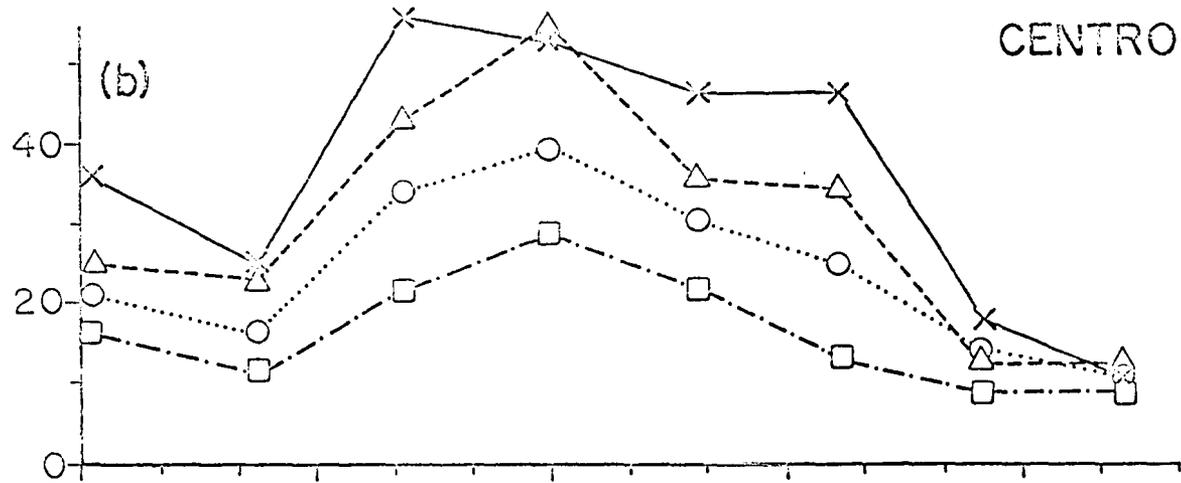
Leucaena was the highest yielding legume at 100 and 70% daylight, but was very sensitive to dense shade. Greenleaf desmodium was the

Figure 23. Dry matter yield of three forage legumes harvested at 8-week intervals over a 15 month period. Average of three replications.

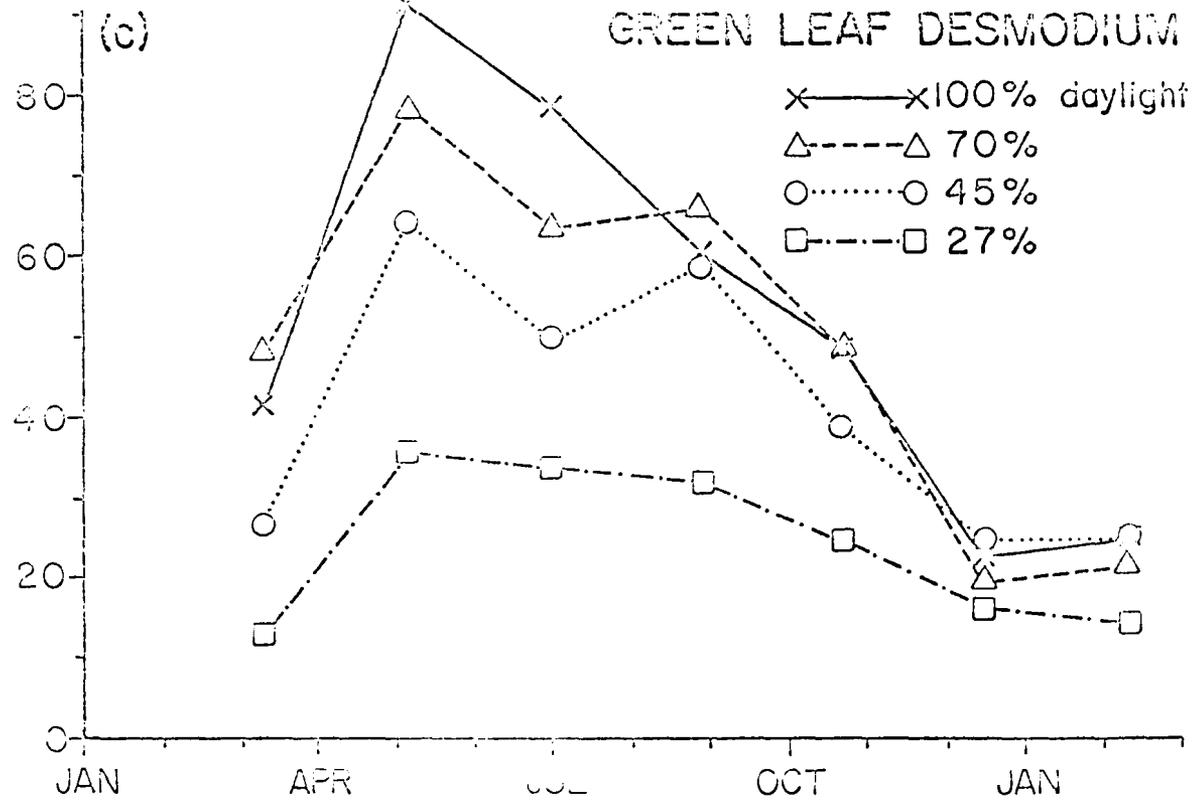
SIRATRO



CENTRO



GREEN LEAF DESMODIUM



DRY MATTER YIELD KG/HA/DAY

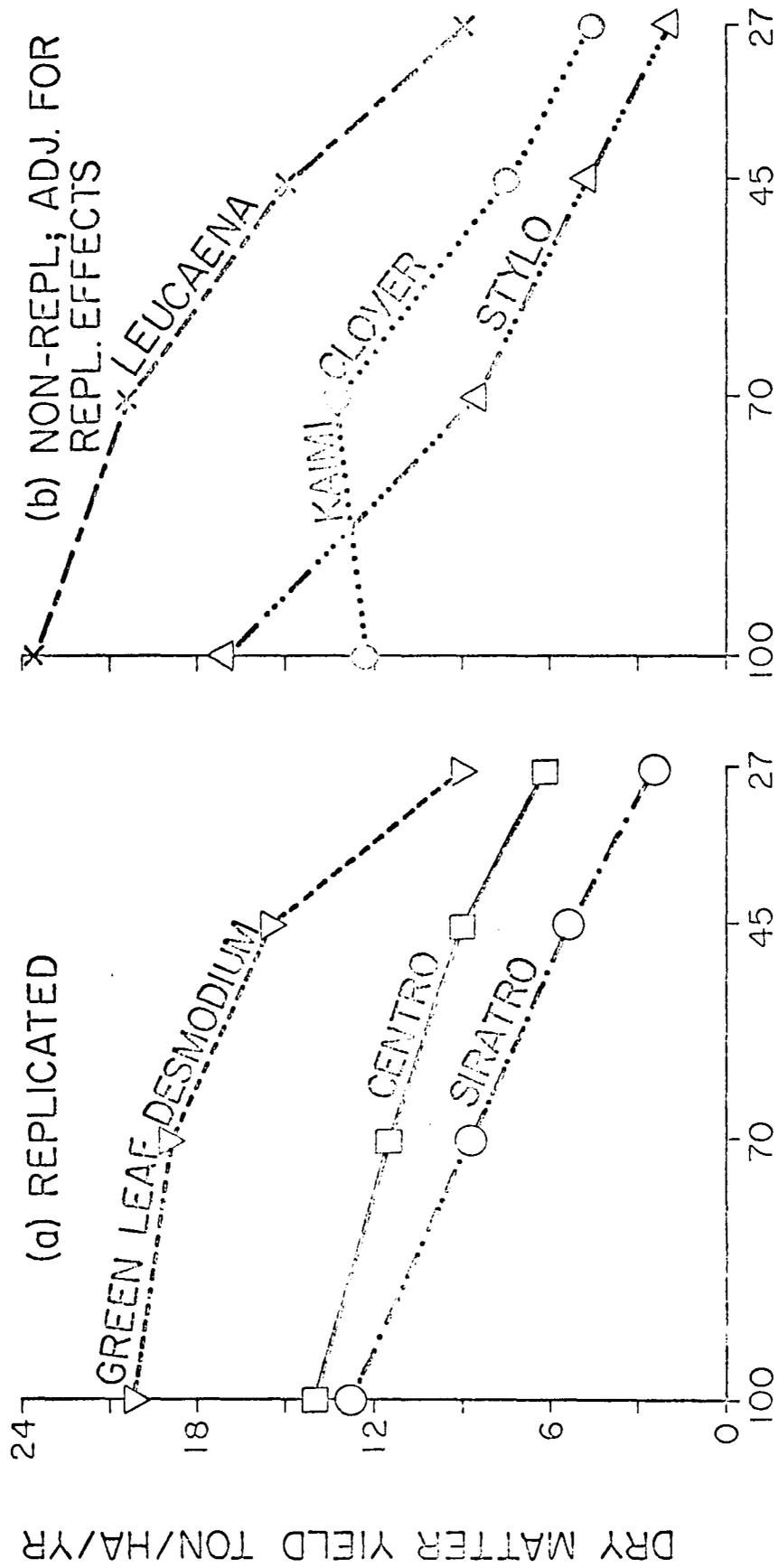


Figure 24. The effect of shading on the annual dry matter yield of six forage legumes.

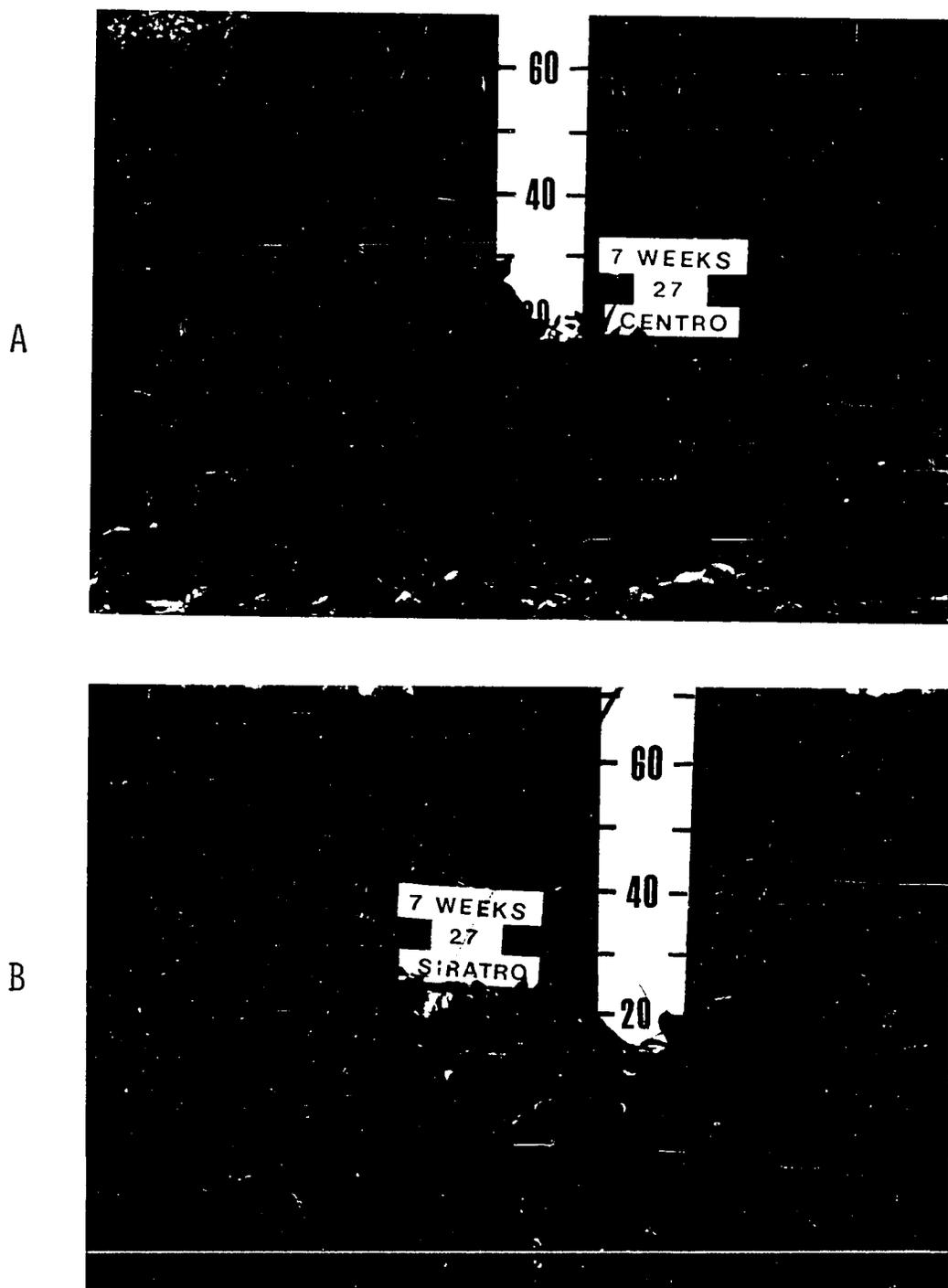


Figure 25. The growth of A) centro, B) siratro, C) greenleaf desmodium, D) kaimi clover, E) leucaena and F) stylo under shade.

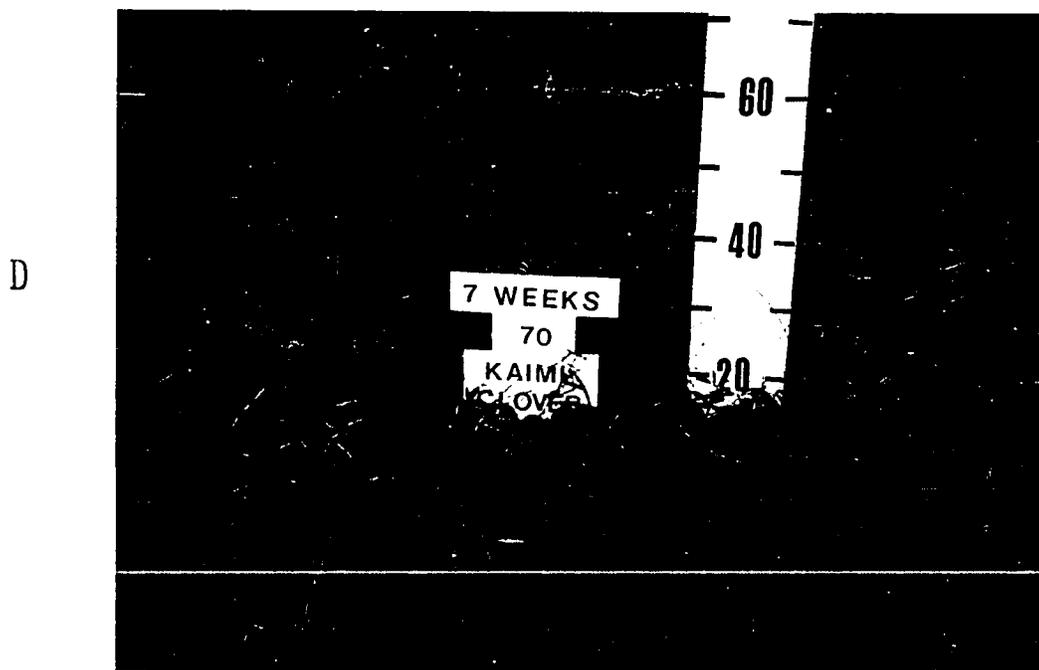
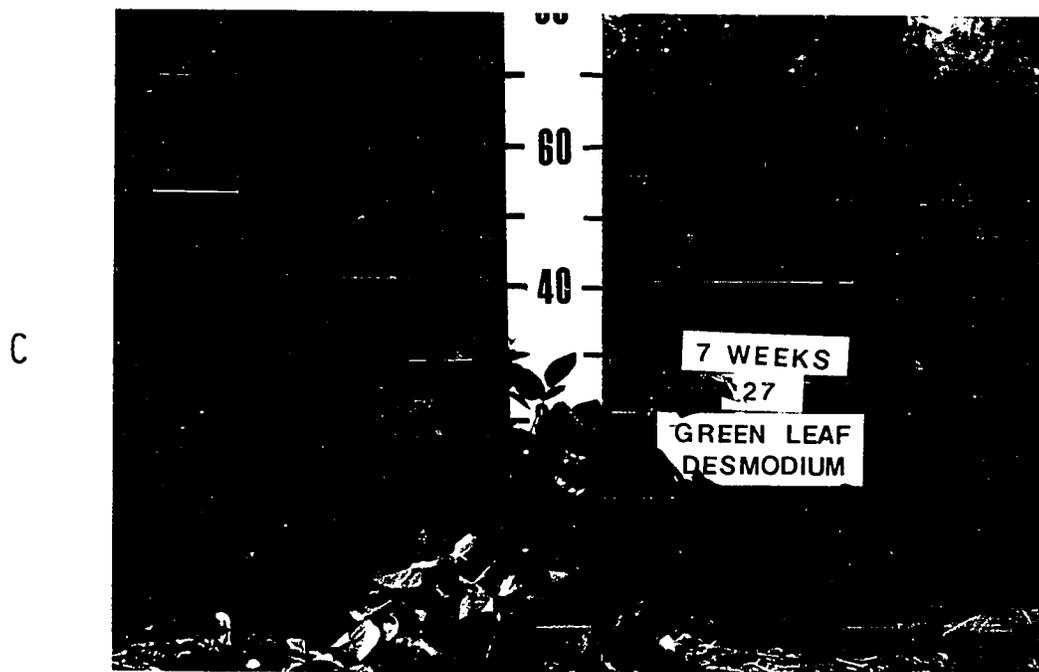


Figure 25. Continued...

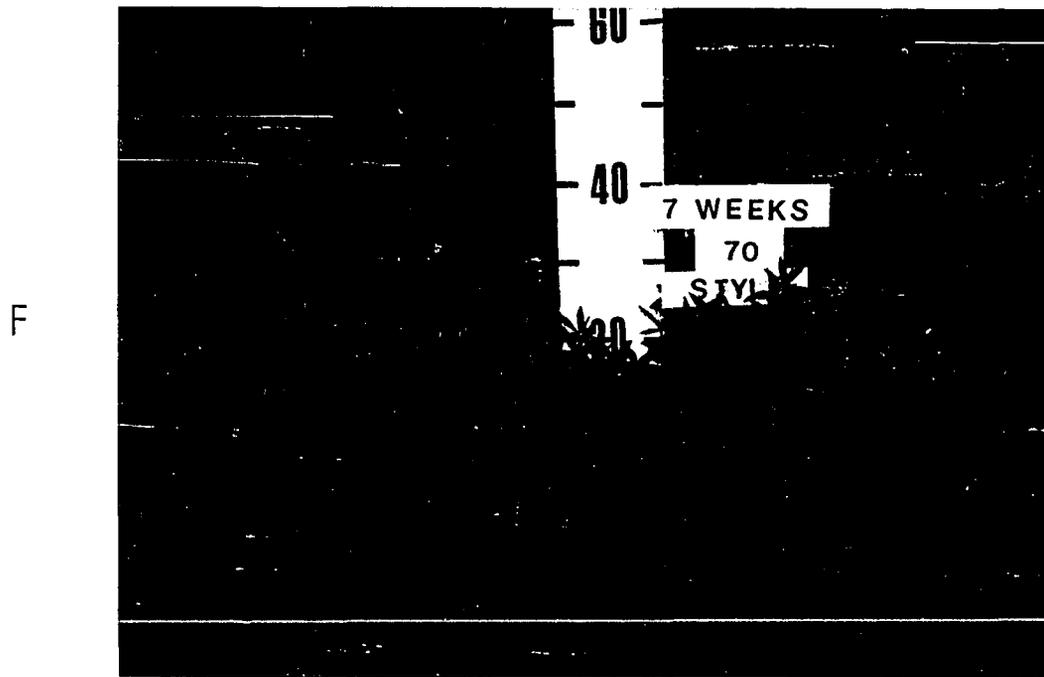
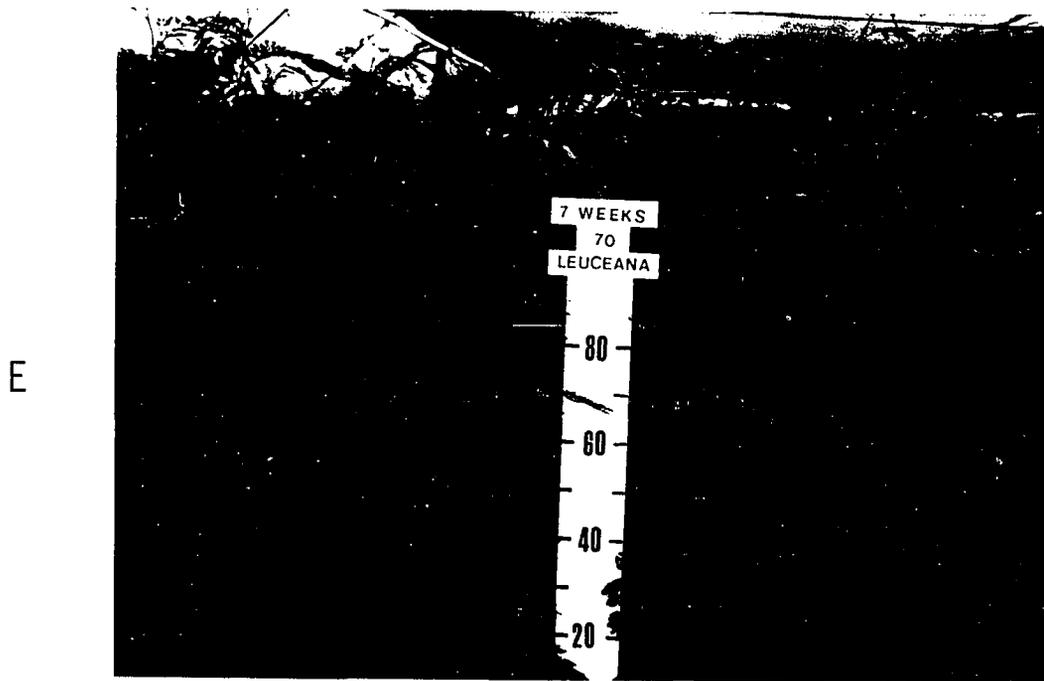


Figure 25. Continued.

most productive at 45 and 27% daylight.

The yield of 21 ton ha⁻¹ yr⁻¹ of greenleaf desmodium obtained at Paia is similar to earlier Hawaiian results obtained with greenleaf desmodium grown in cinder-filled plots at 240 m elevation and cut three times a year (Whitney, 1967). Others (Younge *et al.*, 1964; Plucknett and Fox, 1965; Younge and Plucknett, 1966; Whitney and Green, 1969) have reported yields of 10-21 ton DM ha⁻¹ yr⁻¹ from trials at different locations in Hawaii. Olsen and Moe (1971) reported over 16 ton DM ha⁻¹ yr⁻¹ for greenleaf desmodium and *Stylosanthes guyanensis* in Uganda. However, Malaysian experiments showed slightly lower annual yields for mixtures of grass plus stylo, centro, or siratro (Ng and Wong, 1976).

Ranacou (1972) reported that yields of greenleaf desmodium and centro were not as severely depressed by shading (100, 70, 50, and 30 of full daylight) as were the yields of glycine (*Glycine wightii* (R. Grah. ex. Wight and Arn.) Verdc.) siratro or stylo. These results are consistent with our findings. Poor growth of siratro at low light intensities has also been reported by Ludlow *et al.* (1974).

Dry matter content. In contrast with the grasses (Chapter IV), there was little or no effect of shading on dry matter content of any of the six legumes. As for the grasses no seasonal differences in DM content was found. However, there were differences among legume species, with the highest DM content in leucaena and kaimi clover (23-26 %) and the lowest in siratro (16-18 %). These species effects could be significant considerations for developing pasture programs which would insure adequate dry matter intake by grazing animals.

Plant height. Plant heights of greenleaf desmodium, leucaena and stylo after 8 weeks regrowth were significantly higher in the shade than in full daylight (Table 10). The greatest height increase was recorded for greenleaf desmodium, in which plants grown under 70% daylight were approximately double the height of plants grown in full daylight at both seasons.

Similar results were obtained by Wolf and Blaser (1972) for field-grown alfalfa (*Medicago sativa* L.) which was shaded (100, 70, 45 and 27% of full daylight) for 18 days.

The sward height of the climbing legumes centro and siratro is a measure of plant volume. Although the yields decreased with decreased light intensity, the height of the plant mass did not differ between light intensities, because plants grown in the shade were more elongated and had wider but thinner leaves, resulting in a lower weight per volume plant mass under shade.

Nitrogen percentage, nitrogen yield and apparent N-fixation.

Percentage N in the harvested legumes (DM basis) varied with season (Figure 22) but was not affected by shading, at any harvest date. This is consistent with the findings by Bathurst and Mitchell (1959) on temperate legumes, but differs from our findings in grasses (Chapter IV) in which the N-percentage increased significantly with decreasing light intensity.

The lowest N-levels in the dry forage were measured during spring and early summer and the highest values during the cool season for all legumes.

Table 10. The effect of shading on plant height of six forage legumes.

Legume species	Plant height at indicated harvest and light intensity							
	August 25 harvest				February 10 harvest			
	100	70	45	27	100	70	45	27
	----- cm -----							
centro	28	28	28	28	17	15	16	17
siratro	29	26	27	23	14	14	15	14
greenleaf desmodium	43	73	76	60	17	34	36	25
leucaena	125	136	128	136	41	90	63	65
stylo*	16	31	23	16	20	18	18	26
kaimi clover*	20	26	23	16	11	11	11	11
Average**	<u>100</u>	<u>156</u>	<u>135</u>	<u>112</u>	<u>100</u>	<u>153</u>	<u>139</u>	<u>134</u>

*Unreplicated; data adjusted for replication effect.

**Calculated as percent of height at 100% daylight. Last four (upright) legumes only.

Percentage N differed between species ($P < .01$) with the N-percentage in centro (3.2-3.8) being about 0.5% higher than in siratro (2.8-3.4) and with siratro being higher than greenleaf desmodium (2.7-3.4) most of the year. The low N-percentage in greenleaf desmodium might be partly due to an increasing proportion of stem resulting from loss of the densely shaded bottom leaves during the last few weeks prior to harvesting.

Percentages of N in forage of the unreplicated legumes were 3.2-3.8 in leucaena and 2.6-3.1 in stylo and kaimi clover.

Decrease in total N yield with decreasing light intensity followed the decrease in DM yield, since the percentage-N in the forage did not vary among light intensities (Table 11). However there was less seasonal variation in N yield than in DM yield, because the high DM yields measured during the summer season contained a lower percentage of N.

The very high DM and N yields measured for leucaena confirm earlier findings in Hawaii (Brewbaker *et al.*, 1972) and Australia (Hutton and Bonner, 1960) that this legume has an exceptional capacity for producing large quantities of high-nitrogen forage.

The N yield of greenleaf desmodium ($540 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in full daylight) is somewhat higher than earlier results from Hawaii (Whitney *et al.*, 1967; Whitney and Green, 1969); probably because the earlier experiments were conducted at higher elevations and at sites with lower total solar radiation levels. Also our experiment was irrigated, while the field experiment conducted by Whitney and Green (1969) was not.

Table 11. The effect of shading on the annual nitrogen yield and apparent nitrogen-fixation (legume N-yield less average N-yield of adjacent minus-N grasses) of six forage legumes.

Legume species	Nitrogen yields at various light intensities (% of daylight)				Apparent N-fix. at 2 light intensities	
	100	70	45	27	100	70
	----- kg N/ha -----					
centro	461	410	293	205	366	315
siratro	362	265	160	83	267	170
greenleaf desmodium	540	528	414	245	445	433
leucaena*	751	710	456	285	656	615
stylo*	459	213	151	80	364	118
kaimi clover*	314	361	186	128	219	266
Average**	100	86	56	35		

*unreplicated; treatments adjusted for replication effects.

**Calculated as percent of yield at 100% daylight.

Apparent N-fixation at 100 and 70% daylight (Table 11) was estimated as legume forage N yields less $95 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (the average forage N yields of corigrass, guineagrass, and Mealani digitgrass grown adjacent to the legume plots at 100 and 70% daylight) (See Chapter IV).

Leucaena was the highest yielder of N with estimated N-fixation exceeding $600 \text{ kg ha}^{-1} \text{ yr}^{-1}$. This equals the maximum levels which have been reported for temperate legumes grown under very good growth conditions in New Zealand (Melville and Sears, 1953), Australia (Henzell and Norris, 1962) and Hawaii (Rotar *et al.*, 1976).

Nitrogen fixation by greenleaf desmodium and centro in the present study was higher than the 380 and $270 \text{ kg ha}^{-1} \text{ yr}^{-1}$ fixed, respectively, in cinder plots at higher elevation in Hawaii (Whitney *et al.*, 1967), and the $280 \text{ kg N fixed ha}^{-1} \text{ yr}^{-1}$ by greenleaf desmodium in a field experiment at 640 m elevation under conditions of low night temperatures and dry periods (Whitney, 1969).

Acetylene reduction. The effects of shading on acetylene reduction in soil cores from beneath the six forage legumes during the period August 1976-February 1977 are shown in Table 12.

The highest acetylene-reduction values were measured for greenleaf desmodium and centro. Although the values declined at the lowest light intensities, these two legumes still had much higher rates of acetylene reduction than the other legumes under heavy shade. The dry matter yields of these two legumes indicated that they were also the most tolerant to shade, and the higher acetylene-reduction activity is probably also a reflection of superior carbon assimilation

Table 12. The effect of shading on the acetylene reduction of tropical forage legumes. Average of six harvests during the period August 16, 1976 to February 9, 1977.

Legume species	Acetylene reduction of legume root nodules at various light intensities (% of daylight)				Correlation of C ₂ H ₂ reduction with	
	100	70	45	27	DM	light int.
	----- $\mu\text{mol C}_2\text{H}_2\text{-red m}^{-2}\text{h}^{-1}$ -----				r	r
centro	432	450	429	318	0.80	0.71
siratro	144	108	60	39	0.996**	0.995**
greenleaf desmodium	468	423	339	222	0.99**	0.95*
leucaena*	204	105	87	75	0.80	0.93
kaimi clover*	198	180	147	75	0.92	0.92
stylo*	135	96	39	15	0.96*	0.99**

*unreplicated.

under shaded conditions. Also, the rooted stolons of both greenleaf desmodium and centro had numerous nodules at the soil surface while such was not the case of the other legumes. Generally the acetylene-reduction data were highly correlated with DM yields ($r=0.80$ to 0.996) and with light intensity ($r=0.92$ to 0.995 , except for centro which was 0.71) (Table 12).

Acetylene-reduction activity was also measured at two weeks prior to harvest, and 2, 4, and 7 weeks after the August 25 harvest. The data are not shown here, but acetylene reduction was lowest at two weeks after harvesting for all six legumes and at all light intensities especially under moderate to heavy shading (50-85% of normal under 100% and 70% daylight vs. 0-65% of normal under heavy shade). Defoliation had the least effect on acetylene-reduction activity in greenleaf desmodium and kaimi clover and the most effect on centro and siratro.

Decreased acetylene reduction following defoliation or shading or both has been reported earlier for white clover (*Trifolium repens* L.) by Moustafa *et al.* (1969). The deleterious effects of defoliation and shading on nodulation of pasture legumes have also been reported for temperate legumes by Butler *et al.* (1959) and for tropical legumes by Whiteman (1970) and Whiteman and Lulham (1970). The decreased total activity was due to decrease in nodule mass, rather than to decreased specific activity (Chu and Robertson, 1974). Halliday and Pate (1976) reported that defoliation caused acetylene reduction to drop to about 10% of pre-defoliation levels within hours. However, by one week after defoliation, acetylene-reduction capacity had been restored to approximately 30% of that of the untreated control plants.

Mineral composition. Mineral levels in the forage legumes at 100, 70, and 45% daylight did not differ significantly ($P < 0.05$) at any season except that K content increased with decreasing light intensity during the summer time (Table 13). Dense shading (27% daylight) resulted in a) higher levels of Ca and K during the summer, b) higher levels of Mg during the cool season, and c) lower levels of P and Cu during the cool season than in the other light intensity treatments.

The P values were all above the critical levels of about 0.23% reported by Andrew and Robins (1969) for cattle production. The highest levels were reported for centro (0.36-0.39%) and the lowest for leucaena (0.22-0.30%). The P level in greenleaf desmodium (0.26-0.34%) is above the highest levels reported from a P fertilizer field trial in Australia (0.22-0.26%) (Bryan and Evans, 1973).

Potassium values increased significantly ($P < 0.01$) with decreasing light intensity during the summer season. During the cool season the K values were only slightly higher in shaded forage. Highest values were found in greenleaf desmodium and siratro (2.38-3.01%) and lowest in kaimi clover (1.21-1.82%). Our results correspond with levels in different *Desmodium* spp. reported from Australia (Bryan and Evans, 1973).

Calcium values were slightly higher in densely shaded forage during the summer, with little variation in Ca content among species over both seasons.

The Mg values were not affected by season in full daylight, but were significantly higher during the cool season at 27% daylight. The Mg values of siratro and stylo forage (0.42-0.62%) were about 50% higher than in the forage of the other legumes (0.28-0.38%).

Table 13. The effect of shading on the mineral content of six forage legumes at two seasons.
(sun = full daylight; shade = 27% daylight).

Element	Season	centro		siratro		greenleaf		leucaena*		stylo*		kaimi clover*	
		sun	shade	sun	shade	sun	shade	sun	shade	sun	shade	sun	shade
P (%)	summer	0.35	0.37	0.26	0.31	0.27	0.26	0.22	0.22	0.31	0.35	0.29	0.29
	winter	0.39	0.36	0.32	0.33	0.33	0.34	0.30	0.28	0.33	0.33	0.28	0.32
K (%)	summer	2.37	2.71	2.38	3.01	2.39	2.68	1.98	2.55	2.03	2.58	1.47	1.82
	winter	1.70	1.91	2.40	2.89	2.59	2.62	2.60	2.74	2.32	2.39	2.21	1.78
Ca (%)	summer	0.96	1.04	0.87	1.07	0.97	1.05	0.89	0.92	1.16	1.27	0.82	0.92
	winter	1.10	1.04	0.87	1.00	1.00	1.10	1.21	1.23	1.00	0.94	0.77	0.90
Mg (%)	summer	0.33	0.33	0.46	0.51	0.28	0.28	0.29	0.29	0.42	0.46	0.28	0.29
	winter	0.33	0.38	0.47	0.62	0.27	0.32	0.30	0.30	0.43	0.50	0.28	0.35
S (%)	summer	0.31	0.29	0.21	0.22	0.18	0.16	0.27	0.28	0.25	0.23	0.15	0.14
	winter	0.27	0.25	0.21	0.19	0.18	0.18	0.33	0.32	0.26	0.24	0.16	0.20
Cu (ppm)	summer	26	24	16	14	17	17	23	23	21	21	15	15
	winter	21	14	15	8	18	14	26	24	22	16	13	11
Zn (ppm)	summer	39	38	31	33	34	34	28	27	40	44	33	31
	winter	45	38	35	30	39	39	36	31	42	39	35	35

*unreplicated.

The S content was highest in centro and leucaena (0.25-0.33%) and lowest in greenleaf desmodium and kaimi clover (0.14-0.20%), with no significant differences among light intensities or seasons.

The Cu contents were generally lower in the heavily shaded plots, especially during the cool season. The highest values were measured for centro and leucaena (14-26 ppm) and the lowest for siratro and kaimi clover (8-16 ppm).

The Zn content did not vary significantly between seasons or light intensities. The highest Zn values were recorded for stylo and centro (38-45 ppm) and slightly lower values for the other legumes (27-39 ppm).

SUMMARY AND CONCLUSION

Six tropical forage legumes were evaluated on an Oxic Haplustoll in Hawaii (100 meters above sea level) over a 20-month period under four light regimes (100, 70, 45 and 27% daylight using polypropylene netting) in the field. Centro (*Centrosema pubescens*), greenleaf desmodium (*Desmodium intortum*), siratro (*Macroptilium atropurpureum*), kaimi clover (*Desmodium canum*), "Hawaiian Giant" leucaena (*Leucaena leucocephala*), and "Schofield" stylo (*Stylosanthes guyanensis*) were all established from scarified and inoculated seeds.

The DM yields were highest in full daylight (12.2-23.5 ton ha⁻¹ yr⁻¹), with the highest yields recorded for leucaena and greenleaf desmodium and the lowest for kaimi clover and siratro. The highest DM yields at 27% daylight were recorded for greenleaf desmodium and leucaena (9 ton ha⁻¹ yr⁻¹) and the lowest for stylo (2.2 ton ha⁻¹ yr⁻¹) and siratro (2.6 ton ha⁻¹ yr⁻¹).

The average relative DM yields for greenleaf desmodium and centro at 100, 70, 45 and 27% daylight were 100, 86, 69 and 45. At the same levels of daylight, the relative yields were 100, 69, 41 and 20 for siratro and 100, 50, 35 and 12 for stylo.

The legumes tested may thus be ranked with respect to shade tolerance as follows: centro = greenleaf desmodium > leucaena > kaimi clover > siratro = stylo. DM production was 2 to 3 times higher during the summer than during the cool season. Dry matter content was slightly lower in the shaded forage (1-2%), compared with full daylight, with no significant difference among shade levels at any harvest date.

Percentage N was not affected by shading, was highest during the cool season, and was significantly higher in centro and leucaena (3.2-3.8%) than in greenleaf desmodium, stylo or kaimi clover (2.6-3.1%). Total N-yields were between 314-751 kg ha⁻¹ yr⁻¹ in full daylight and 80-285 in 27% daylight.

Acetylene reduction was significantly depressed by defoliation. Acetylene reduction levels 2 weeks after harvesting were only 50-85% at 100 and 70% daylight and 0-65% at 45 and 27% daylight compared to pre-defoliation levels. Recovery was nearly complete by 4 weeks after harvesting. Greenleaf desmodium and kaimi clover were least and centro and siratro most affected by harvesting. Acetylene reduction was highly correlated to DM yields at different light intensities ($r=0.80$ for centro and leucaena and $r=0.92-0.996$ for the others). Acetylene reduction and light intensity were also highly correlated ($r=0.92-0.995$, except for centro which was 0.71). During the cool season acetylene reduction was drastically decreased for centro, but was only

slightly decreased for the other 5 legumes.

Leucaena had the greatest apparent N-fixation (legume N-yield less average N-yield of adjacent minus -N grasses), fixing an estimated $615 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in full daylight. Apparent N fixation values for the other legumes (in full daylight) were: $445 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for greenleaf desmodium, 365 kg for centro and stylo and 265 kg for siratro and kaimi clover.

The levels of P, Ca, Mg, S, Cu and Zn were not affected by shading at any season except for small effects at 27% daylight. Dense shade increased the levels of Mg during the cool season and Ca and K during the summer season and decreased the levels of P and Cu during the cool season.

Plant height for the upright growing legumes greenleaf desmodium, leucaena and stylo increased significantly with shading at both seasons.

In general, the responses to shade by the legumes studied were decreased DM yield and nitrogenase activity, slightly decreased DM content, and elongated growth. Shading had little effect on mineral content.

CHAPTER VI

THE EFFECT OF DIFFERENT LIGHT INTENSITIES ON ACETYLENE REDUCTION, DRY MATTER ACCUMULATION AND GRAIN YIELD OF SOYBEAN, COWPEA, BUSHBEAN AND PIGEON PEA.

INTRODUCTION

The dependence of most plant growth processes on photosynthesis (and hence sunlight) is well established (see review by Evans, 1972). Most plants are able to adapt to changes in light regimes through both morphological and physiological changes. Shading of legumes generally causes elongated growth, reduced specific leaf weight (SLW), and increased leaf area per unit of plant weight (LAR) (Straley and Cooper, 1972; Beuerlein and Pendleton, 1971; Bowes *et al.*, 1972).

Cumulative dry weights and relative amounts of nitrogen in the above ground parts during growth in full daylight have been recorded for soybean by Hanway and Weber (1971) and Egli and Leggett (1973); while top and root growth at different morphological stages have been reported for soybean by Mayaki *et al.* (1976) and Sivakumar *et al.* (1977). Similar data have been reported for bushbean and climbing bean (*Phaseolus vulgaris* L.) in full daylight by Graham and Rosas (1977). The effect of shading on total N in different plant parts during growth was recorded for faba beans (*Vicia faba* L.) by Sprent and Bradford (1977).

Although shading has been known for many years to affect growth and yield, only a few studies have been made on the effect of shading on nitrogen fixation. Chu and Robertson (1974) found that shading reduced both nodule number and size on white clover and similar results have been reported for birds foot trefoil (McKree, 1962), cowpea (Dart and Mercer, 1964), lupin (Sprent, 1973), and soybean (Yoshida, 1973; Lawn and Brun, 1974). Sprent and Bradford (1977) reported that shading of field beans delayed nodule senescence.

The assessment of biological nitrogen fixation in the field using the acetylene-reduction technique (Hardy *et al.*, 1973) has been widely accepted as a useful assay for N-fixation. Using this method, Sprent (1973) found that shading of lupin decreased the N fixation activity of the plant in proportion to the logarithm of relative irradiance. This was largely due to smaller amounts of nodule tissue formed under shade, while the specific nodule activity was only slightly reduced. Sprent and Bradford (1977) found that shading of faba beans generally caused a decrease in nodule activity during early growth, but that nodules on shaded plants became more active during the later part of the growing season. This was associated with delayed senescence of the leaves in shaded plants (Sprent *et al.*, 1977).

Several studies have indicated the importance of photosynthetic products to symbiotic nitrogen fixation (Virtanen *et al.*, 1955; Wheeler, 1971; Lawn and Brun, 1974). Seasonal and diurnal variations in nitrogen fixation indicate that the process is quite sensitive to the supply of photo-synthetic assimilates (Bergersen, 1970; Mague and Burris, 1972; Sloger *et al.*, 1975).

Total acetylene reduction by most legumes usually increase with plant age until the start of pod filling and then decreases markedly. However differences among different species and varieties have been reported (e.g. Hardy *et al.*, 1968; Harper and Hageman, 1972; Lawn *et al.*, 1974; Lawn and Brun, 1974; Sloger *et al.*, 1975; Sprent and Bradford, 1977; Graham and Rosas, 1977). The decrease in nitrogen fixation during pod filling has been reported to be a result of an inadequate supply of assimilates from the shoot to the nodules (Lawn and Brun, 1974; Lawrie and Wheeler, 1975). Thus nitrogen-fixation, especially during the reproduction phase, may be subject to the effect of both plant maturation characteristics and light intensity.

This study was initiated to determine the effect of different light intensities on the performance of several grain legumes during the summer and cool seasons with respect to 1) the cumulative dry weights of roots, nodules, stems, leaves and pods during growth, 2) number of nodules, nodule weight and C_2H_2 -reduction, 3) plant height, 4) nitrogen content and 5) grain yield, pod number per plant, seed number per pod and seed weight.

MATERIALS AND METHODS

Light intensity experiment. Planting of grain legumes were established in each of two seasons on an Oxic Haplustoll near Paia, Hawaii. The experimental site was located approximately $20^{\circ} 55'N$ latitude and $156^{\circ}W$ longitude at about 100 m elevation. Phosphorous and potassium were applied 9 months prior to the first planting (April-July) at a rate of 150 kg/ha of P as treble superphosphate, and 180 kg/ha of K as muriate of potash. Lime was applied at 3400 kg/ha to increase the pH

to about 6.3.

Bushbean cv. Burpee Tenderpod (*Phaseolus vulgaris* L.), soybean cv. Kahala (*Glycine max* L.), cowpea selection TVu 1190 (*Vigna unguiculata* Walp.) were planted April 9th 1976 (summer crop).

These varieties were planted again November 4th, 1976 (cool-season crop) except that cowpea TVu 1190 was replaced TVu 4557. Cowpea TVu 1190 was, however also planted as a non-replicated treatment. Pigeon pea CITA 4 (*Cajanus cajan* (L.) Millsp.) was planted November 11th, 1975 as a non-replicated treatment, and pods were harvested at varying intervals during the following 14 months. Four different light regimes were obtained by shading with different densities polypropylene screening: 100, 70, 45 and 27% of full daylight, erected as described in Chapter IV.

Three replications of a split plot arrangement in a completely randomized block were used, with light regimes as whole plots and species as sub plots. Each sub plot consisted of six rows 2.9 m long and spaced 42 cm apart. Plant populations were varied by varying intra-row spacing, e.g. 6.5, 9.2, 13.2, and 18.3 cm for soybean, bushbean, cowpea TVu 1190, and cowpea TVu 4557 respectively, which corresponded to 365,000, 260,000, 180,000 and 130,400 plants per ha (Appendix Figures 1 and 2).

Prior to planting seeds were scarified and inoculated with commercial peat cultures^{3/}. The plots were watered as needed, using impulse sprinklers. Each block was watered separately to allow for reduced water use under low light intensities.

^{3/}Supplied by the Nitragin Co., Milwaukee, Wis.
No endorsement is implied.

Three plants were sampled at random from each plot at weekly intervals from 3 weeks after seeding to maturity for the April 9th planting and at 1-3 week intervals for the November 4th planting. Acetylene-reduction activity, number and dry weight of nodules, plant height, and dry weights of roots, stems, leaves, pods and seeds were determined at each sampling. Acetylene reduction was determined on plants which were excavated and the roots gently cleaned of soil. The nodulated roots were then cut from the tops and immediately transferred into 1000 ml plastic containers, one root system per container, with minimal agitation in order to maintain nodule attachment to the roots. Acetylene was introduced within 10 minutes of sampling (10% by volume) by first removing 100 ml of air with a syringe and then adding 100 ml of acetylene. After incubation for 1½ hours, 0.5 ml of gas was removed and injected into Varian Aerograph model 940 gas chromatograph equipped with a hydrogen flame ionization detector. Separation was achieved using a 1/8-inch by 5 feet stainless steel column packed with "Poropak R". Injector and detector temperatures were maintained at 110 and, 140 C respectively. Purified N₂ carrier gas at 30 ml/min provided retention times for C₂H₄ and C₂H₂ of 1.0 and 1.5 min, respectively. Results were calibrated against standard gases supplied by Gaspro Inc. The roots, nodules, and top portions of the plants were dried at 55 C and individually weighed. The 3 plants per treatment in each replication were then combined prior to grinding for total N determination. At maturity the four center rows were harvested, dried at 45 C, and weights of seeds, number of pods per plant, number of seeds per pod and 1000

seed weight were recorded. The nitrogen content of seeds, and combined root, nodule and top samples was determined by Kjeldahl digestion (using CuSO_4 and selenized Hengar granular catalysts) followed by measurement of NH_4 by the diffusion process (using modified Conway dishes) or an automatic NH_4 analyzer.

Nitrogen fertilizer experiment on bushbean. Due to the very low 1000 seed weight recorded for bushbean in full daylight, and the very low acetylene-reduction data recorded for bushbean, compared to the other grain legumes, an additional experiment was conducted to evaluate the effects of N fertilizer on growth of bushbean under 100 and 70% of full daylight.

Three replications of a split plot arrangement in a completely randomized block were used, with light regimes as whole plots and N-levels as sub plots; 30 kg/ha of nitrogen as urea was applied to the plus-N treatments at the time of planting, followed by 40 kg N/ha six weeks after planting.

Plants were established March 27, 1977, and spacing, seed inoculation and irrigation were done as in the first experiment. Plant samples were taken 3, 4 and 7 weeks after emergence to assay for acetylene reduction and for plant weight determination. At 4 weeks leaf areas were determined by correlation with a known weight of a standard area of photocopy paper on which the leaves were copied. At maturity the plants were harvested and characterized as described for the first experiment.

RESULTS AND DISCUSSION

SOYBEAN

Plant growth characteristics. Shading of soybean caused the typical morphological changes associated with shade (Boardman, 1977) bigger and thinner leaves and longer internodes. Plant height of soybean increased linearly for the first 9 weeks after emergence to a maximum of 60 cm during the summer crop, with the tallest plants occurring at 45% daylight followed by 70, 27 and 100% daylight (Figures 26 and 27; Appendix Figure 3). During the cool season, maximum plant height of 30 cm (at 27% daylight) was reached one week earlier than during the summer season, with decreasing plant height in the following order: 27 > 70 > 45 > 100% daylight. Increasing soybean plant height with shading has also been reported by Caviness and Downey (1968) and Yoshida (1973).

Nodulation and N-fixation. The nodule number of soybean (summer planting) increased linearly until the beginning of pod fill (7-9 weeks after emergence) reaching about 65 nodules per plant for 100, 70, and 45% daylight, and 44 nodules per plant for 27% daylight (Figure 28; Table 14). Nodule number declined rapidly after 9 weeks under all light intensities. Maximum nodule mass occurred two weeks after the peak of nodule number, reaching 700 mg/plant for 100 and 70% daylight, 600 mg/plant for 45% daylight and 300 mg/plant for 27% daylight.

The number of nodules per plant was not significantly reduced by moderate shade, but was consistently lower at 27% daylight (Table 14). Intense shade also reduced nodule size so that the total nodule mass

SOYBEAN

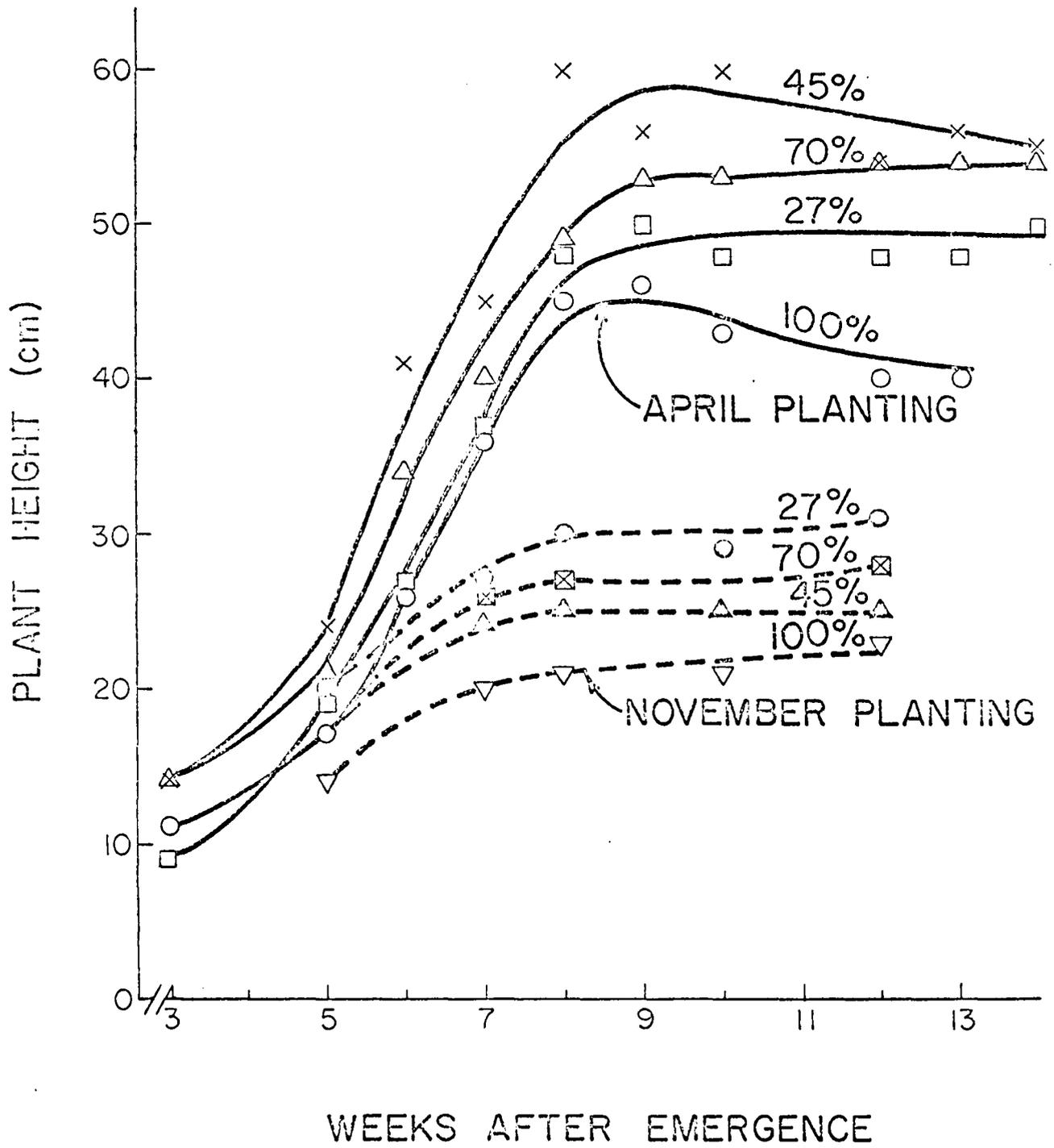


Figure 26. The effect of shading on plant height of Kahala soybean grown during two seasons.

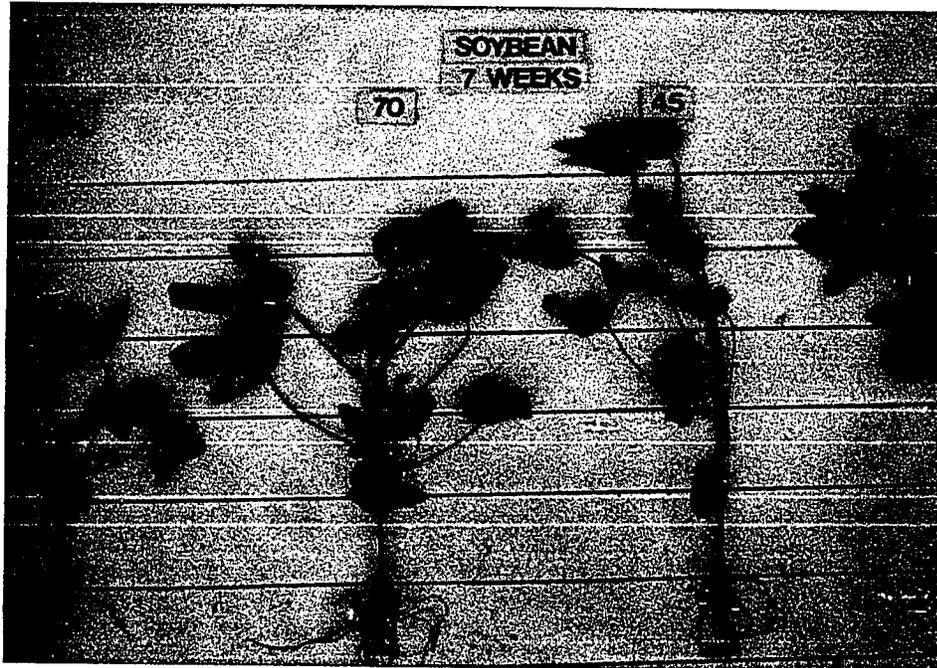


Figure 27. The effect of shading on growth of soybean during the summer season.

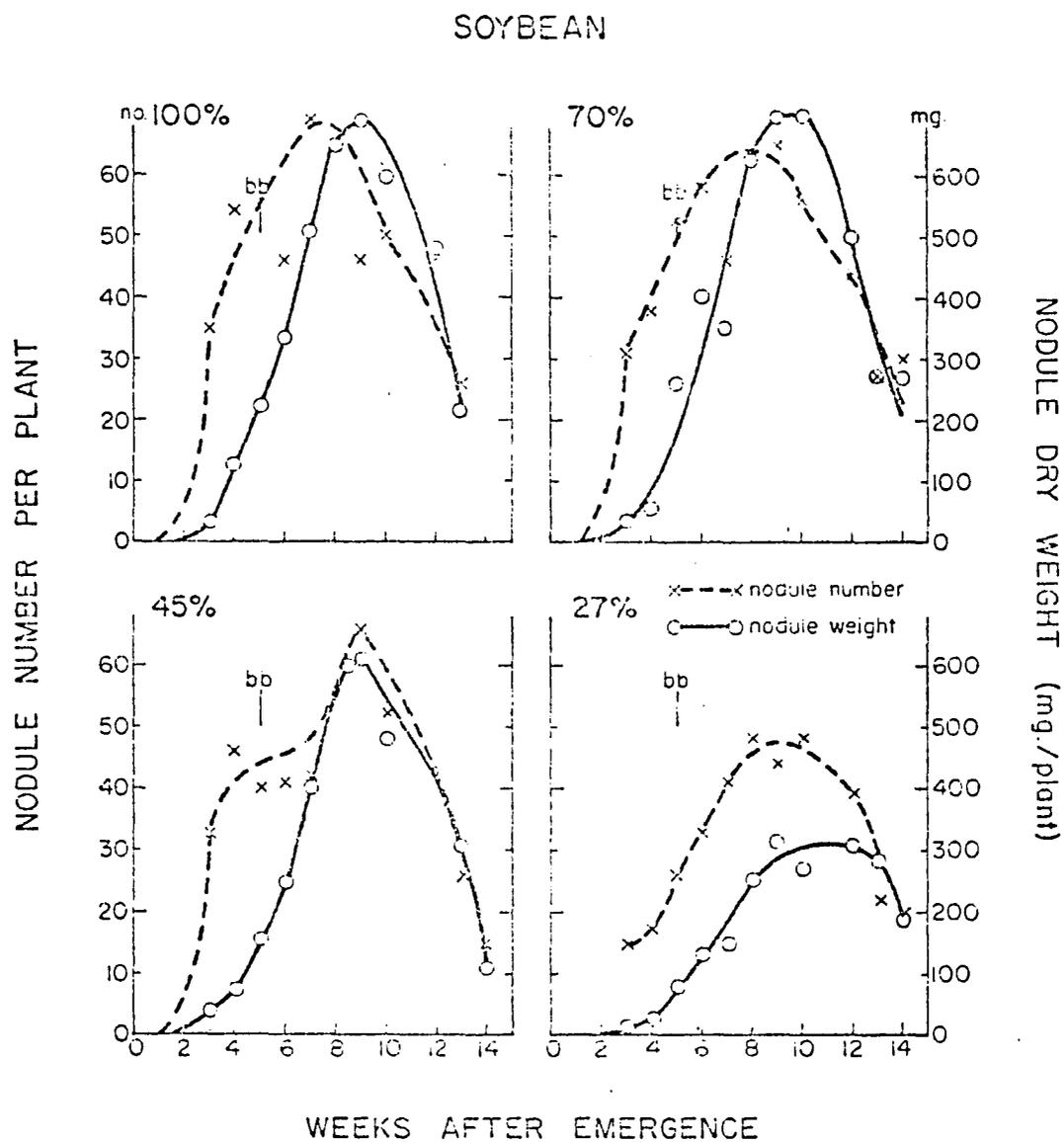


Figure 28. The effect of shading (100%=full daylight) on nodule number and nodule dry weight of Kahala soybean grown during the summer season (bb=beginning bloom).

Table 14. The effect of shading on the number of nodules, nodule dry weight and acetylene reduction per plant, and the specific nodule activity and nodule size of Kahala soybean grown during the summer.

Light intensity	Characteristics at indicated weeks after emergence						
	3	5	7	8	9	11	13
a) <i>Total nodule number per plant.</i>							
100	36 a [†]	49	71 a	67 a	60	33	25
70	33 a	53	46 b	64 a	65	38	27
45	31 a	40	42 bc	70 a	66	53	26
27	16 b	35	29 c	36 b	44	21	22
	*	ns	**	*	ns	ns	ns
b) <i>Total nodule dry weight per plant (mg).</i>							
100	35	228	527 a	650 a	704 a	333 ab	189
70	38	263	351 a	629 a	703 a	377 ab	270
45	36	159	402 a	599 a	610 a	523 a	105
27	13	206	146 b	251 b	312 b	169 b	281
	ns	ns	*	**	*	*	ns
c) <i>Acetylene reduction per plant ($\mu\text{mol/h}$).</i>							
100	2.5	26 a	50 a	23 b	47 a	11	0.0
70	3.8	25 a	41 b	30 b	26 b	9	4.1
45	2.8	19 ab	33 b	39 a	28 ab	24	7.3
27	0.8	13 b	12 c	22 b	17 b	10	3.4
	ns	*	**	*	*	ns	ns
d) <i>Specific nodule activity ($\mu\text{mol/h/gm dry nodule}$).</i>							
100	79	113	102	38	63	42	0
70	72	95	98	47	36	25	14
45	65	125	81	64	52	45	40
27	54	95	81	65	60	60	16
e) <i>Nodule size (mg/nodule).</i>							
100	1.0	4.7	7.4	9.7	11.7	10.0	8.5
70	1.2	5.0	7.6	9.8	10.8	9.9	10.0
45	1.2	4.0	9.6	8.6	9.2	9.9	11.2
27	0.8	5.9	5.0	7.0	7.1	8.0	12.8

[†] Means in the same column followed by the same letter are not significantly different at the 5% level (Bayes LSD).

* Significant at the 5% level.

** Significant at the 1% level.

ns Non significant.

per plant under 27% daylight was significantly lower than under full daylight or moderate shade at most sampling dates. The effect of shading on nodule number and nodule weight was similar during both seasons, although total nodule number per plant during the cool season was about 50%, and nodule weight only 25% of the summer season (Tables 14 and 15). During the summer season soybean nodules attained an average maximum weight of 11 mg/nodule. Maximum weight per nodule peaked at 9 weeks after emergence for plants grown under 100 and 70% daylight and at 13 weeks for plants grown under 45 and 27% daylight. Average nodule weight was smaller during the cool season than during the summer. Nodule size also decreased with decreasing light intensity at both seasons (Table 14 and 15). The smaller nodule size at a given sampling date can be partly explained on the basis of delayed physiological maturity under shade. Reduction in nodule mass, nodule number, nodule size, or all three due to shading of soybean has also been reported by Sampaio and Döbereiner (1968), Bergersen (1969), Yoshida (1973), Lawn and Brun (1974), and Kry (1976). Rocha *et al.* (1970) reported that when soybean were grown under shade (27, 45 and 70% of daylight) the nodule number was not affected by shading, but nodule mass decreased linearly with decreasing light intensity.

Maximum acetylene reduction during the summer was 40-50 $\mu\text{mol C}_2\text{H}_4$ produced per plant per hour for 45, 70 and 100% daylight and 20 $\mu\text{mol C}_2\text{H}_4$ produced per plant per hour for 27% daylight at early pod filling --7-8 weeks after emergence (Figure 29; Table 14). Acetylene reduction was decreased significantly only under the most intense shade during the period 5 to 9 weeks after emergence. Before and after this period, shading had no significant effect on acetylene

Table 15. The effect of shading on the number of nodules, nodule dry weight and acetylene reduction per plant, and specific nodule activity and nodule size of Kahala soybean grown during the cool season.

Light intensity	Characteristics at indicated weeks after emergence			
	5	7	8	6
a) <i>Total nodule number per plant.</i>				
100	27 b [†]	22 b	20 ab	21
70	54 a	43 a	34 a	29
45	37 b	21 b	24 ab	30
27	11 b	15 b	8 b	19
	*	*	*	ns
b) <i>Total nodule dry weight per plant (mg).</i>				
100	39 b	139 ab	139 ab	143 a
70	122 a	195 a	244 a	131 a
45	40 b	92 bc	121 ab	104 ab
27	9 b	28 c	27 b	39 b
	*	*	*	*
c) <i>Acetylene-reduction per plant (μmol/h).</i>				
100	5.5 b	21.2 ab	14.2 a	1.8
70	22.3 a	22.6 a	17.7 a	3.7
45	5.2 b	10.6 bc	9.2 b	3.8
27	0.6 b	1.3 c	1.7 c	1.3
	**	*	**	ns
d) <i>Specific nodule activity (μmol/h/gm dry nodule).</i>				
100	138	154	139	9
70	172	117	89	26
45	125	120	76	41
27	60	57	39	32
e) <i>Nodule size (mg/nodule).</i>				
100	1.4	6.3	6.7	6.8
70	2.3	4.5	6.9	4.5
45	1.1	4.4	5.0	3.5
27	0.8	1.9	3.4	2.1

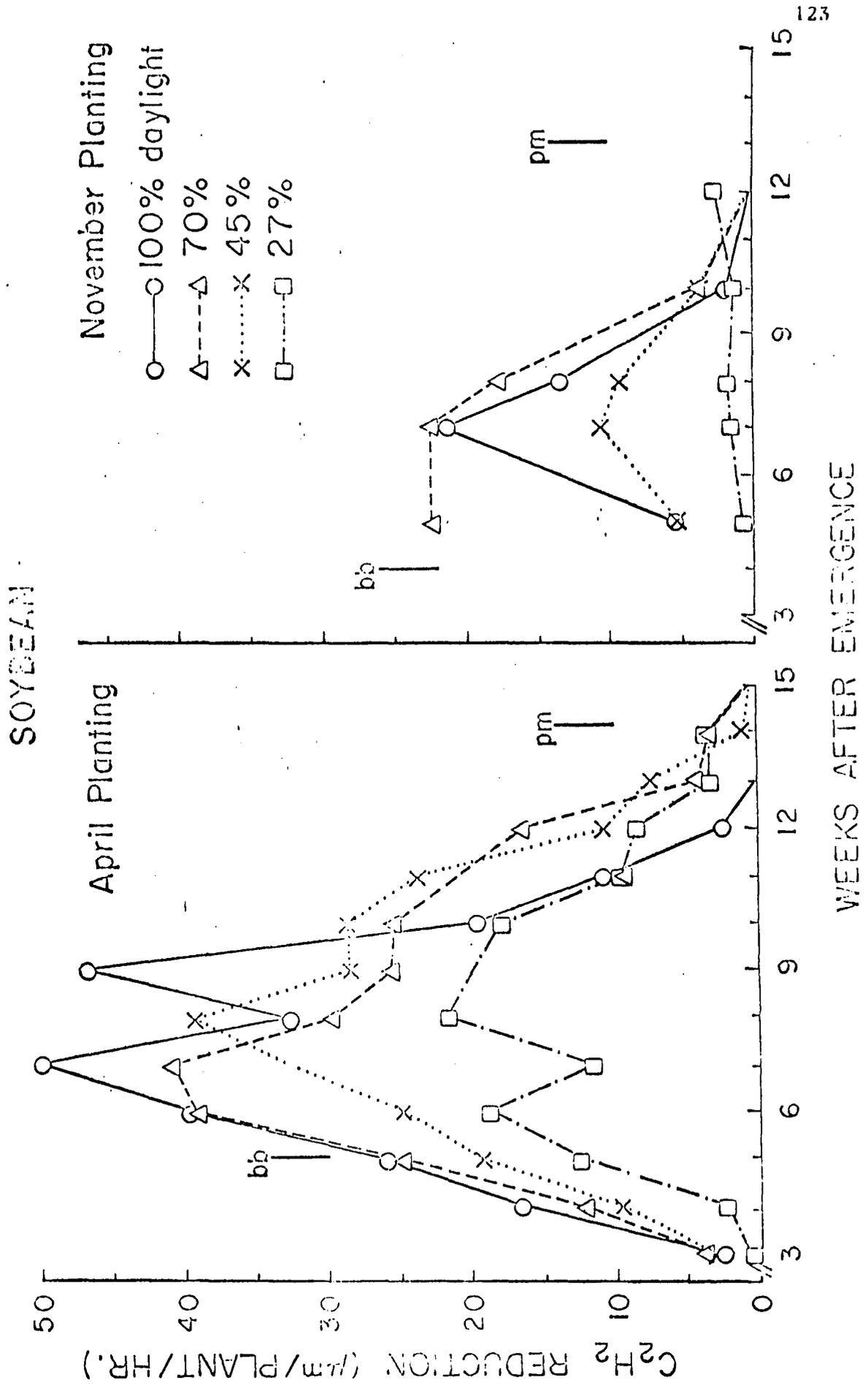
[†] Means in the same column followed by the same letter are not significantly different at the 5% level (Bayes LSD).

* Significant at the 5% level.

** Significant at the 1% level.

ns No significant difference.

Figure 29. The effect of shading on acetylene reduction of
Kahala soybean grown during two seasons.
(bb=beginning bloom; pm=physiological maturity).



November Planting

- 100% daylight
- △ 70%
- × 45%
- 27%

April Planting

- 100% daylight
- △ 70%
- × 45%
- 27%

C₂H₂ REDUCTION (µm/PLANT/HR.)

reduction. At the time of maximum acetylene reduction, more than 50% of the total DM production had been accumulated.

Acetylene reduction per gram of nodule dry weight (hereafter referred to as specific nodule activity) decreased linearly from 120 $\mu\text{mol/g}$ at 4 to 5 weeks after emergence to about 45 $\mu\text{mol/g}$ at 11 weeks at all light intensities. Specific nodule activity then remained at about 15 $\mu\text{mol/g}$ until maturity (Table 14).

Acetylene reduction during the cool season reached a maximum of only 22 $\mu\text{mol/plant per hour}$ at 7 weeks after emergence which is much lower than during the summer. Also acetylene reduction in the cool-season crop decreased sharply after 8 weeks, probably caused by tendency of this crop to mature much earlier than the summer crop. Rates of acetylene reduction and nodule activity recorded in full daylight in this study are similar to those reported for other soybean varieties (Hardy *et al.*, 1968, 1971; Harper and Hageman, 1972; Sloger *et al.*, 1975; Graham and Rosas, 1977). Acetylene reduction in soybean grown in Brazil under 100, 70, 45 and 27% daylight decreased inproportion to decreasing light intensity (Rocha *et al.*, 1970), which is in variance to this investigation, where the acetylene reduction over the whole growing period was decreased only under the most intense shade. In two greenhouse studies in Georgia, Kry (1976) found the highest acetylene reduction at 82 and 60% daylight when soybeans were grown under 100, 82, 60 and 38% daylight.

Decreases in nodule mass with shading have been reported to be highly correlated with decreased root dry weights. One gram of root tissue supported 50 mg nodule tissue on *Lupinus arboreus* (Sprent, 1973) when grown at light intensities between 100 and 10% daylight. Soybean

plants grown in pots at 100, 82, 60 and 38% daylight supported 440 mg nodule tissue per gram of root tissue regardless of light intensity (Kry, 1976). In this investigation there was a highly significant linear relationship for the summer crop between nodule and root weights ($r = 0.93$) regardless of shading treatment or age from 5 - 12 weeks after emergence, with each gram of root tissue supported 786 mg of nodule tissue (Figure 30). During the cool season each gram of root tissue supported 873 mg of nodule tissue ($r = 0.78$). These data are from field experiments, where some root tissue were lost during sampling, consequently the nodule weight per gram of root weight would be higher than in a pot experiment (e.g. Kry, 1976). Low soil N-content in this experiment would also explain the high nodule weights per gram root weight, as suggested by the data of Kry (1976) from a greenhouse experiment, where each gram of root supported 440 mg nodule at zero-N and 200 mg nodule at 60 kg N/ha.

Dry matter and N accumulation. Dry matter (DM) accumulation for roots, nodules, stems, leaves and pods at different light intensities were season-dependent. The maximum accumulation during the summer was 9 ton/ha while during the cool season only 2.4 ton/ha were harvested (Figures 31 and 32). Although Kahala soybean is considered to be photoperiodically insensitive, the cool-season crop started flowering 3.5 weeks after emergence -- 10 days earlier than the summer crop. This served to restrict the formation of additional photosynthetic surface and caused earlier competition for photosynthates by the developing grain. There was no significant difference between the final DM yield at 100 and 70% daylight at either season. However, DM

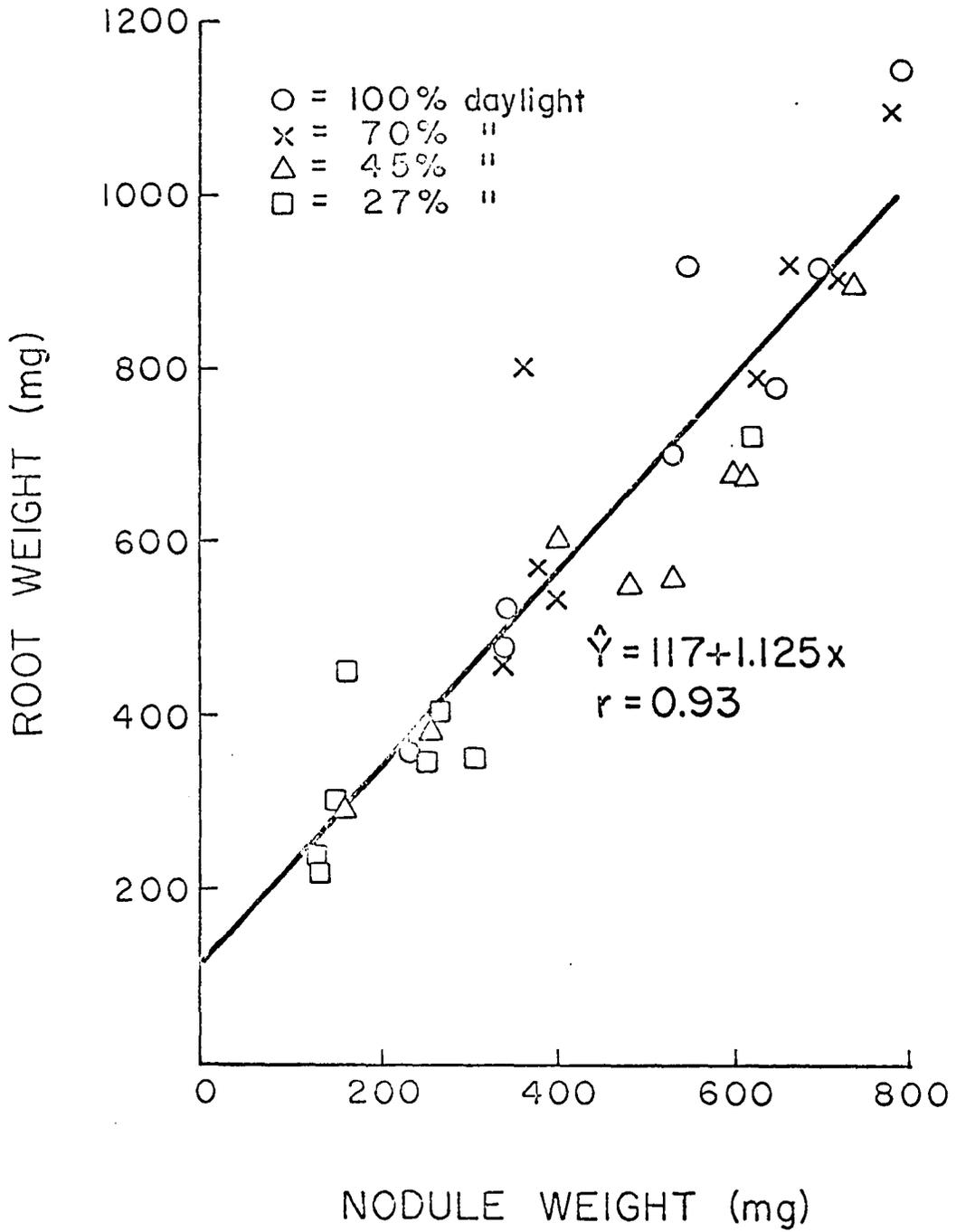


Figure 30. Relationship between root and nodule dry weights of soybean over all shading treatments and sampled 4-12 weeks after emergence during the summer season.

SOYBEAN

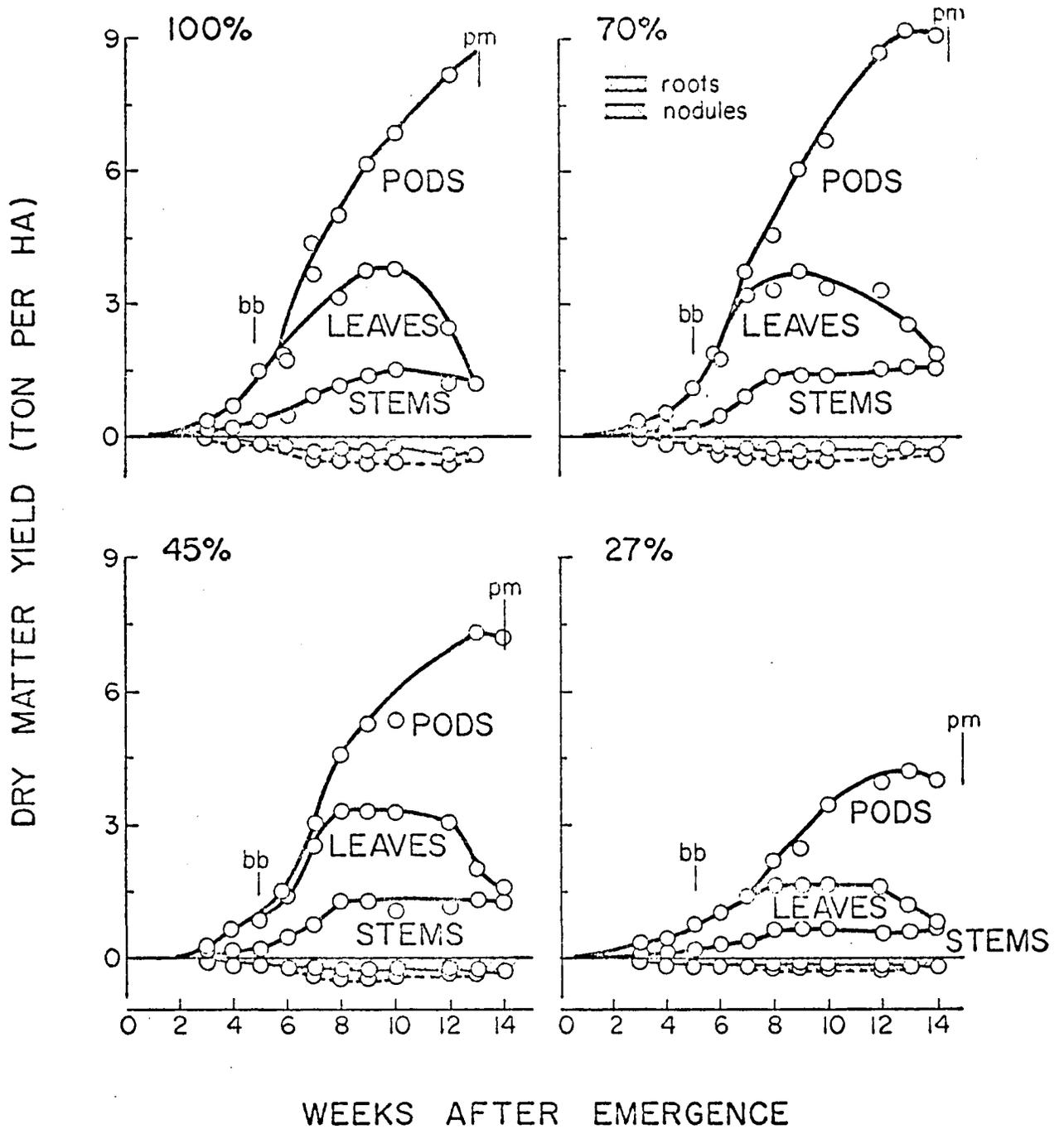


Figure 31. The effect of shading on dry matter accumulation of Kahala soybean grown during the summer season. (bb=beginning bloom; pm=physiological maturity).

SOYBEAN

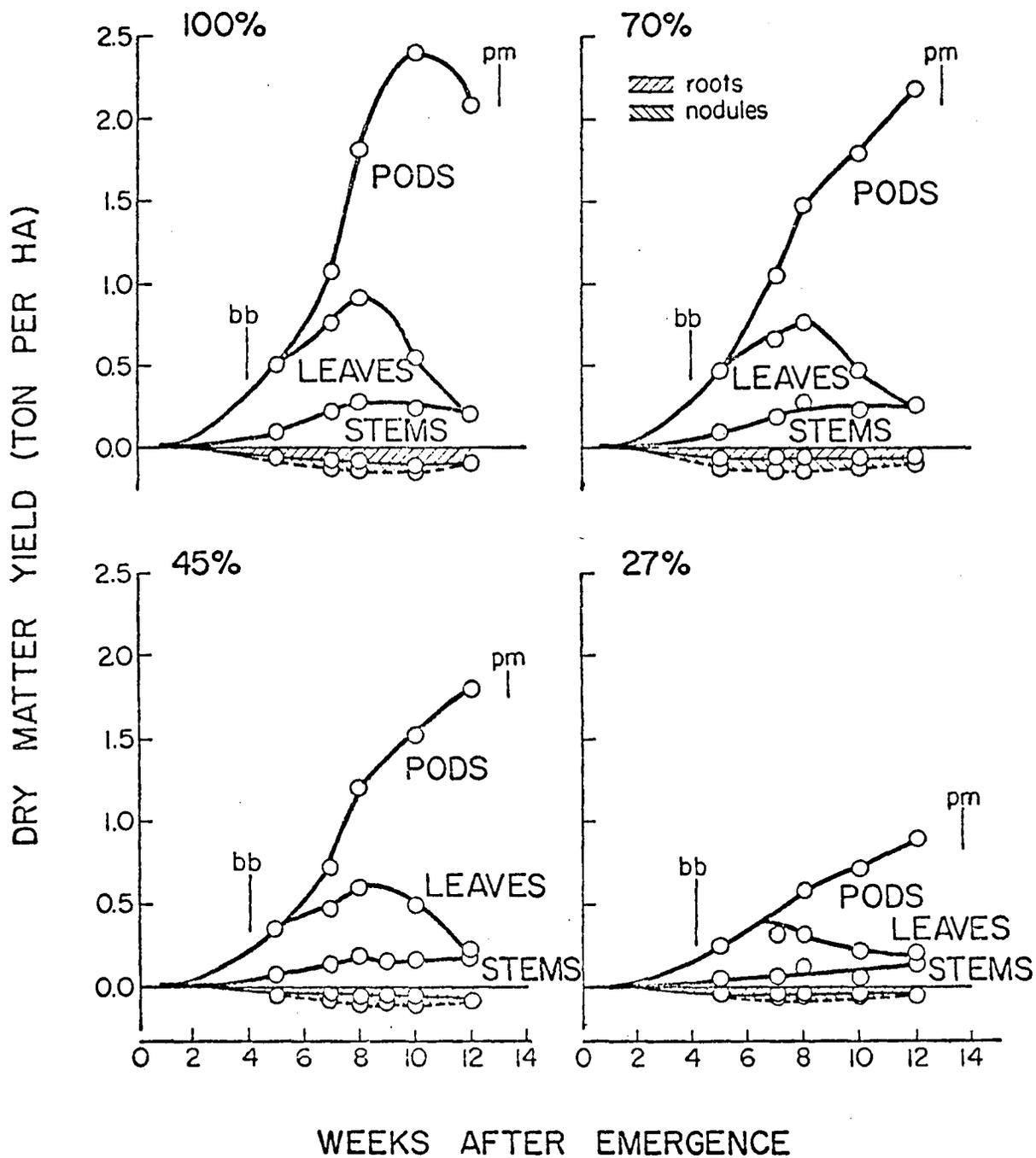


Figure 32. The effect of shading on dry matter accumulation of Kahala soybean grown during the cool season. (bb=beginning bloom; pm=physiological maturity).

accumulation was significantly restricted by more severe shading, especially during the period 5-12 weeks after emergence. Nitrogen levels of the total plant (tops, roots and nodules) were quite constant (3.0 - 3.8%) during the growth period and accumulative N yields were therefore primarily a function of DM yields (Table 16). The total N yield for the different treatments ranged from 144-350 kg N/ha for the summer crop and 28-103 kg N/ha for the cool-season crop.

The top/root ratio changed significantly with stage of maturity, but there were no differences among light intensities (Table 17). The lowest top/root ratio of 4.6 was recorded at 4 and 5 weeks after emergence, after which the ratio increased linearly to 22 at maturity. The rate of increase in top/root ratio with age corresponds well with earlier findings by Mayaki *et al.* (1976) and Sivakumar *et al.* (1971). McKee (1962) and Sprent (1973) reported that shading increased the top/root ratio of lupin and birds-foot trefoil, but this effect apparently does not occur in soybean.

Grain yield. The maximum seed yields of 5.2 ton/ha for the summer harvest and 1.38 ton/ha for the cool-season harvest were obtained in full daylight (Table 18). The relative yields for 100, 70, 45 and 27% daylight were: 100, 81, 79 and 52 for the summer harvest and 100, 99, 74 and 38 for the cool-season harvest. Number of seeds per pod was not influenced by shading at either season. The average 1000 seed weight was 243 gm for the summer crop. During the cool season, 1000 seed weight for the 100, 70 and 45% daylight treatments was 207, while the seed weight at 27% daylight was significantly lower (179 gm per 1000 seed). The determining factor for maximum

Table 16. The effect of shading on nitrogen percentage and nitrogen yield of total plant of Kahala soybean grown during two seasons.

Light intensity	Characteristics at indicated weeks after emergence								
	3	4	5	6	7	8	10	12	13
----- Percentage N in plants -----									
Summer planting									
100	3.21	3.10	3.08	3.04	3.30	3.42	3.18	3.27	3.75
70	3.23	3.12	3.09	3.14	3.25	3.53	3.49	3.30	3.17
45	3.01	3.05	3.00	3.24	3.37	3.25	2.95	3.68	3.33
27	3.11	3.04	3.00	3.12	3.16	3.20	3.14	3.29	3.37
Cool-season planting									
100	-	-	3.75	-	3.88	3.54	3.36	3.61	
70	-	-	3.75	-	4.13	3.30	3.28	3.83	
45	-	-	3.52	-	3.93	3.66	3.22	3.16	
27	-	-	3.26	-	3.74	3.47	3.21	3.47	
----- Total N yield in kg/ha -----									
Summer planting									
100	13	30	54	66	165	192	235	280	349
70	13	23	43	69	136	180	251	286	350
45	10	22	31	56	114	163	169	199	279
27	7	14	28	34	50	77	118	113	139
Cool-season planting									
100	-	-	23	-	49	72	85	103	
70	-	-	23	-	49	54	63	94	
45	-	-	15	-	32	49	47	61	
27	-	-	9	-	14	21	18	28	

Table 17. The effect of shading of soybean on the top/root ratio.

Light intensity	Top/Root ratio at indicated weeks after emergence											
	3	4	5	6	7	8	9	10	11	12	13	14
a) Summer crop												
100	5.3	4.6	5.6	5.9	7.1	9.0	10.0	13	13	10	22	
70	6.3	4.6	4.6	5.4	7.0	7.1	9.0	14	14	13	22	20
45	5.6	5.6	5.3	6.3	7.7	9.0	8.3	13	20	20	20	22
27	6.7	6.3	4.8	7.0	7.7	8.3	8.5	13	14	14	17	20
b) Cool-season crop												
100	-	-	5.6	-	8.3	8.1	-	14	-	20		
70	-	-	5.0	-	7.7	9.0	-	16	-	20		
45	-	-	6.7	-	7.7	11.1	-	14	-	17		
27	-	-	6.8	-	9.0	12.5	-	15	-	15		

Table 18. The effect of shading on the performance of Kahala soybean. Plant density of 365,000 per ha. Average of three replications.

Light intensity	Days to maturity	Pods per plant	Seeds per pod	1000 seed weight	Seed yield		%N	Total N kg/ha	
					per plant	per ha.			
					gm.	gm.	tons		
<u>April '76-July '76</u>									
100	99 b*	30 a	2.0 a	239	14.2 a	5.2 a	6.27 ab	325 a	
70	112 a	24 a	1.9 ab	253	11.5 b	4.2 b	6.44 ab	271 ab	
45	107 a	25 a	1.8 b	245	11.2 b	4.1 b	6.46 a	263 b	
27	114 a	16 b	1.9 ab	233	7.3 c	2.7 c	6.20 b	166 c	
LSD _{.05}	7	7	0.13	-	2.2	0.8	0.25	56	
<u>November '76-February '77</u>									
100	96 c	10.0 a	1.8 a	202 a	3.78 a	1.38 a	6.03 b	83 a	
70	97 bc	9.3 a	1.9 a	210 a	3.75 a	1.37 a	6.09 b	84 a	
45	98 bc	7.2 b	1.9 a	205 a	2.80 b	1.02 b	6.76 a	70 a	
27	102 a	4.6 c	1.7 b	179 b	1.41 c	0.52 c	6.67 a	34 b	
LSD _{.05}	2.5	0.8	0.13	18	0.50	0.17	0.41	15	

*Means in the same column followed by the same letter are not significantly different at the 5% level (Bayes LSD).

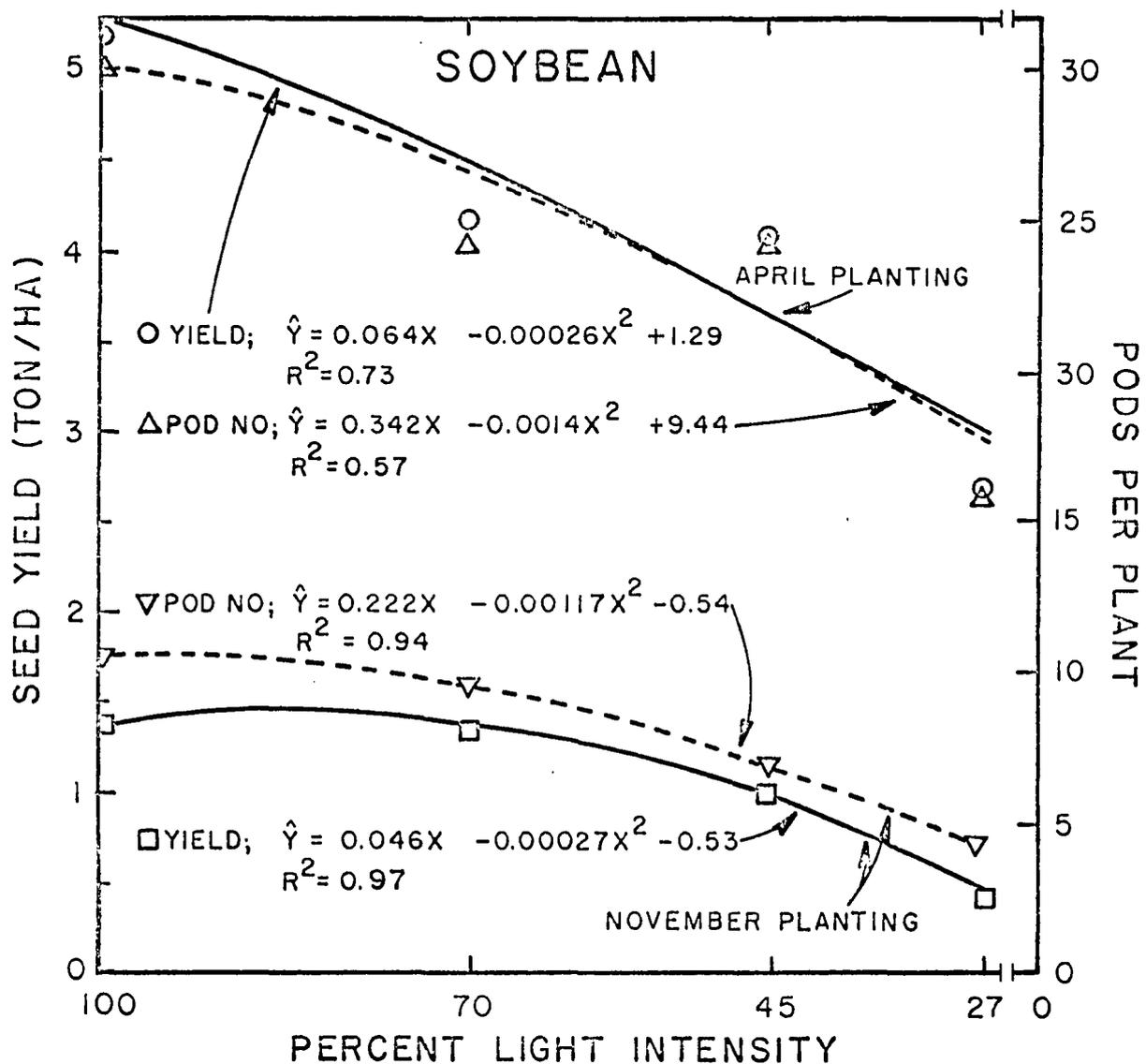


Figure 33. The effect of shading on the seed yield and number of pods per plant of Kahala soybean.

yield was the number of pods per plant (Figure 33). The N-percentage in the seeds was relatively constant, ranging from 6.03 - 6.76% for both seasons.

The N-yield of the grain was between 166-325 kg/ha during the summer season and only 34-84 kg/ha during the cool season. The very low yield during the cool season was related to the very short vegetative growth period of only 3-4 weeks, compared to 5 weeks during the summer season, and lower total solar radiation during the cool season.

COWPEA

Plant growth characteristics. The TVu 1190 selection of cowpea had a viny habit and did not flower when grown during the summer season (Figure 34). At 13 weeks after emergence average vine length was 3 m, with no difference among light intensities. However, significantly fewer vines were formed under 45 and 27% daylight. Also the vines and leaves were thinner with decreasing light intensity. Cowpea TVu 1190 was also grown during the cool season as a non-replicated treatment. At this season there was very little tendency toward formation of viny stems (Figure 35) and flowering and grain production took place.

The TVu 4557 selection of cowpea was grown during the cool season only. It had a bushy habit in full daylight; but at 70 and 45% daylight, about one third of the plants were viny. Under 27% daylight the plants were very retarded with no tendency toward viny growth.

The pods on the cowpea TVu 1190 were very long (30 cm) and



Figure 34. Growth of cowpea TVu 1190 during the summer season at 45% daylight.

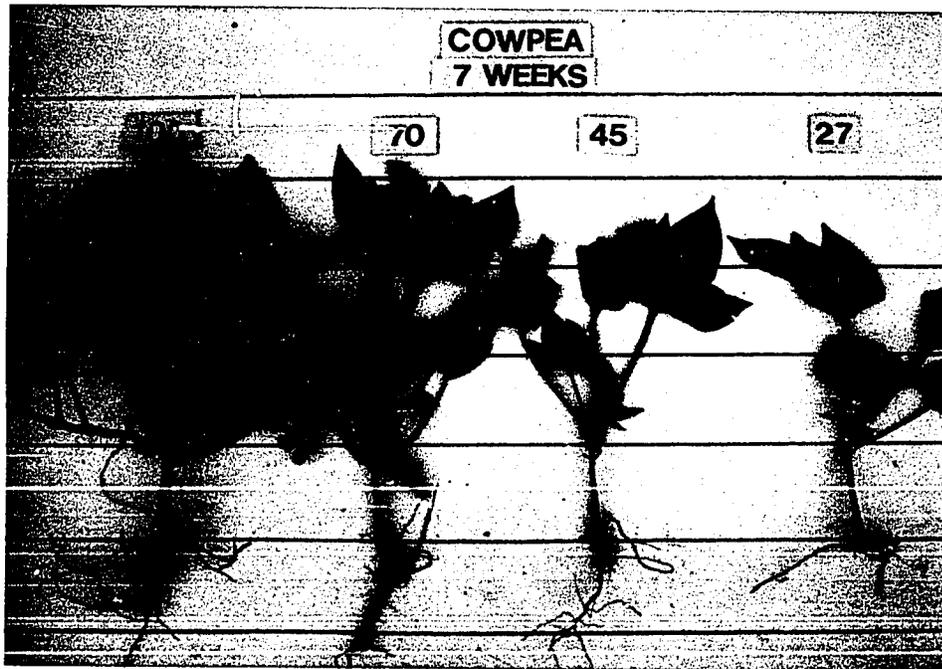


Figure 35. The effect of shading on growth of cowpea TVu 1190 during the cool season.

drooped to the ground level resulting in the loss of 40-80% of the grain due to rat damage. No rat damage was observed on the cowpea TVu 4557 which has shorter (15 cm) pods which were positioned above the plants (see photographs, Figure 36).

Nodulation and N-fixation. Cowpea TVu 1190 (summer crop) produced a maximum of 32 nodules per plant (with a total dry weight of 440 mg) under full daylight 9 weeks after emergence (Table 19, Figure 37). Plants grown under 27% daylight only produced 16 nodules per plant (143 mg dry weight) at the same age. During the cool season, cowpea TVu 4557 grown in full daylight produced a maximum of 16 nodules per plant (136 mg dry weight) 7 weeks after emergence (Table 20). Both nodule number and weight were reduced in both varieties with reduced light intensity and drastically so at 27% daylight. The relatively high nodule number and weight recorded for cowpea TVu 1190 at 13 weeks is probably related to the failure of this variety to flower during the summer season. Nodule size in both cowpea varieties at 27% daylight was about 30-40% of the size attained under full daylight during the main period of vegetative growth. Nodules produced under 70 and 45% daylight were intermediate in size (Tables 19 and 20). Under intense shade nodule size continued to increase until maturity. Reduction in nodule size due to shading of cowpea has also been reported by Dart and Mercer (1964).

Acetylene reduction varied significantly among treatments, with the lowest rates at 27% daylight for all sampling dates and for both varieties. The highest rates were obtained at 100% daylight for most sampling dates for cowpea TVu 1190 (summer season) (Figure 38) and

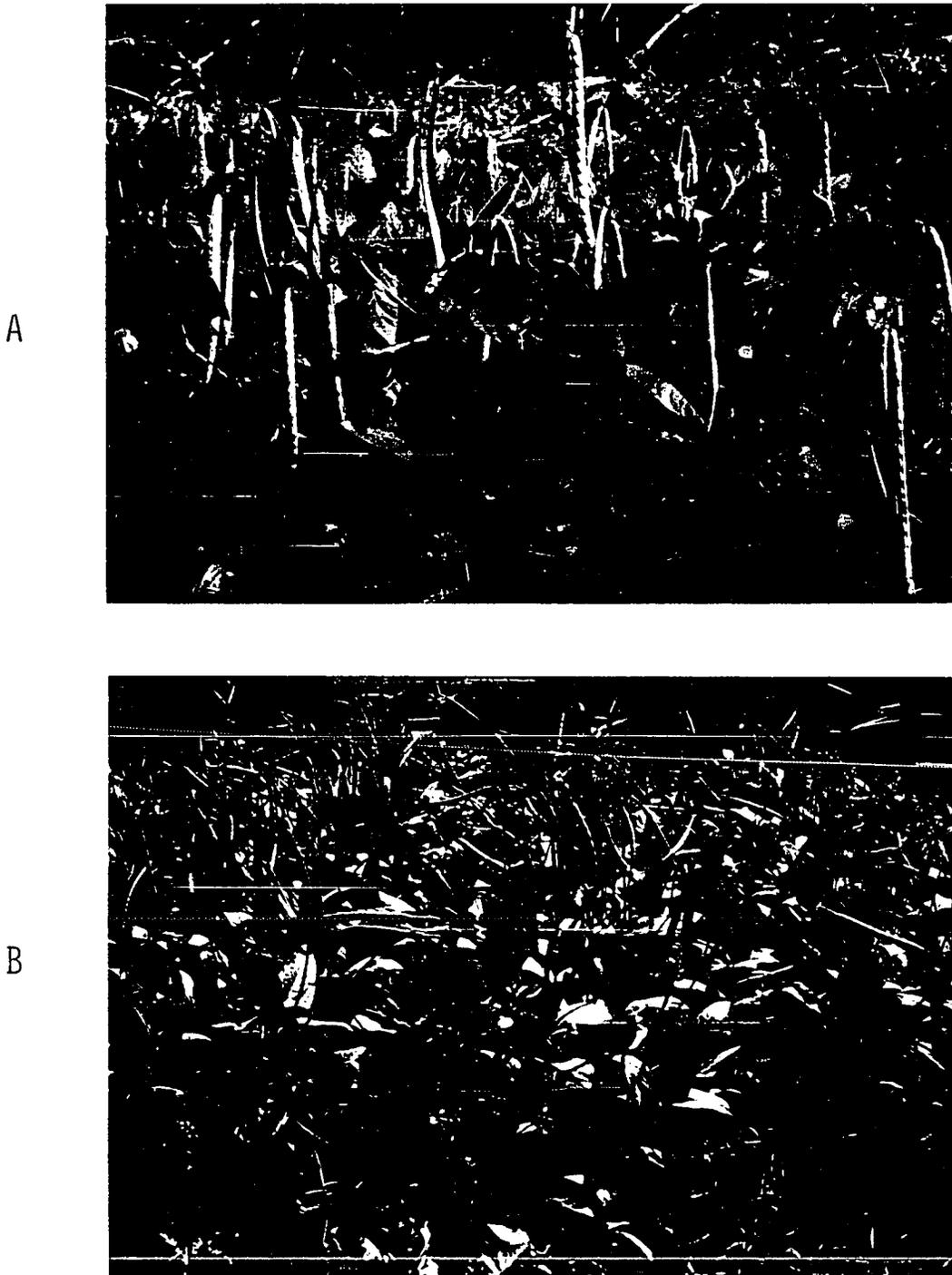


Figure 36. A) Cowpea TVu 1190 with pods hanging to the ground, which resulted in heavy loss from rat damage.
B) Cowpea TVu 4557 pods held high above the ground, no rat damage.

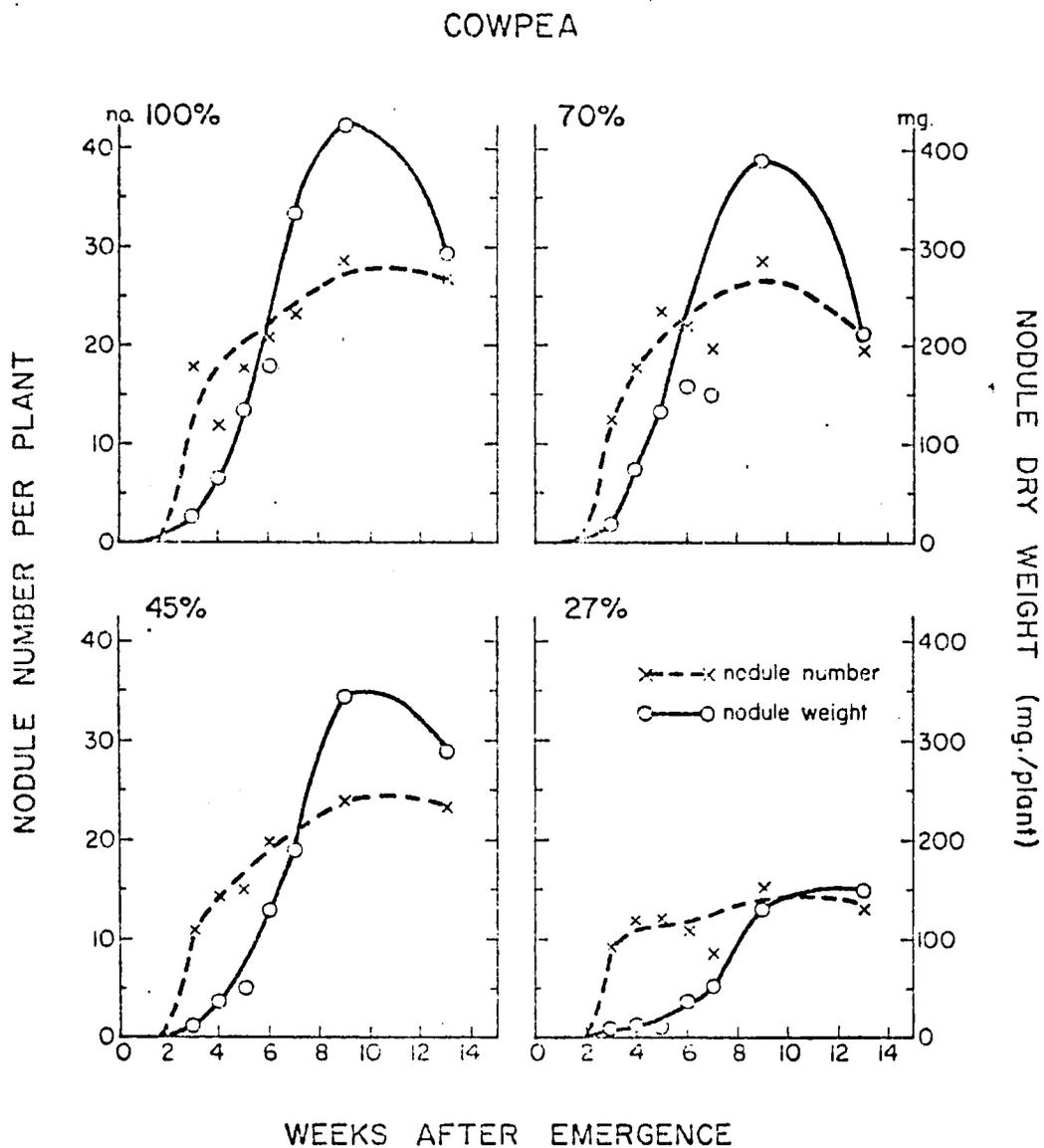


Figure 37. The effect of shading (100%=full daylight) on nodule number and nodule dry weight of cowpea TVu 1190 grown during the summer season (no flowering).

Table 19. The effect of shading on the number of nodules, nodule dry weight and acetylene reduction per plant, and specific nodule activity and nodule size of cowpea TVu 1190 grown during the summer.

Light intensity	Characteristics at indicated weeks after emergence						
	3	4	5	6	7	9	13
a) <i>Total nodule number per plant.</i>							
100	19 a [†]	20	18 ab	25 a	24 a	42 a	33
70	14 b	19	24 a	23 ab	21 a	30 ab	21
45	11 bc	14	15 b	20 ab	19 a	23 b	22
27	8 c	13	10 b	11 b	8 b	16 b	13
	*	ns	*	*	**	*	ns
b) <i>Total nodule dry weight per plant (mg).</i>							
100	31 a	75 a	146 a	303 a	346 a	541 a	302
70	22 ab	76 a	154 a	156 ab	165 b	428 b	229
45	8 b	45 ab	50 b	139 b	192 b	342 b	294
27	8 b	15 b	26 b	51 b	56 c	143 c	153
	*	*	**	*	**	**	ns
c) <i>Acetylene reduction per plant ($\mu\text{mol/h}$).</i>							
100	7.6 a	12.6 a	18 ab	39 a	33 a	30 a	27 a
70	3.9 ab	16.7 a	23 a	21 a	14 bc	25 ab	18 a
45	1.1 b	6.5 b	10 b	21 a	20 b	12 bc	23 a
27	1.1 b	1.9 c	2 c	8 b	6 c	8 c	8 b
	*	**	**	*	**	*	*
d) <i>Specific nodule activity ($\mu\text{mol/h/gm}$ dry nodule).</i>							
100	248	173	119	133	98	46	98
70	141	210	181	157	103	62	71
45	141	118	190	160	121	34	84
27	124	117	117	168	97	99	46
e) <i>Nodule size (mg/nodule).</i>							
100	1.6	3.8	8.1	12.1	14.4	12.9	9.2
70	1.6	4.0	6.4	6.0	7.9	14.3	10.9
45	0.7	3.2	3.3	7.0	10.0	14.9	13.4
27	1.0	1.2	2.6	4.6	7.0	8.9	11.8

[†] Means in the same column followed by the same letter are not significantly different at the 5% level (Bayes LSD).

* Significant at the 5% level.

** Significant at the 1% level.

ns No significant difference.

Table 20. The effect of shading on the number of nodules, nodule dry weight, and acetylene reduction per plant, and specific nodule activity and nodule size of cowpea TVu 4557 grown during the cool season.

Light intensity	Characteristics at indicated weeks after emergence			
	5	7	9	11
a) <i>Total nodule number per plant.</i>				
100	12	11 b [†]	9 ab	4
70	11	9 b	9 ab	4
45	11	16 a	13 a	7
27	8	4 b	4 b	8
	ns	ns	*	ns
b) <i>Total nodule dry weight per plant (mg).</i>				
100	62 a	104 a	114 a	16
70	37 b	60 a	33 b	14
45	40 ab	84 a	136 a	43
27	12 c	8 b	13 b	23
	*	*	**	ns
c) <i>Acetylene reduction per plant ($\mu\text{mol/h.}$).</i>				
100	15.2 a	15.4 a	5.4 ab	0
70	9.9 ab	6.0 b	1.0 b	0
45	8.0 bc	11.6 a	12.4 a	0
27	2.3 c	0.8 c	0.2 b	0
	*	**	*	ns
d) <i>Specific nodule activity ($\mu\text{mol/h/gm dry nodule}$).</i>				
100	216	160	48	
70	259	101	21	
45	249	162	78	
27	176	83	11	
e) <i>Nodule size (mg.DW./nodule).</i>				
100	5.2	9.5	12.7	4.0
70	3.4	6.7	3.7	3.5
45	3.6	5.3	10.5	6.1
27	1.5	2.0	3.3	2.7

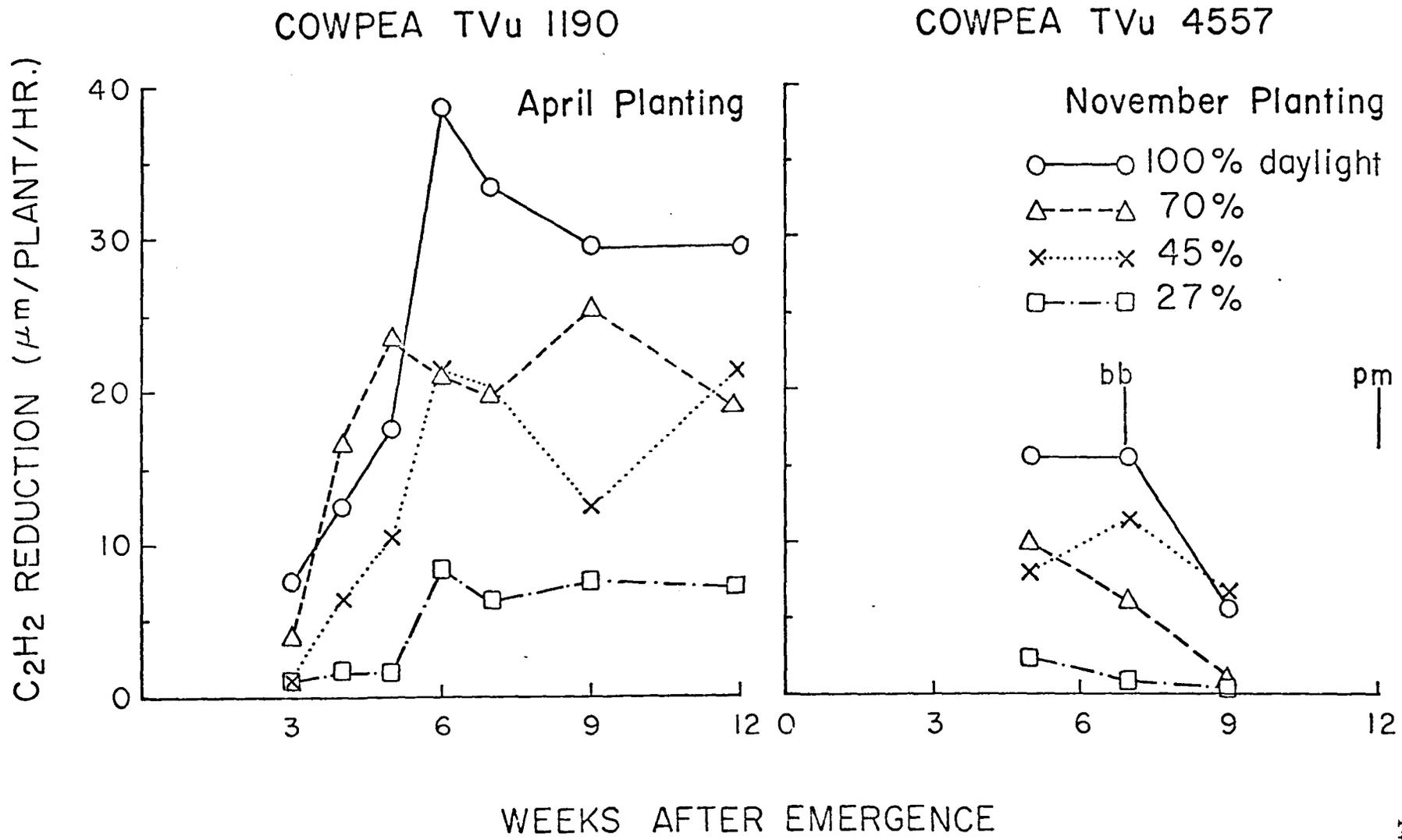
[†] Means in the same column followed by the same letter are not significantly different at the 5% level (Bayes LSD).

* Significant at the 5% level.

** Significant at the 1% level.

ns No significant difference.

Figure 38. The effect of shading on the acetylene-reduction activity of cowpea TVu 1190 grown during the summer (no flowering) and cowpea TVu 4557 grown during the cool season (flowering). (bb=beginning bloom; pm=physiological maturity).



70% being highest for cowpea TVu 4557 (cool season) (Figure 38, Tables 19 and 20). Acetylene reduction increased with time for cowpea TVu 1190 during the first 6 weeks after emergence. Acetylene reduction subsequently remained constant at about 30 μmol per plant per hour for the 100% daylight, 20 for 70 and 45% daylight, and 8 μmol per plant per hour for 27% daylight. Specific nodule activity was higher in cowpea than in bushbean or soybean. Maximum specific activity in full daylight was 248 $\mu\text{mol/g}$ nodule dry weight per hour 3 weeks after emergence, whereas under 27% daylight maximum activity (168 $\mu\text{mol/g}$ nodule dry weight per hour) was reached at 6 weeks; 3 weeks later (Table 19). The average specific nodule activity during the period 3-7 weeks after emergence was 150 $\mu\text{mol/g}$ nodule dry weight per hour after which it decreased to about 80 $\mu\text{mol/g}$ nodule dry weight per hour at 13 weeks after emergence.

Acetylene reduction in cowpea TVu 4557 which was grown during the cool season was highest at 5 and 7 weeks (≈ 15 $\mu\text{mol/plant}$ per hour under full daylight). Although the nodule weight continued to increase after 5 weeks, the acetylene reduction decreased, due to reduced specific nodule activity. The specific activities (in $\mu\text{mol/g}$ nodule dry weight per hour) were about 240 at 5 weeks, 140 at 7 weeks, 40 at 9 weeks, and zero at 11 weeks. Plants grown under 27% daylight had substantially lower activity at all sampling dates.

During the cool season cowpea TVu 4557 flowered and produced grain within 100 days, whereas cowpea TVu 1190 failed to flower over a 110 day experimental period during the summer. Thus the longer period of nodule activity in cowpea TVu 1190 was probably due to lack of competition for photosynthetic assimilates by the developing seeds.

Blomquist and Kust (1972) concluded that after pod filling commences, translocation from a given leaf occurs primarily to the pods in the axil of that leaf and at the second node below that leaf, while very small amounts are translocated to the roots and nodules (Hume and Criswell, 1972). Prior to pod filling most of the assimilates reaching the roots appear to come from lower leaves on the plant (Thainer *et al.*, 1959). Lawn and Brun (1974) reported that treatments designed to reduce the source-sink ratio (i.e. by shading and defoliation) of soybean, decreased nodule activity, while nodule activity was increased above the control when the source/sink ratio was increased by supplemental light or by depodding. This was interpreted as evidence that the decline in symbiotic nitrogen fixation during pod filling was primarily due to diversion of assimilate to the pods.

Rates of acetylene reduction and nodule activity for cowpea in full daylight are similar to those reported for other grain legumes species (Dart and Day, 1971; Lawrie and Wheeler, 1973; Sprent, 1973, 1977). However, the adverse effects of shading on nodule number, nodule mass and acetylene reduction in cowpea is much greater than that reported for soybean and bushbean.

The decrease in nodule mass with shading has been reported to be associated with decreased root dry weights (Sprent, 1973; Yoshida, 1973; Kry, 1976). A similar relationship was found in this investigation. Root weights of cowpea TVu 1190 (summer crop) were highly correlated with nodule weights; with each gram of roots supporting 224 mg of nodule tissue at the 100, 70 and 45% daylight treatments during the period 3-9 weeks after emergence ($r=0.94$) (Figure 39).

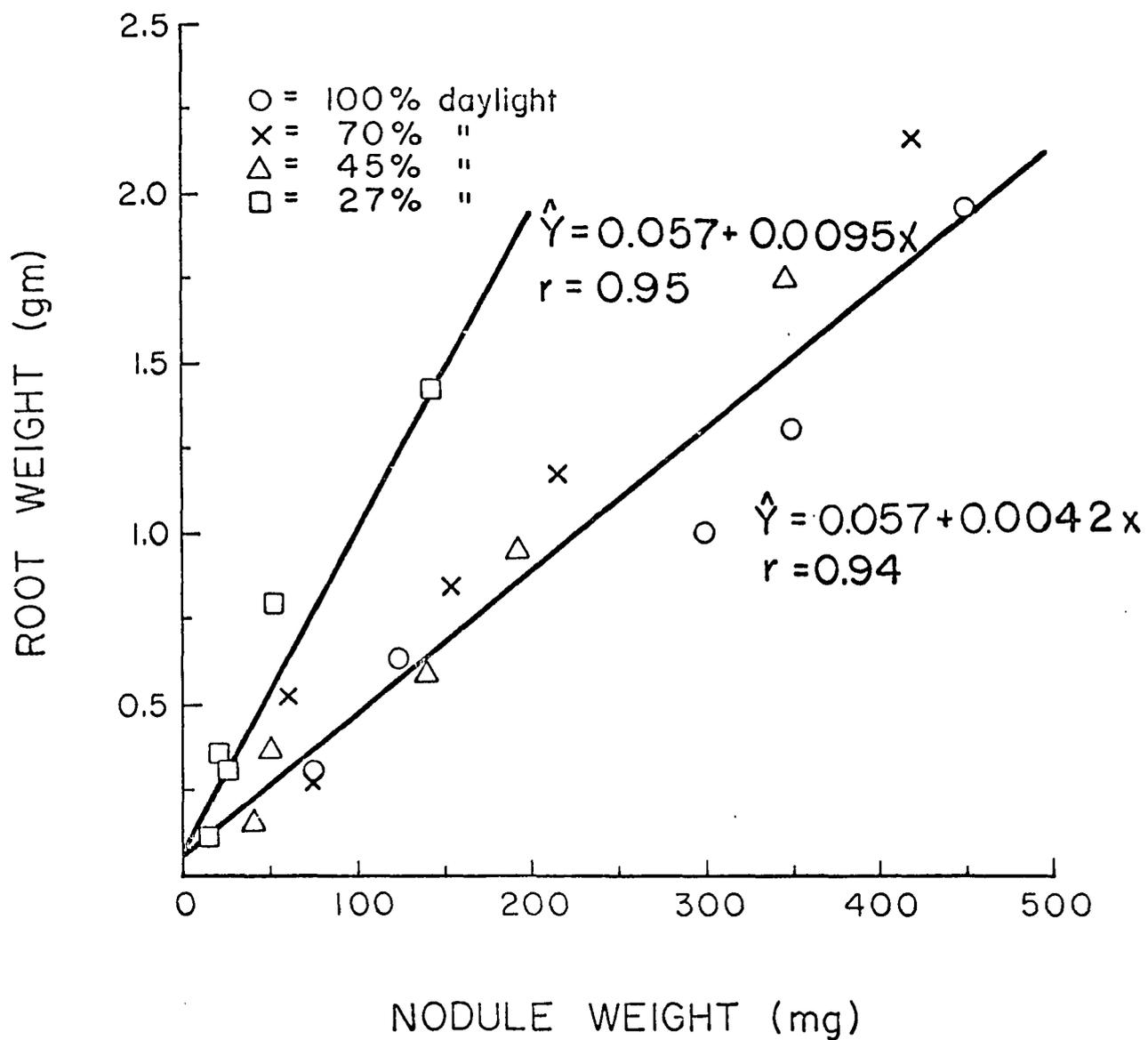


Figure 39. Relationship between root and nodule dry weights of cowpea TVu 1190 during the period 3-9 weeks after emergence grown during the summer season.

During this same period each gram of root tissue in the 27% daylight treatment supported 100 mg of nodule tissue ($r=0.95$). In cowpea TVu 4557 (cool-season crop) each gram of root tissue supported 210 mg of nodule tissue; ($r=0.78$), during the period 5-7 weeks after emergence.

Dry matter and N accumulation. Total DM accumulation (leaves, stems, roots and nodules) of cowpea TVu 1190 after 13 weeks of growth during the summer was 15.9 ton/ha in full daylight, 14.8 ton/ha at 70% daylight, 9.8 ton/ha at 45% daylight and 4.1 ton/ha at 27% daylight. Total DM yield was not significantly reduced by the 70% daylight treatment, but more severe shade was detrimental to plant growth.

Total DM accumulation of cowpea TVu 4557 (cool season) after 11 weeks of growth (2 weeks before maturity) ranged from 1.9 ton/ha of tops and roots at full daylight to only 0.5 ton/ha at 27% daylight (Figure 40). Thus both varieties proved quite sensitive to shading. This is consistent with earlier reports that the vegetative growth of cowpea was reduced by shading (Adedipe and Ormrod, 1975; Tarila *et al.*, 1977).

The total growth period for soybean, bushbean and cowpea during the cool season were about the same, but the proportion of the different plant parts at a given age differed markedly. Cowpea TVu 4557 first started flowering 7-8 weeks after emergence, at which time 25-50% of the total pod DM of soybean and bushbean had already been formed. At maturity (13-14 weeks after emergence) about half of the total DM in cowpea TVu 4557 was found in the seeds and pods, compared to 85 - 90% for bushbean and soybean, indicating that cowpea was less efficient in translocating photosynthate from the leaves to the grain. However,

COWPEA TVu 4557

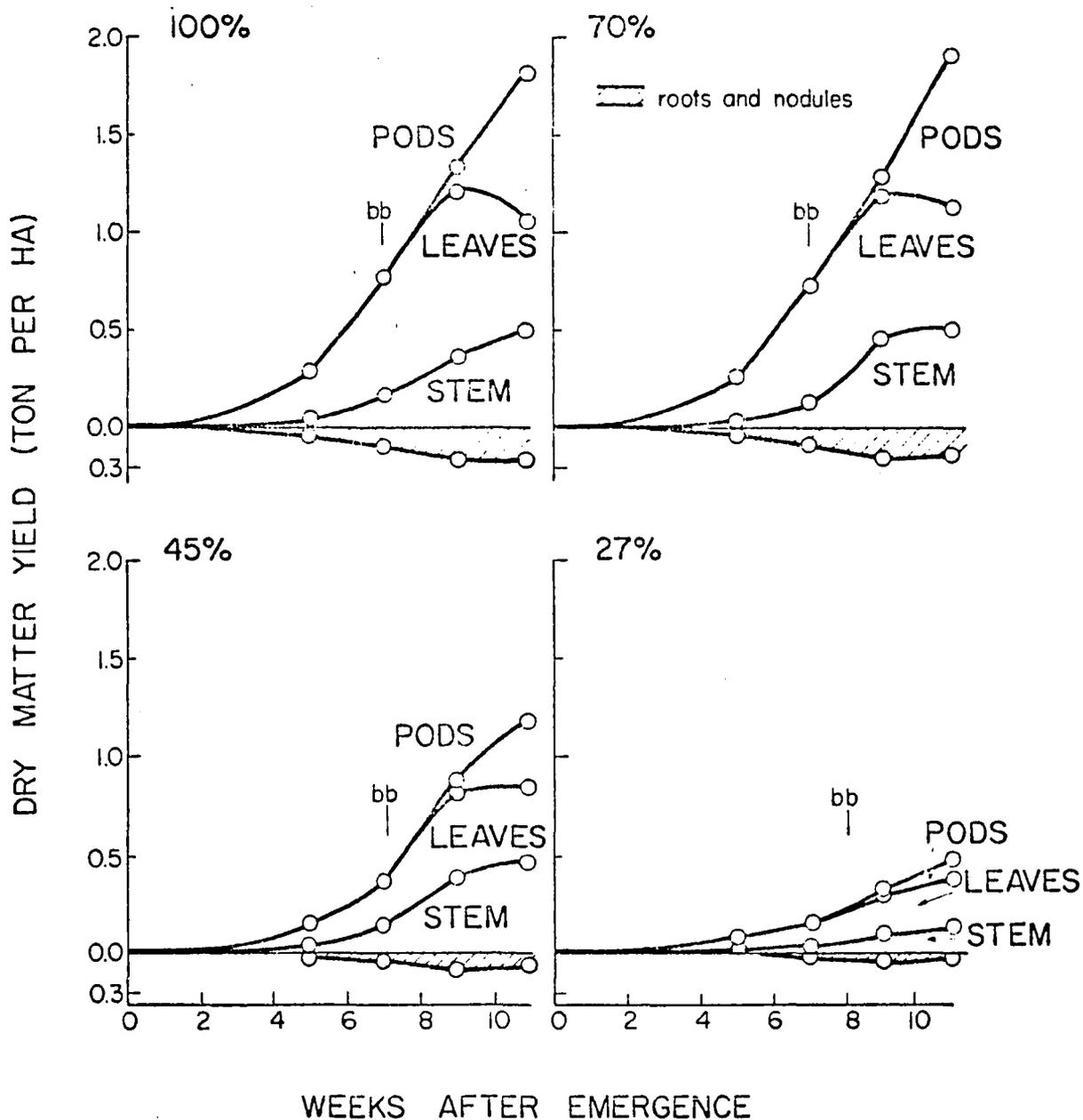


Figure 40. The effect of shading on the dry matter accumulation of cowpea TVu 4557 grown during the cool season. (bb=beginning bloom; pm=physiological maturity)

in spite of this grain yields were equal to or higher than the other species and more N remained in the residues.

When cowpea TVu 1190 was grown during the cool season (as a non-replicated treatment), the plants flowered and produced grain. Adjusted total DM yields of cowpea TVu 1190 were 30% higher than cowpea TVu 4557 in full daylight and were double cowpea TVu 4557 yields at 27% daylight.

The N-percentage for both cowpea varieties decreased with age, but was not greatly affected by light intensity treatments (Table 21). The total N yield for the non-flowering cowpea TVu 1190 for the 13 week period of summer growth varied between 109-361 kg/ha, depending on light intensity, while the N yield of cowpea TVu 4557 grown during the cool season peaked at 11-36 kg/ha 2 weeks before seed maturity (Table 21).

The top/root ratio of cowpea TVu 1190 remained at 8-10 for all light intensities during the first 7 weeks after emergence, after which it increased to 16 at 13 weeks after emergence (Table 22). The top/root ratio of TVu 4557 (cool-season crop) increased only slightly with age, and was not affected by shading. That shading has no effect on top/root ratio of cowpea was earlier reported by Dart and Mercer (1964). However, it appears that other factors such as variety and season do have strong effects on top/root ratio of this crop.

Grain yield. Grain was only harvested during the cool season since cowpea TVu 1190 grown during the summer did not flower. The grain yield of cowpea TVu 4557 decreased drastically with decreasing light intensity (Table 23). The relative grain yields at 100, 70, 45 and 27%

Table 21. The effect of shading on nitrogen percentage and nitrogen yield of total plant of cowpea TVu 1190 (summer season) and cowpea TVu 4557 (cool season).

Light intensity	Characteristics at indicated weeks after emergence						
	3	4	5	6	7	9	13
----- Percentage N in plants -----							
Summer planting (cowpea TVu 1190).							
100	3.45	3.46	2.95	3.16	3.23	2.95	2.36
70	3.14	3.05	2.86	3.26	2.80	2.66	2.65
45	3.47	3.30	2.75	2.50	3.14	2.64	2.70
27	3.00	3.67	3.47	2.83	2.55	2.86	2.65
Cool season planting (cowpea TVu 4557).							
100	-	-	3.49	2.96	2.83	1.96	-
70	-	-	3.29	2.93	2.37	1.80	-
45	-	-	3.31	3.08	2.42	1.93	-
27	-	-	3.19	2.98	2.40	2.31	-
----- Total N yield in kg/ha -----							
Summer planting (cowpea TVu 1190).							
100	7	27	35	72	110	297	352
70	6	18	34	55	85	232	361
45	4	16	23	36	62	176	273
27	3	8	21	19	49	99	109
Cool season planting (cowpea TVu 4557).							
100	-	-	12	26	42	36	-
70	-	-	10	24	35	35	-
45	-	-	5	13	23	23	-
27	-	-	3	5	9	11	-

Table 22. The effect of shading on the top/root ratio of cowpea

Light intensity	Top/root ratio at indicated weeks after emergence							
	3	4	5	6	7	9	11	13
a) Summer crop (cowpea TVu 1190).								
100	8	9	7	8	10	16	-	16
70	8	8	9	9	9	14	-	16
45	8	8	8	9	8	14	-	16
27	8	8	9	9	10	11	-	13
b) Cool-season crop (Cowpea TVu 4557).								
100	-	-	7	8	9	-	10	-
70	-	-	8	9	8	-	13	-
45	-	-	7	8	9	-	9	-
27	-	-	7	9	9	-	14	-

Table 23. The effect of shading on the performance of cowpea TVu 4557 during the cool season. Plant density of 130,400 per ha. Average of three replications.

Light intensity	Days to maturity	Pods per plant	Seeds per pod	1000 seed weight	Seed yield		%N	Total N kg/ha
					per plant	per ha.		
				gm	gm	tons		
December '76-February '77								
100	99 c*	8.9 a	7.6 a	138	9.3 a	1.22 a	3.50 a	43 a
70	100 c	6.7 b	8.0 a	139	7.4 b	0.97 b	3.59 a	35 b
45	102 b	3.4 c	7.4 a	133	4.1 c	0.53 c	3.65 a	20 c
27	105 a	1.0 d	6.2 b	134	0.9 d	0.11 d	3.66 a	4 d

* Means in the same column followed by the same letter are not significant different at 5% level (Bayes LSD).

daylight were 100, 80, 43 and 9. A reduction in grain yields of cowpea under low light intensity has also been reported by Ezedinma (1973) and Tarila and Ormrod (1977). The grain yield and number of pods per plant decreased significantly at each shade level (Figure 41). The number of seeds per pod was significantly reduced at 27% daylight, but 1000 seed weight was not affected by shading. Total N-yield of cowpea TVu 4557 ranged from 4-43 kg/ha depending on light intensity with N yield closely related to grain yield (and hence light intensity) since the N percentage did not vary significantly between treatments (2.62-2.98).

BUSHBEAN

Plant growth characteristics. Plant growth under different levels of shading showed typical morphological adaptations. These included longer internodes and petioles and wider but thinner leaves. Shading of bushbean also caused elongated petiole growth with the result that the lower leaf laminae were elevated nearer the top of the canopy so that the leaves were subjected to less self-shading. In addition, the leaf area ratio (LAR) of 4-week old bushbean plants increased with decreasing radiation (1.8 dm²/g plant DM at 100% daylight vs. 2.3 dm²/g at 70% daylight). Leaf area index (LAI) was also higher under 70% than under 100% daylight, providing a greater available photosynthetic area under light shade.

No significant difference in plant height was recorded between summer and cool season, or among shade levels, but plants grown in the shade were about 5 cm taller than plants grown in full daylight (Figure 42).

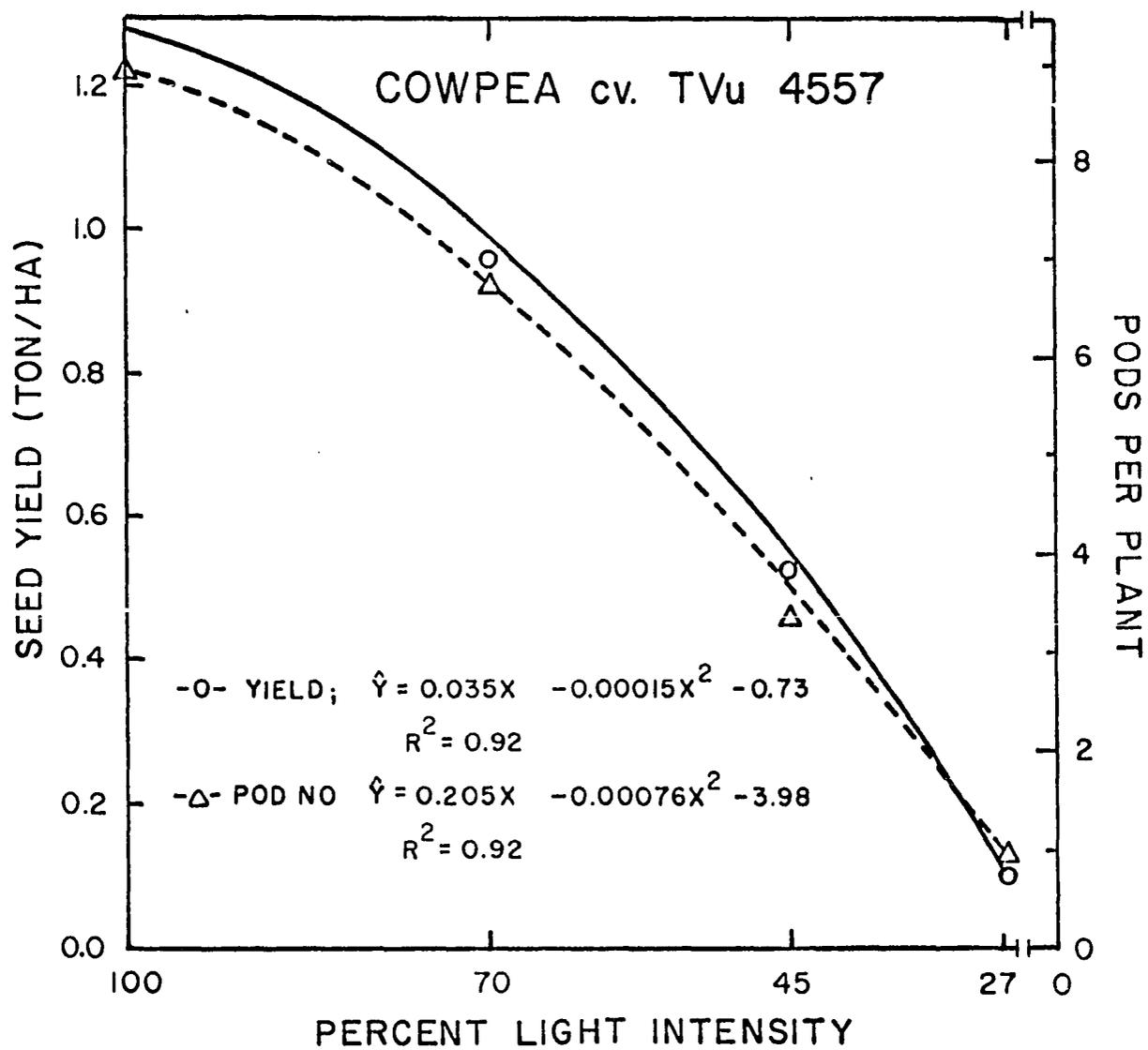


Figure 41. The effect of shading on the seed yield and number of pods per plant of cowpea TVu 4557 grown during the cool season.

BUSHBEAN

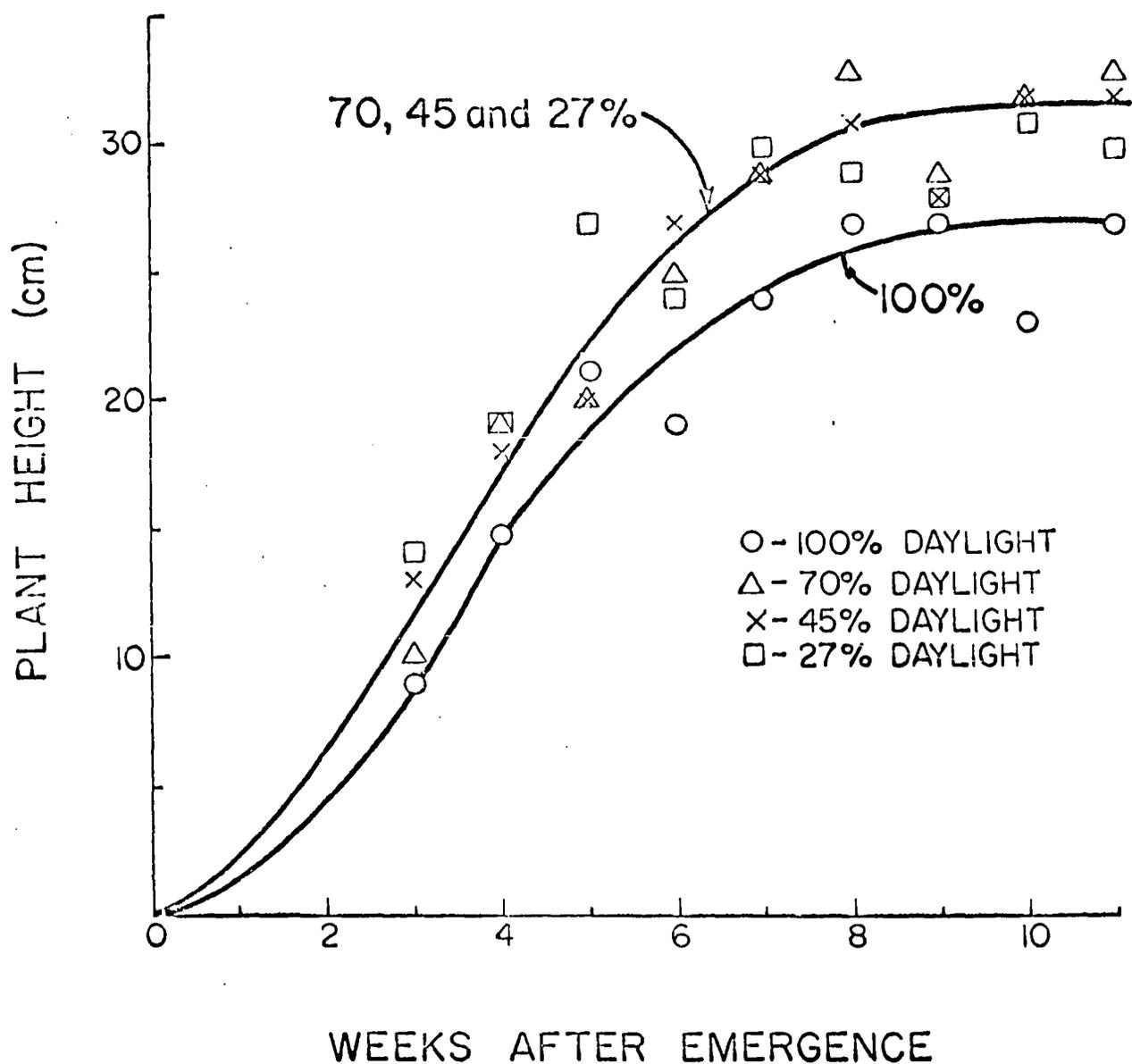


Figure 42. The effect of shading on plant height of bushbean grown during the summer season.

Nodulation and N-fixation. Nodule number was affected less by shading than nodule weight on bushbean (Figure 43), for both the summer and cool-season plantings (Tables 24 and 25).

The nodule number in bushbean reached a maximum at 3-4 weeks after emergence for all light intensities at both seasons, except that under the most intense shade during the cool season, nodule number per plant peaked 5 weeks after emergence. At both seasons nodule mass was highest at 5 weeks after emergence for 100% daylight, at 6 weeks for 70% daylight and 1-2 weeks later for 45 and 27% daylight. Shading effects were noted after the third week; both nodule number and nodule mass per plant were depressed as light intensity was reduced.

Nodule weight varied greatly between seasons and among sampling dates. The average maximum nodule weight for bushbean during the summer season was 1.8 mg/nodule and for the cool season 1.0 mg/nodule. Nodules formed under shaded conditions were generally smaller than in full daylight (Tables 24 and 25). The adverse effect of shading on nodule number, nodule mass, nodule size, or all three, have also been reported for other species by Butler *et al.* (1959), McKee (1962), Sprent (1973, 1977) and Chu and Robertson (1974).

Acetylene reduction during the summer peaked at early bloom (4 weeks after emergence) with a maximum of 8-10 $\mu\text{mol C}_2\text{H}_4$ produced/plant per hour for 45, 70 and 100% daylight and 3 $\mu\text{mol C}_2\text{H}_4$ produced/plant per hour for 27% daylight at early bloom (Figure 44). By 5 weeks after emergence the activity had dropped to only half that measured at 4 weeks; due mainly to reduced specific nodule activity (from approximately 120 to 60 $\mu\text{mol/g dry nodule per hour}$). DM yield at 4 weeks after emergence was only about 8% of the total DM yield.

BUSH BEAN

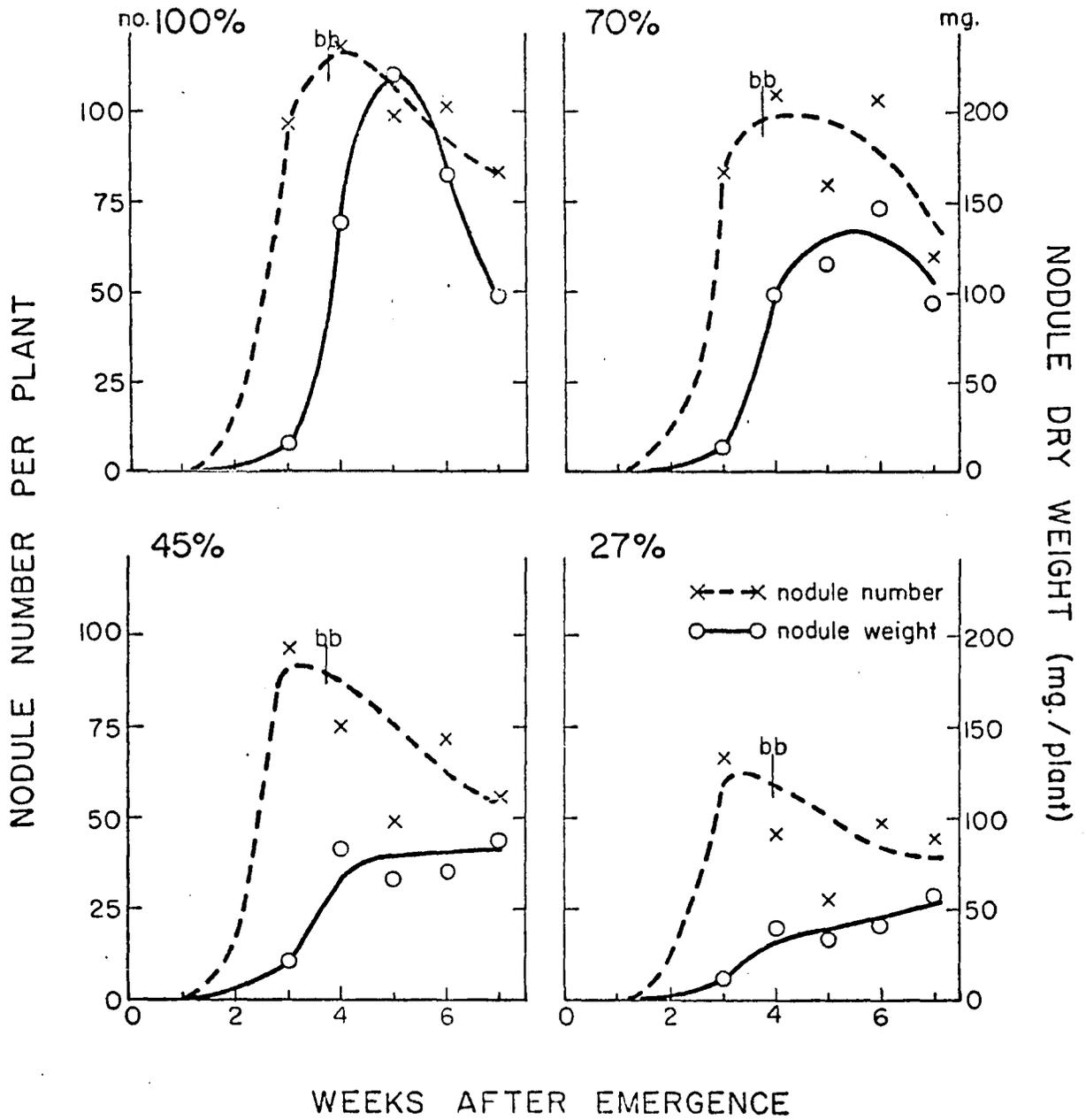


Figure 43. The effect of shading (100%= full daylight) on nodule number and nodule dry weight of bushbean grown during the summer season (bb=beginning bloom).

Table 24. The effect of shading on the number of nodules, nodule dry weight and acetylene reduction per plant, and specific nodule activity and nodule size of bushbean grown during the summer.

Light intensity	Characteristics at indicated weeks after emergence					
	3	4	5	6	7	8
a) <i>Total nodule number per plant.</i>						
100	96	121 a [†]	99 a	101	86	-
70	83	104 ab	79 ab	104	68	-
45	97	69 bc	64 ab	72	62	-
27	60	46 c	40 b	49	45	-
	ns	*	*	ns	ns	
b) <i>Total nodule dry weight per plant (mg).</i>						
100	17	143 a	175 a	164 a	97	-
70	14	98 ab	116 ab	146 a	93	-
45	23	83 ab	67 bc	72 ab	88	-
27	11	19 b	33 c	40 b	58	-
	ns	*	*	*	ns	-
c) <i>Acetylene-reduction per plant ($\mu\text{mol/h}$).</i>						
100	2.3	10.6 a	5.0	2.7	3.1	0.1
70	0.7	8.1 ab	4.8	3.4	3.3	0.4
45	2.0	7.7 ab	4.6	4.0	3.4	0.7
27	1.8	3.1 b	1.8	2.3	2.4	0.8
	ns	*	ns	ns	ns	ns
d) <i>Specific nodule activity ($\mu\text{mol/h/gm dry nodule}$).</i>						
100	177	92	29	19	46	-
70	34	123	50	26	33	-
45	228	98	74	72	38	-
27	191	212	42	93	43	-
e) <i>Nodule size (mg/nodule).</i>						
100	0.18	1.18	1.77	1.62	1.13	-
70	0.16	0.94	1.47	1.40	1.37	-
45	0.24	1.20	1.05	1.00	1.42	-
27	0.18	0.41	0.83	0.82	1.29	-

† Means in the same column followed by the same letter are not significantly different at the 5% level (Bayes LSD).

* Significant at the 5% level.

ns No significant difference

Table 25. The effect of shading on the number of nodules, nodule dry weight and acetylene reduction per plant, and specific nodule activity and nodule size of bushbean grown during the cool season.

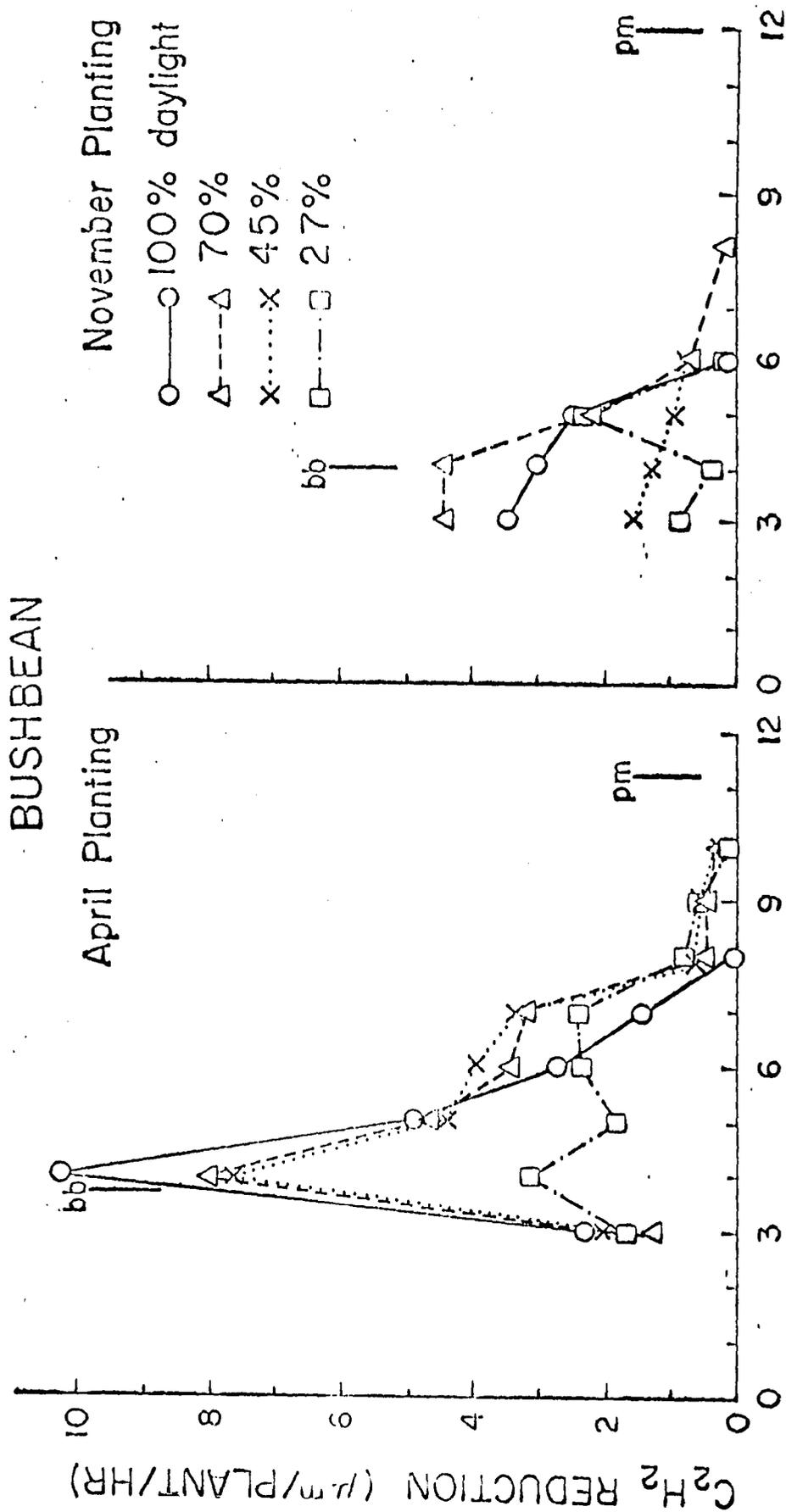
Light intensity	Characteristics at indicated weeks after emergence				
	3	4	5	6	8
a) <i>Total nodule number per plant.</i>					
100	-	101 a [†]	56	13 b	0
70	-	121 a	90	70 a	7
45	-	65 ab	54	32 b	5
27	-	29 b	62	16 b	4
		*	ns	*	ns
b) <i>Total nodule dry weight per plant (mg).</i>					
100	-	37	30	13 b	0
70	-	58	65	40 a	9
45	-	18	27	21 a	3
27	-	7	40	8 b	4
		ns	ns	*	ns
c) <i>Acetylene reduction per plant (μmol/h).</i>					
100	3.5	3.0	2.5	0.2	-
70	4.6	4.5	2.2	0.6	0.2
45	1.6	1.3	1.2	0.7	0.0
27	0.9	0.3	2.4	0.1	0.0
	ns	ns	ns	ns	ns
d) <i>Specific nodule activity (μmol/h/gm dry nodule).</i>					
100	-	77	72	13	-
70	-	70	30	12	-
45	-	41	30	32	-
27	-	13	85	12	-
		ns	ns	ns	
e) <i>Nodule size (mg/nodule).</i>					
100	-	0.37	0.54	1.00	-
70	-	0.48	0.72	0.56	0.78
45	-	0.28	0.50	0.66	0.60
27	-	0.24	0.65	0.50	0.50

† Means in the same column followed by the same letter are not significantly different at the 5% level. (Bayes LSD).

* Significant at the 5% level.

ns No significant difference.

Figure 44. The effect of shading on the acetylene-reduction activity of bushbean grown during two seasons (bb=beginning bloom; pm=physiological maturity).



WEEKS AFTER EMERGENCE

Thus this bushbean variety (Burpee Tenderpod) would have been almost entirely dependent on soil N for the major part of its growth and reproductive development. Shading had no statistical significant effect on acetylene reduction in bushbean at either season, except for the summer crop at 4 weeks, where 27% daylight resulted in significantly lower activity than full daylight. In this experiment the acetylene-reduction rates were highest in unshaded treatments during the first 5 weeks, after which acetylene reduction in the shaded treatments became higher than in full daylight. This was associated with delayed senescence of leaves under shade, a result similar to that noted for *Vicia faba* L. by Sprent and Bradford (1977). The results for bushbean are considerably lower than the maximum acetylene-reduction rates of 20-30 $\mu\text{mol}/\text{plant}$ per hour reported by Graham and Rosas (1977) for bushbean and climbing bean. The fixation period reported by Graham and Rosas was also much longer, reaching a peak at 9 weeks after emergence, compared to 4 weeks in the present experiment. The data reported here correspond more closely to the 6 $\mu\text{mol C}_2\text{H}_4$ produced/plant per hour for dark red kidney beans (Janssen and Vitosh, 1974) or the even lower acetylene-reduction values reported from glass-house experiments by Sprent, (1976).

The mentioned acetylene-reduction data are all measured at one light intensity only. To my knowledge nobody has measured the effect of shading on the acetylene reduction over the total growth period.

Although few experiments have been reported concerning shading effects on acetylene reduction, some comparisons can be made. Sprent (1976a) showed that acetylene reduction per plant of *P. vulgaris* did not differ when grown at light levels of 4500 and 7000 lux in

controlled environments. In this investigation there was a highly significant linear relationship between nodule weight and root weight for the summer crop at 100, 70 and 45% daylight ($r=0.95$) at time of maximum acetylene reduction (4 weeks after emergence), with each gram of root tissue supporting 385 mg of nodule tissue. At 27% daylight each gram of root tissue only supported 100 mg of nodule tissue (Figure 45).

Dry matter and N accumulation. Dry matter accumulation rates for roots, nodules, stems, leaves and pods by the summer crop of bushbean was similar for full daylight and moderate shade (≈ 4 ton/ha at 8 weeks), but was substantially reduced by severe shade (≈ 2.5 ton/ha) (Figure 46). After 8 weeks no further increase in DM yield took place in full daylight and symptoms of senescence appeared (Figure 47). Nitrogen deficiency symptoms appeared at 7 weeks in bushbean plants in full daylight and this coincided with a significantly lower level of N in these plants (2.5% vs. 2.8% for plants grown under 70% daylight and 3.0% under 45 and 27% daylight) (Table 26). Nitrogen percentage of the tops plus roots decreased with age from about 3.0% at 4 weeks to about 2.3% at maturity with the N percentage being lowest at full daylight and highest under heavy shade for most sampling dates. Total N yield increased linearly during the first 8 weeks to 74-113 kg N/ha, depending on light intensity, after which there was nil or very little increase in N accumulation (Table 26). The N content of fallen leaves were excluded in these calculations under the assumption that most of the N in the leaves was translocated before leaf fall.

DM and total N accumulation for the cool-season crop followed the

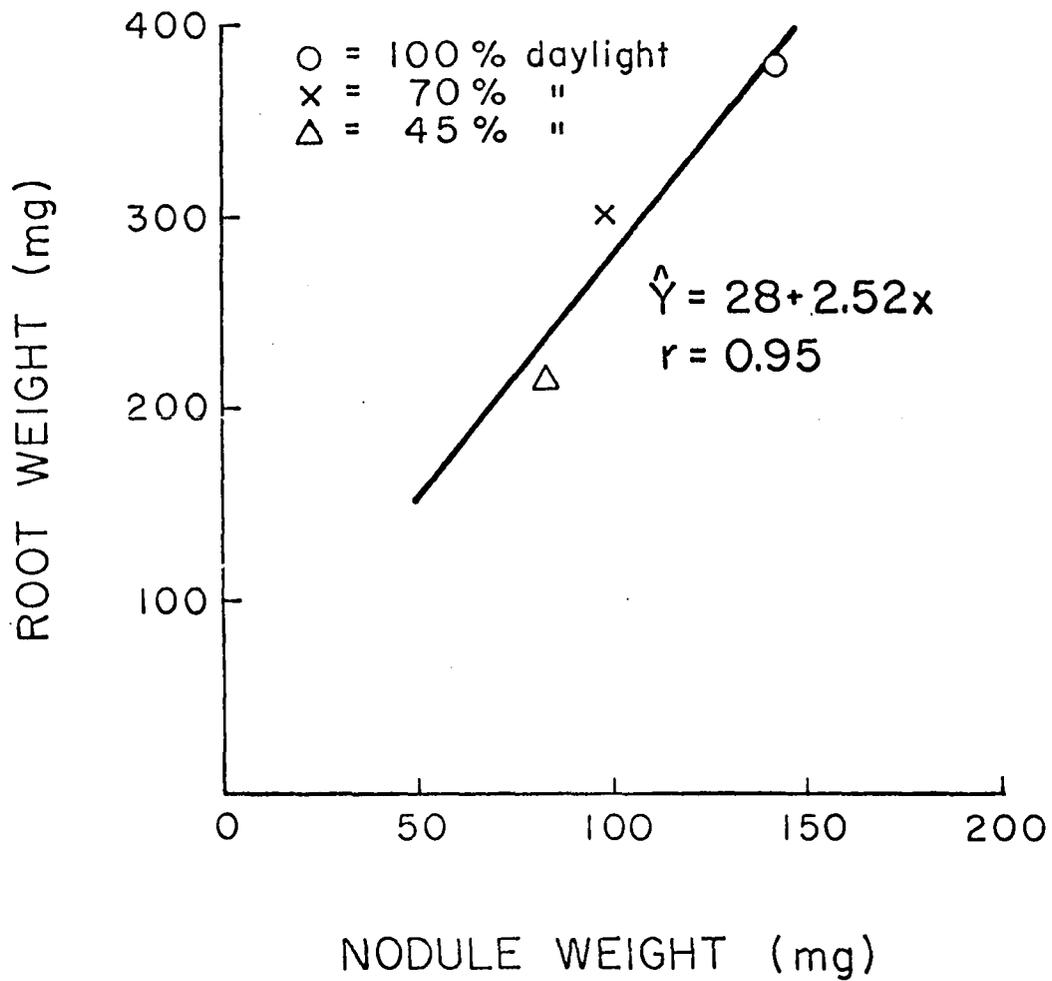


Figure 45. Relationship between root and nodule dry weights of bushbean four weeks after emergence during the summer season.

BUSHBEAN

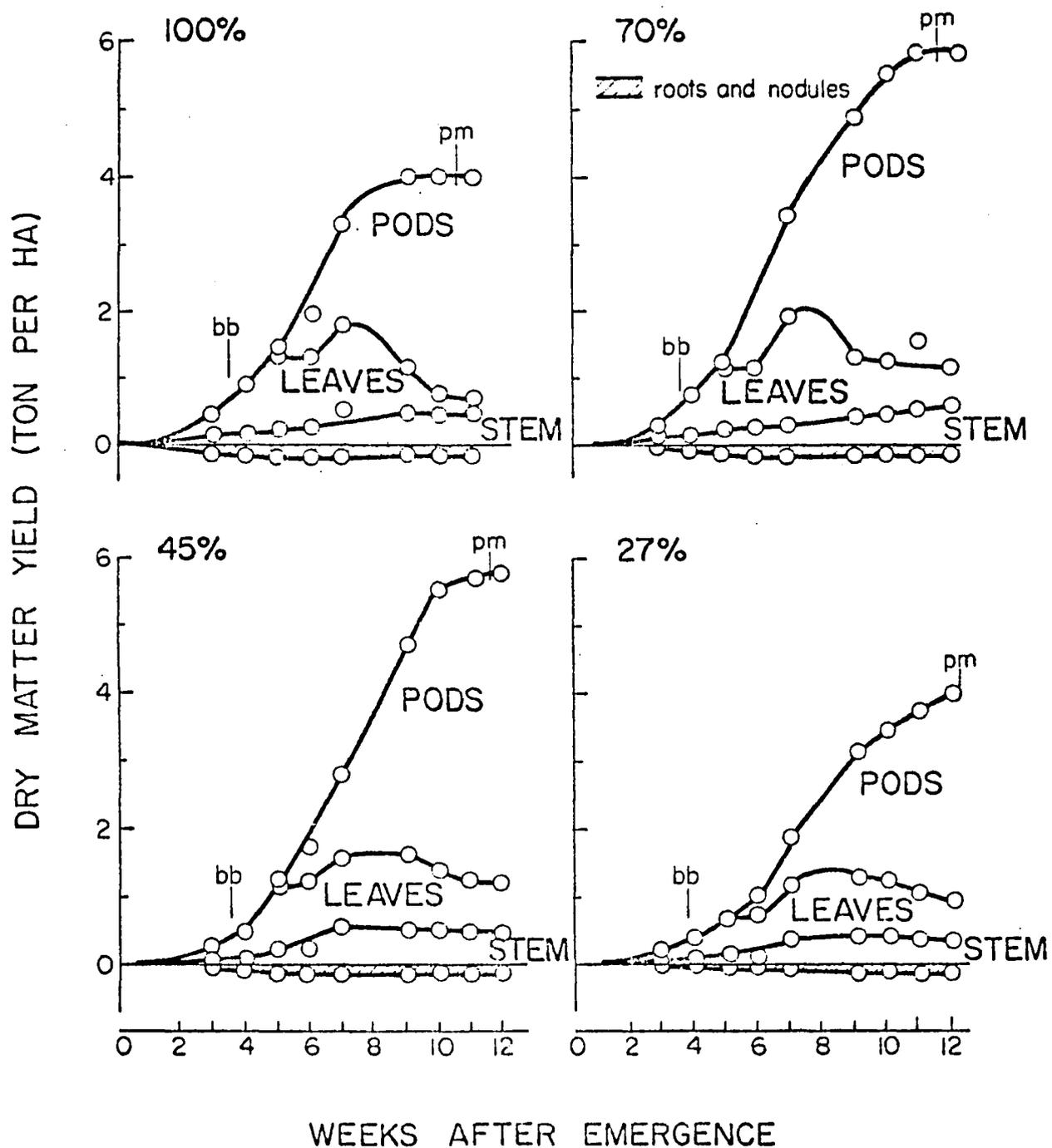


Figure 46. The effect of shading on the dry matter accumulation of bushbean grown during the summer season (bb=beginning bloom; pm=physiological maturity).

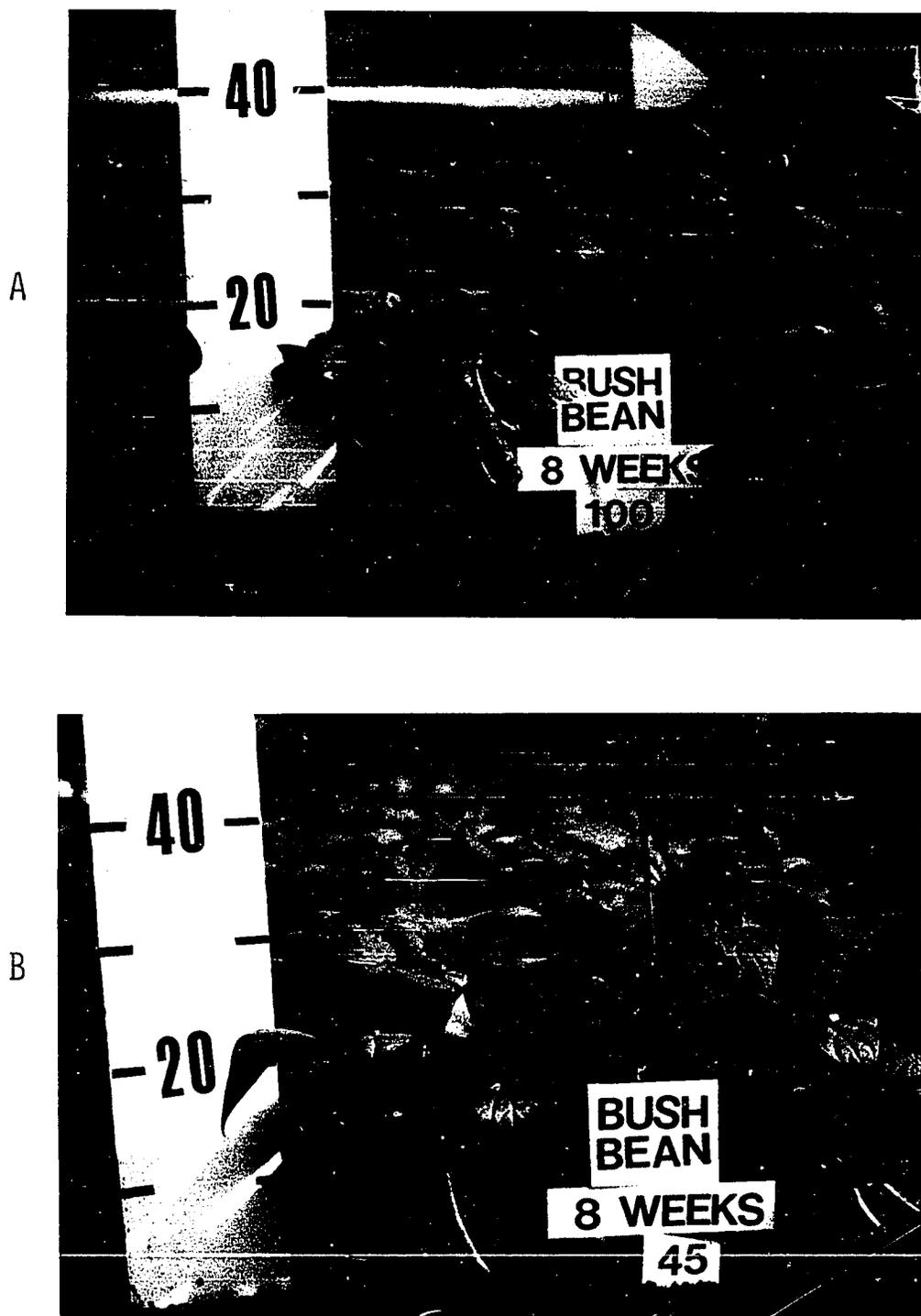


Figure 47. Growth of bushbean 8 weeks after seeding at A) 100% daylight and B) 45% daylight during the summer season.

Table 26. The effect of total plant shading on nitrogen percentage and nitrogen yield of bushbean grown during two seasons.

Light intensity	Characteristics at indicated weeks after emergence								
	3	4	5	6	7	8	9	10	11
----- Nitrogen percentage -----									
Summer planting.									
100	3.62	2.94	2.74	2.74	2.53	2.51	2.08	2.25	2.33
70	3.87	2.76	2.69	2.86	2.84	2.46	2.25	2.19	2.27
45	3.69	2.95	2.95	2.46	3.07	2.66	2.30	2.31	2.29
27	3.65	3.10	3.05	2.49	3.03	2.78	2.62	2.53	2.26
Cool season planting.									
100	3.26	3.26	3.02	2.60	-	2.31	-	-	-
70	3.63	3.27	3.20	2.77	-	2.41	-	-	-
45	3.38	3.38	3.60	3.00	-	2.75	-	-	-
27	3.30	3.56	3.60	3.47	-	2.83	-	-	-
----- Total N yield in kg/ha -----									
Summer planting.									
100	18	31	46	59	89	91	86	92	95
70	13	24	38	53	104	113	116	124	135
45	12	17	41	47	91	111	116	125	113
27	9	13	23	28	60	74	85	78	87
Cool season planting.									
100	11	19	36	46	-	56	-	-	-
70	12	21	48	52	-	56	-	-	-
45	10	15	34	45	-	51	-	-	-
27	7	10	23	33	-	34	-	-	-

same patterns as for the summer crop during the first 6 weeks after emergence. Subsequently, however, growth rates were depressed resulting in lower final yields (Figure 46, Table 26). The top/root ratio did not differ among light intensities, but increased with age at both seasons (Table 27), as was recorded for cowpea and soybean.

Grain yield. Maximum grain yield in bushbean of 3.3 ton/ha for the summer crop and 2.0 ton/ha for the cool-season crop was recorded at 70% daylight, followed by 45, 100 and 27% daylight for both seasons (Table 28). The relative grain yields at 100, 70, 45 and 27% daylight were 100, 122, 103 and 78 for the summer harvest and 100, 142, 114 and 71 for the cool-season harvest. Low yields of bushbean in full daylight were probably due to inadequate N supply. The plants fixed very little N and were therefore almost entirely dependent on soil N. Early leaf senescence in full daylight was probably also due to inadequate N since the plants were unable to rapidly replace chlorophyll destroyed by the sun. The 1000 seed weight was only 247 grams in full daylight and 300-310 grams in the shade for the summer harvest, and 265 grams in full daylight and 352-360 grams in the shade for the cool-season harvest. The higher seed weight during the cool season suggests that during the summer season even the shaded plants may have been deficient in N. Seed N percentage was also higher by 0.15-0.66% during the cool season; a further indication of greater N stress in the summer crop of bushbean. The bushbean started flowering 25-30 days after emergence for both seasons. The lower yield of bushbean during the cool season was probably due to the lower total irradiance during this period as compared to the summer

Table 27. The effect of shading on the top/root ratio of bushbean

Light intensity	Top/root ratio at indicated weeks after emergence									
	3	4	5	6	7	8	9	10	11	12
a) Summer crop										
100	11.1	6.0	7.7	10	13	20	30	27	30	-
70	9.0	6.6	7.6	10	14	24	32	32	31	30
45	7.7	6.0	9.9	12	16	25	30	30	25	26
27	7.1	6.7	9.0	9	14	21	25	30	27	29
b) Cool-season crop										
100	9.0	9.8	13	20	-	25	-	-	-	-
70	7.7	7.9	14	20	-	25	-	-	-	-
45	10.0	9.0	16	20	-	31	-	-	-	-
27	9.0	7.6	14	24	-	26	-	-	-	-

Table 28. The effect of shading on the performance of Burpee tenderpod bushbean.

Light intensity	Days to maturity	Pods per plant	Seeds per pod	1000 seed weight	Seed yield		%N	Total N kg/ha
					per plant	per ha		
				gm.	gm.	tons		
<u>April '76-July '76</u> †								
100	81 c	11.5 a	3.6	247 b	10.3 ab	2.7 ab	2.62 b	71 ab
70	88 b	11.6 a	3.6	304 a	12.9 a	3.3 a	2.70 ab	90 a
45	89 b	10.1 b	3.4	310 a	10.7 ab	2.8 ab	2.79 ab	77 ab
27	93 a	8.2 c	3.3	300 a	8.2 b	2.1 b	2.98 a	63 b
LSD .05	1.3	1.3	-	36	3.0	0.8	0.32	22
<u>November '76-February '77</u>								
100	83 c	6.5 a	3.0	265 b	5.3 c	1.37 c	3.28 a	44 b
70	95 b	6.0 b	3.6	360 a	7.8 a	2.03 a	2.85 b	58 a
45	96 b	5.5 c	3.2	352 a	6.2 b	1.60 b	3.16 a	51 ab
27	100 a	3.6 d	3.2	358 a	4.2 d	1.01 d	3.34 a	35 c
LSD .05	3	0.4	0.7	45	0.8	0.22	0.21	8

† Means in the same column followed by the same letter are not significantly different at 5% level (Bayes LSD).

season. The limiting plant character affecting yield was the number of pods per plant, since shading had no significant effect on the number of seeds per pod. The relationship between seed weight and pod number at varying light intensities is shown in Figure 48.

NITROGEN FERTILIZER EXPERIMENT ON BUSHBEAN

During the first two weeks after emergence the non-fertilized plants were very yellow. However, these plants became equally as green as the N-fertilized plants by 3-4 weeks after emergence.

Nodule number at 3, 4 and 7 weeks after emergence did not differ significantly between light intensities or between nitrogen levels, although there was a strong indication of reduced nodule number when the plants were fertilized or grown in full daylight (Table 29).

Total nodule dry weight per plant and acetylene reduction were significantly higher with non-fertilized plants at 70% daylight at 3 and 4 weeks after emergence. This was associated with increased nodule size in the non-fertilized plots plus significantly greater specific nodule activity (Table 29). These results are similar to the findings of Kry (1976) who tested soybeans at different light intensities (100, 82, 60 and 38%) with and without N fertilizer.

The total DM yield of tops and roots were higher for the fertilized plots, with the difference increasing with age (Table 30). The nitrogen percentage at 3 weeks was higher for the fertilized plots but this was reversed at 4 weeks, (especially at 70% daylight) at which time high acetylene-reduction levels were measured in the non-fertilized plots. A second application of 45 kg N/ha at 5 weeks after emergence reversed the situation again, with N percentage in the

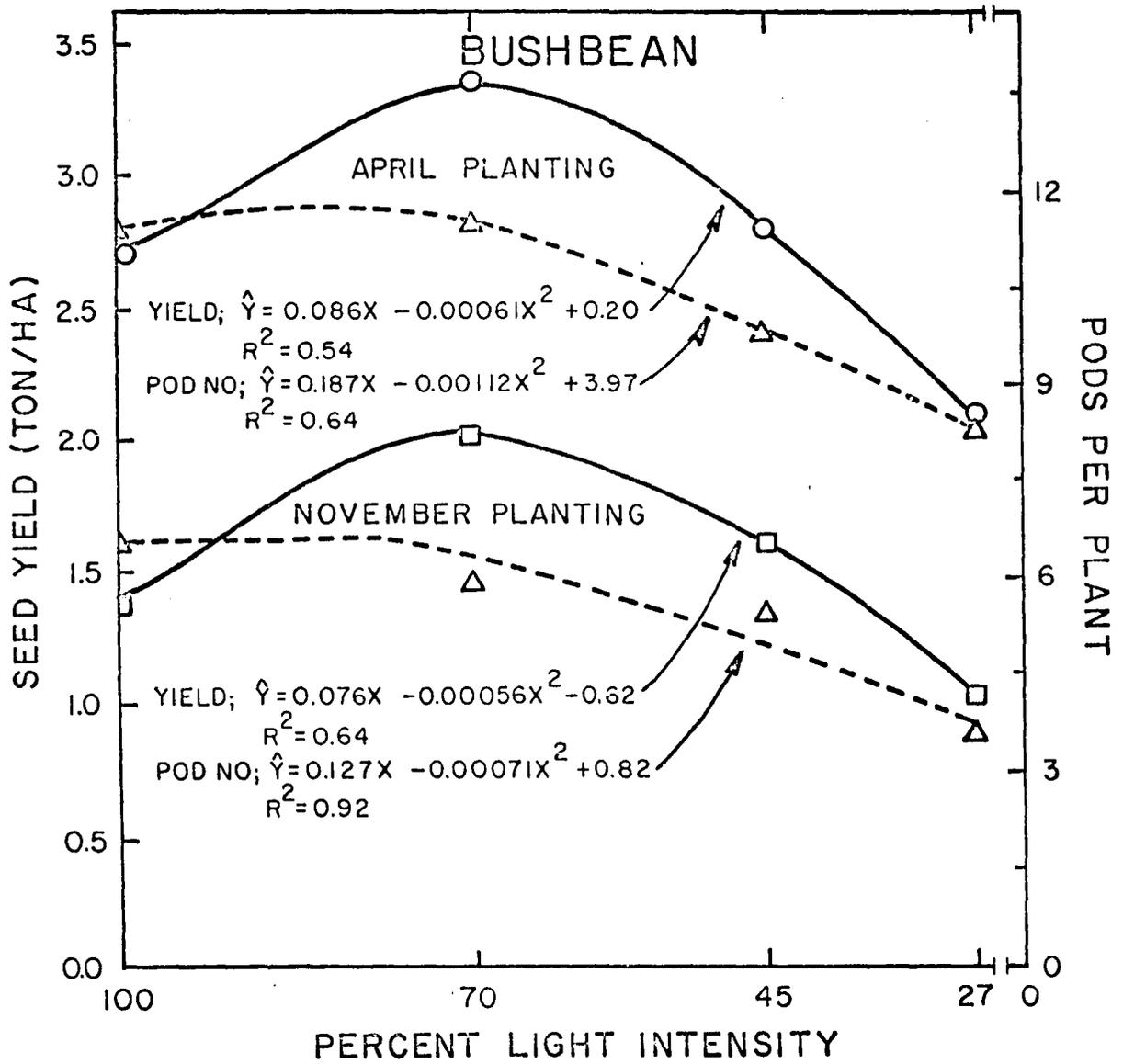


Figure 48. The effect of shading on the seed yield and number of pods per plant of bushbean grown during two seasons.

Table 29. The effect of shading and nitrogen fertilizer on the number of nodules, nodule dry weight and acetylene reduction per plant, and specific nodule activity and nodule size of bushbean.

Light intensity	kg N per ha	Characteristics at indicated weeks after emergence		
		3	4	7
a) <i>Total nodule number per plant.</i>				
100	75	67	66	8
100	0	112	69	7
70	75	101	45	11
70	0	140	129	27
b) <i>Total nodule dry weight per plant (mg).</i>				
100	75	17	41	8
100	0	33	42	10
70	75	23	28	20
70	0	69	140	57
c) <i>Acetylene reduction per plant ($\mu\text{mol/h}$).</i>				
100	75	2.0	6.6	0.7
100	0	4.4	6.3	0.2
70	75	2.4	1.7	1.8
70	0	14.8	11.7	1.4
d) <i>Specific activity ($\mu\text{mol/h/gm dry nodule}$).</i>				
100	75	50	94	16
100	0	104	102	10
70	75	92	11	30
70	0	195	100	22
e) <i>Nodule size (mg/nodule).</i>				
100	75	0.25	0.62	1.00
100	0	0.30	0.61	1.43
70	75	0.23	0.62	1.82
70	0	0.50	1.08	2.11

Table 30. The effect of shading and nitrogen fertilizer on dry matter yield, N percentage, N yield and top/root ratio of bushbean

Light intensity	kg N per ha	Characteristics at indicated weeks after emergence		
		3	4	7
a) <i>Total DM yield of tops (kg/ha)</i>				
100	75	237	614 b	2463 a
100	0	203	459 b	2137 ab
70	75	248	769 a	2716 a
70	0	206	649 ab	1883 b
		ns	*	*
b) <i>Total DM yield of roots (kg/ha)</i>				
100	75	36	68	126
100	0	33	61	123
70	75	36	75	130
70	0	26	56	127
		ns	ns	ns
c) <i>Total N yield (kg/ha)</i>				
100	75	11	19	59
100	0	9	18	55
70	75	10	25	76
70	0	8	24	49
d) <i>Nitrogen percentage</i>				
100	75	3.82	2.74	2.73
100	0	3.51	2.78	2.42
70	75	3.49	2.98	2.67
70	0	3.35	3.17	2.41

fertilized plants exceeding the non-fertilized plants at 7 weeks.

Top/root ratio was not affected by N fertilization or shading, but increased with age from 6-7 at 3 weeks after emergence to about 20 at 7 weeks after emergence.

Pods of the bushbean are usually harvested green. In this experiment half of the plot was harvested as green pods, (or green beans) and half as dry beans. The green beans were harvested every 4 days 7-9 weeks after emergence. The number of pods per plant and pod weight were greater for the fertilized plots resulting in a greater total yield of green beans in the N-fertilized plots (19.7 ton/ha vs. 14.2 ton/ha for non-fertilized bushbean)(Table 31). Similarly, seed yield was highest at 70% daylight and with N fertilizer (Table 32). Almeida *et al.* (1973) reported a 52% increase in bean yield in Brazil when 40 kg/ha of N was added. A 32% increase in bean yield was reported in Cuba, when 90 kg/ha of N was added (Sistachs, 1970). El-Beheidi (1970) reported a 26% increase in bean yield in Egypt when 60 kg/ha of N was added. Residue (pod husks, haulms and roots) yields were also higher in the fertilized plots (Table 32).

Shading and N fertilization had no significant effect on N percentage in the seed, while the N percentage was significantly higher in the residue from the fertilized plots (Table 32). The N-fertilizer recovery was 44% in full daylight and 52% in the shade.

The 1000 seed weight of fertilized bushbean was 23% higher in full daylight and 12% higher in the shade than non-fertilized bushbean. This indicates that nitrogen availability is of great importance for pod filling. The number of seeds per pod and number of pods per plant

Table 31. The effect of shading and nitrogen fertilizer on green bean yield and pod number per plant of bushbean. Plant density of 260,000 per ha. Average of three replications.

Light intensity	N-fert. treatment	Pods per plant	Green pod yield			Percent DM	DM yield
			per pot	per plant	per ha		
	kg/ha		gm	gm	ton	%	t/ha
100	75	13.1	5.51	72	18.8	13.4	2.51
100	0	10.7	5.36	57	14.9	12.2	1.82
70	75	13.2	5.96	79	20.5	12.2	2.50
70	0	9.6	5.38	52	13.4	11.9	1.60

Table 32. The effect of shading and nitrogen fertilizer on the performance of bushbean. Plant density of 260,000 per ha. Average of three replications.

Light intensity	N-fert. treat.	Days to maturity	Pods per plant	Seeds per pod	Seed weight	Seed yield	Residues		N-percentage		N-yield		
							pod husks	haulms + roots	seed	resid.	seed	resid.	total
%	kg/ha				g/1000	-----	ton/ha	-----	---- % ----	-----	kg/ha	-----	
100	75	86	10.4	3.6	319	3.16	0.58	0.70	2.57	1.13	82	14	96
100	0	82	8.8	3.5	258	2.05	0.51	0.53	2.57	0.93	53	10	63
70	75	92	10.6	3.7	339	3.49	0.63	0.88	2.68	1.13	93	17	110
70	0	86	8.3	3.5	302	2.26	0.53	0.53	2.62	1.02	59	11	70
<u>ANOVA</u>													
Light intensity		**	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	ns
N fertilizer		**	*	*	**	**	*	**	ns	*	**	**	**

* Significant at the 5% level.
 ** Significant at the 1% level.
 ns No significant difference.

were significantly higher in fertilized plots, but were not affected by shading. Harvesting at the dry bean stage resulted in fewer pods than when green beans were harvested, probably because removal of the green pods allowed more photosynthate to become available for development of pods from later flowers.

Shading was accompanied by changes in morphology (Table 33). The data for leaf area ratio (LAR) indicated that the leaf area per unit of plant weight was significantly higher in the shade. Shading decreased leaf thickness, but N fertilization increased thickness. The leaf area per unit of soil area (leaf area index) at four weeks after emergence was 50% higher in the shade. The higher yield of shaded plants appeared to be primarily a result of the greater photosynthetic area in the shade plus the better positioning of the leaves due to their elongated petioles.

From this experiment it can be concluded that because of the low rate of nitrogen fixation in bushbean cv. Burpee Tenderpod application of N fertilizer at the time of planting was important for maximizing the number of pods per plant, while the second application 5 weeks later was important for pod filling and seed development.

PIGEON PEA

Pigeon pea was planted November 11th 1975, and pods were harvested every 70-90 days over the period 6-15 months after planting (Table 34). The total seed yield was 13 t/ha at full daylight or slightly less than 1 ton per month of grain. The proportional yields for 100, 70, 45 and 27% daylight were 100, 73, 41 and 15, respectively,

Table 33. The effect of shading and levels of nitrogen fertilizer on the specific leaf weight, leaf area index and leaf area ratio of 4 weeks old bushbean.

Light intensity	kg N/ha	S L W (mg/cm ²)	L A I (cm ² /cm ²)	L A R (cm ² /g)
100	75	3.77	1.07	166
100	0	3.29	1.03	178
70	75	2.92	1.68	226
70	0	2.66	1.48	230
<u>ANOVA</u>				
Light intensity		**	**	**
N fertilizer		*	ns	ns

* Significant at the 5% level.
 ** Significant at the 1% level.
 ns No significant difference.

Table 34. The effect of shading on the yield, seed size and seed number per pod on pigeon pea. Unreplicated. Plant population 40,000 per ha.

Light intensity	Grain yield at				Total grain yield	Seeds per pod	Seed weight	Grain nitrogen	
	8 May	20 Jul.	21 Oct.	1 Jan.				percent	yield
	ton/ha						g/1000	%	kg/ha
100	3.0	4.9	1.6	3.5	13.0	3.5	107	3.80	494
70	2.6	3.7	1.1	2.0	9.4	3.4	99	3.87	364
45	2.7	1.5	0.6	0.6	5.2	3.4	91	4.17	221
27	0.8	0.8	0.2	0.2	2.0	3.3	86	4.14	83

indicating that this crop is highly sensitive to shading. Both seed size and number of seeds/pod decreased with decreasing light intensity. Nitrogen percentage in the grain was lowest in full daylight and highest at 45% daylight. The N yield of the grain decreased linearly with decreasing light intensity with a total N yield in full daylight of 494 kg/ha over a 15 month growing period (equivalent to about 1 kg N per day).

SUMMARY AND CONCLUSION

Plant growth under different levels of shading showed typical morphological adaptation: longer internodes and petioles, greater LAR, and wider but thinner leaves. Plant height in bushbean was not significantly affected by shading or season, while in soybean the summer crop was double the height of the winter crop and the shaded plants were 15-35% taller than the plants grown in full daylight. Flowering in soybean for the cool-season crop started 3.5 weeks after emergence -- 10 days earlier than the summer crop. This served to restrict growth due to earlier competition for photosynthate by the developing grain. Cowpea TVu 1190 did not flower during the summer season, but did flower when grown during the cool season. TVu 1190 plants had a viny habit during the summer and grew as a semi-bush type plant in the cool season. Light shading of cowpea TVu 4557 caused some plants to become vine-like, while in full daylight all plants were of the bush type.

Nodule number was affected less by shading than nodule weight for all three species at both seasons, resulting in a smaller nodule size with decreasing light intensity. Nodules were also smaller during the

cool season. Maximum nodule number was reached at 3 weeks after emergence for bushbean and 6 weeks after emergence for soybean and cowpea TVu 1190, while maximum nodule weight was reached about 2 weeks later. Acetylene-reduction rates of soybean and cowpea grown during the summer at full daylight averaged 30 $\mu\text{mol C}_2\text{H}_2$ plant per hour during the period 4 to 13 weeks after emergence. During the total growth period acetylene reduction in bushbean was only 4% of the acetylene reduction measured for soybean (equal area basis). This difference in acetylene reduction accounted for the great difference in total N-accumulation, with 350 kg N/ha accumulated for soybean and cowpea and only 120 kg N/ha accumulated in bushbean.

Soybean roots supported the greatest amount of nodule tissue of the three species tested. Each gram of root supported 800 mg of nodule tissue during most of the growing period. Cowpea TVu 1190 supported 220 mg nodule tissue/gm root tissue at 100, 70 and 45% daylight, but only 100 mg at 27% daylight. Similarly, bushbean roots supported less nodule tissue (100 mg nodule/gm root) under heavy shading of bushbean compared to 380 mg nodule/gm root in the other treatments during the time of maximum acetylene reduction.

In bushbean the total DM yields at maturity was 50% higher at 45 and 70% daylight than in full daylight or at 27% daylight. The low DM yield in full daylight could be explained on the basis of a) the dependence of bushbean on soil N for development, b) the high rate of destruction of chlorophyll in full daylight which exceeded the rate of chlorophyll regeneration, and c) the earlier maturation (by 2 weeks) of plants grown in full daylight. The large response to the application of 75 kg N/ha indicates that N is a major limiting

factor for optimum growth in bushbean. Both cowpea varieties (cowpea TVu 1190 during the summer season and cowpea TVu 4557 during the cool season) were affected more by shading than soybean. At 100, 70, 45 and 27% daylight the relative DM yields were 100, 95, 76 and 40 for soybean and 100, 95, 65 and 25 for cowpea.

The top/root ratio differed significantly among species and maturity stages, but not among light intensities. The lowest top/root ratio of 4.6 was measured for soybean at 4-6 weeks after emergence, after which the ratio increased linearly to 20 at late pod filling. The top/root ratio of the other crops similarly increased with age: from 6-30 in bushbean and from 7-16 in cowpea. The N percentage of tops and roots + nodules of soybean did not vary significantly among light intensities or age, with N percentage ranging from 3.0-3.7 for the summer crop and slightly higher for the winter crop. For cowpea the N percentage decreased with age from 3.5-1.8% in cowpea TVu 4557, and from 3.5-2.7% in cowpea TVu 1190 (vegetative growth only) with no difference among light intensities. The N percentage in bushbean decreased with age and with increasing light intensity from 3.8-2.2 at both seasons. The total N-yield for the summer crop was 350 kg N/ha for soybean and cowpea and 130 kg N/ha for bushbean. The N-yield for the cool season crop was much lower for all species. The total growth period for the 3 species tested were about the same, but the proportion of the different plant parts at a given age differed markedly. Cowpea TVu 4557 first started flowering 7-8 weeks after emergence, at which time already 25-50% of the total pod DM of soybean and bushbean had been formed. At maturity about half of the total DM in cowpea TVu 4557 was found in the seeds and pods, compared to

80-90% for bushbean, indicating that cowpea was less efficient in translocating nutrients from the leaves to the grain.

The effect of different light intensities on the final grain yield varied significantly among species, with bushbean being most shade tolerant, soybean intermediate and cowpea most sensitive to shading. The relative yields for 100, 70, 45 and 27% daylight were 100, 132, 108 and 74 for bushbean, (summer + cool season crop) 100, 90, 76 and 45 for soybean (summer and cool season crop) and 100, 80, 43 and 9 for cowpea TVu 4557 (cool season crop). The yields in full daylight (summer and cool season) were 2.4 and 1.4 ton/ha for bushbean 5.2 and 1.4 ton/ha for soybean, respectively, and 1.2 ton/ha for cowpea TVu 4557 (cool season only). The harvest index (grain yield/biological yield) decreased with decreasing light intensity, especially for cowpea and bushbean. The limiting component of yield was the number of pods per plant, since shading had little or no effect on seed number per pod or 1000 seed weight, except for bushbean where 1000 seed weight was significantly lower at full daylight. The much lower seed weight of bushbean in full daylight was assumed to be related to nitrogen deficiency during pod filling and this assumption was confirmed by the results from the N fertilizer trial. Seed weight of bushbean was increased by 24% and seed yield by 50% when 75 kg N/ha was added. The N-percentage in the seeds for the different species was relatively constant, ranging from 6.03-6.76% for soybean, (both seasons) 3.50-3.60% for cowpea TVu 4557, 2.62-2.98 for bushbean summer crop and 2.85-3.34 for bushbean cool season harvest.

Appendix Table 1. The effect of shading on the P content of six tropical grasses.

Species	N-level	Percent phosphorous at light intensity							
		100	70	45	27	100	70	45	27
		Cool season				Summer season			
Mealani digitgrass	0	0.46	0.43	0.44	0.36	0.31	0.35	0.36	0.33
	365	0.28	0.26	0.29	0.28	0.19	0.21	0.25	0.28
guineagrass	0	0.34	0.37	0.37	0.35	0.29	0.34	0.31	0.31
	365	0.24	0.26	0.24	0.24	0.18	0.20	0.21	0.21
corigrass	0	0.29	0.36	0.38	0.40	0.29	0.34	0.40	0.39
	365	0.29	0.29	0.31	0.30	0.29	0.29	0.38	0.24
napiergrass*	0	0.29	0.45	0.34	0.27	0.32	0.35	0.27	0.26
	365	0.28	0.36	0.31	0.27	0.27	0.34	0.27	0.26
kikuyugrass*	0	0.29	0.34	0.42	0.39	0.36	0.39	0.43	0.43
	365	0.25	0.23	0.39	0.33	0.26	0.26	0.31	0.30
signalgrass*	0	0.31	0.38	0.36	0.40	0.21	0.31	0.35	0.35
	365	0.23	0.32	0.25	0.26	0.32	0.27	0.29	0.28

*non-replicated.

Appendix Table 2. The effect of shading on the K content of six tropical grasses.

Species	N-level	Percent potassium at light intensity							
		100	70	45	27	100	70	45	27
		Cool season				Summer season			
Mealani digitgrass	0	1.87	2.17	2.87	3.05	1.79	2.07	2.69	3.19
	365	2.55	2.81	3.17	3.43	1.90	1.52	2.44	2.93
guineagrass	0	1.68	1.90	2.36	2.53	1.52	1.94	2.60	2.95
	365	2.05	2.60	2.58	3.11	2.39	2.88	3.03	2.96
corigrass	0	1.45	1.93	2.18	3.00	1.50	1.84	2.21	2.77
	365	2.35	2.64	3.03	3.42	2.16	2.35	2.14	3.14
napiergrass*	0	3.38	4.63	4.39	4.81	2.95	3.42	3.67	3.86
	365	3.28	3.60	3.92	4.31	2.51	3.06	3.28	3.50
kikuyugrass*	0	1.30	2.07	2.37	4.61	2.41	1.97	2.70	4.07
	365	2.33	2.40	2.88	4.18	2.41	2.54	3.60	3.55
signalgrass*	0	1.93	1.91	2.32	2.71	1.46	1.69	2.70	2.89
	365	2.21	3.02	2.71	3.27	1.51	2.27	2.44	3.17

*non-replicated.

Appendix Table 3. The effect of shading on the Ca content of six tropical grasses.

Species	N-level	Percent calcium at light intensity							
		100	70	45	27	100	70	45	27
		Cool season				Summer season			
Mealani digitgrass	0	0.39	0.36	0.34	0.42	0.33	0.32	0.28	0.35
	365	0.32	0.33	0.39	0.52	0.29	0.30	0.31	0.43
guineagrass	0	0.30	0.29	0.31	0.36	0.35	0.32	0.32	0.38
	365	0.31	0.33	0.32	0.41	0.49	0.47	0.45	0.50
corigrass	0	0.37	0.35	0.34	0.40	0.37	0.35	0.32	0.32
	365	0.38	0.34	0.42	0.43	0.42	0.40	0.38	0.38
napiergrass*	0	0.39	0.28	0.30	0.36	0.25	0.28	0.34	0.30
	365	0.32	0.28	0.31	0.39	0.31	0.31	0.29	0.30
kikuyugrass*	0	0.34	0.34	0.38	0.53	0.36	0.35	0.32	0.34
	365	0.50	0.48	0.54	0.59	0.36	0.34	0.33	0.49
signalgrass*	0	0.27	0.29	0.25	0.45	0.25	0.23	0.18	0.25
	365	0.25	0.36	0.28	0.48	0.24	0.28	0.29	0.35

*non-replicated.

Appendix Table 4. The effect of shading on the Mg content of six tropical grasses.

Species	N-level	Percent calcium at light intensity							
		100	70	45	27	100	70	45	27
		Cool season				Summer season			
Mealani digitgrass	0	0.30	0.31	0.30	0.42	0.20	0.21	0.23	0.33
	365	0.25	0.31	0.32	0.47	0.28	0.33	0.33	0.40
guineagrass	0	0.41	0.41	0.41	0.48	0.32	0.33	0.34	0.34
	365	0.32	0.34	0.35	0.44	0.38	0.39	0.43	0.47
corigrass	0	0.38	0.41	0.39	0.45	0.34	0.38	0.40	0.40
	365	0.38	0.42	0.43	0.50	0.38	0.45	0.44	0.47
napiergrass*	0	0.27	0.35	0.26	0.30	0.32	0.32	0.30	0.28
	365	0.26	0.26	0.28	0.32	0.28	0.26	0.31	0.28
kikuyugrass*	0	0.38	0.37	0.39	0.46	0.38	0.37	0.41	0.37
	365	0.37	0.30	0.38	0.47	0.37	0.32	0.36	0.48
signalgrass*	0	0.37	0.40	0.35	0.41	0.27	0.33	0.30	0.36
	365	0.26	0.44	0.33	0.55	0.25	0.39	0.36	0.52

*non-replicated.

Appendix Table 5. The effect of shading on the S content of six tropical grasses.

Species	N-level	Percent sulphur at light intensity							
		100	70	45	27	100	70	45	27
		Cool season				Summer season			
Mealani digitgrass	0	0.11	0.13	0.18	0.21	0.08	0.11	0.13	0.17
	365	0.13	0.18	0.22	0.24	0.12	0.16	0.16	0.19
guineagrass	0	0.11	0.11	0.13	0.15	0.08	0.10	0.12	0.14
	365	0.10	0.11	0.12	0.16	0.11	0.12	0.14	0.16
corigrass	0	0.11	0.13	0.15	0.23	0.10	0.12	0.15	0.19
	365	0.15	0.20	0.26	0.27	0.14	0.19	0.20	0.26
napiergrass*	0	0.9	0.10	0.13	0.14	0.07	0.10	0.10	0.11
	365	0.11	0.12	0.13	0.16	0.09	0.10	0.12	0.12
kikuyugrass*	0	0.15	0.17	0.19	0.27	0.16	0.19	0.18	0.27
	365	0.20	0.17	0.28	0.30	0.20	0.20	0.21	0.30
signalgrass*	0	0.11	0.13	0.16	0.23	0.9	0.11	0.15	0.19
	365	0.15	0.20	0.19	0.25	0.11	0.14	0.16	0.23

*non-replicated

Appendix Table 6. The effect of shading on the Si content of six tropical grasses.

Species	N-level	Percent silica at light intensity							
		100	70	45	27	100	70	45	27
		Cool season				Summer season			
Mealani	0	2.74	2.58	2.31	2.42	2.20	2.27	2.11	2.01
digitgrass	365	2.45	2.17	1.93	1.98	1.68	1.59	1.54	1.76
guineagrass	0	2.90	2.90	2.80	2.98	2.91	2.74	2.59	2.73
	365	2.80	2.77	2.74	2.66	2.43	2.31	2.34	2.38
corigrass	0	2.73	2.71	2.63	2.50	2.61	2.23	2.35	2.41
	365	2.37	2.29	2.17	2.23	2.35	2.02	1.82	1.70
napierrgrass*	0	2.78	2.75	2.49	2.65	2.72	2.19	2.28	2.38
	365	2.62	2.20	2.37	2.58	2.70	2.12	2.14	2.12
kikuyugrass*	0	2.89	1.94	1.87	1.58	1.49	1.52	1.52	1.61
	365	1.65	1.68	1.68	1.44	1.25	1.20	1.15	1.37
signalgrass*	0	2.35	2.35	2.08	2.29	2.49	2.49	2.07	2.38
	365	1.98	1.91	1.83	2.09	2.40	2.00	1.74	1.66

*non-replicated.

Appendix Table 7. The effected of shading on the Cu content of six tropical grasses.

Species	N-level	Copper content (ppm) at light intensity							
		100	70	45	27	100	70	45	27
		Cool season				Summer season			
Mealani digitgrass	0	3.3	5.3	8.0	7.8	5.0	5.7	6.7	7.7
	365	5.7	8.0	9.7	8.7	6.3	7.3	8.0	9.0
guineagrass	0	3.0	2.3	5.0	4.0	2.3	4.3	5.7	6.7
	365	5.0	6.3	6.7	5.0	6.3	6.3	6.7	8.0
corigrass	0	2.0	5.0	5.2	6.7	4.0	3.3	3.7	5.7
	365	5.0	7.3	7.4	7.0	5.3	5.7	6.3	9.3
napiergrass*	0	6.0	7.0	8.5	8.0	4.0	5.0	6.5	6.8
	365	6.0	8.0	10.0	10.0	5.0	7.0	7.0	7.0
kikuyugrass*	0	3.5	3.0	5.0	9.0	8.0	7.0	8.0	10.0
	365	5.0	5.0	7.0	7.0	9.2	8.0	11.0	12.0
signalgrass*	0	4.0	5.0	7.0	5.0	3.0	3.0	6.0	7.0
	365	5.0	6.5	8.0	8.0	4.0	4.0	8.0	10.0

*non-replicated.

Appendix Table 8. The effect of shading on the Zn content of six tropical grasses

Species	N-level	Zinc content (ppm) at light intensity							
		100	70	45	27	100	70	45	27
		Cool season				Summer season			
Mealani digitgrass	0	28	28	33	24	20	23	22	30
	365	23	25	33	30	21	25	26	29
guineagrass	0	25	24	28	26	17	21	20	20
	365	21	23	22	22	18	19	20	20
corigrass	0	34	33	35	45	33	28	31	33
	365	26	31	28	35	26	27	33	37
napiergrass*	0	20	31	30	31	21	28	25	29
	365	19	32	27	28	17	25	23	27
kikuyugrass*	0	45	29	36	31	37	32	38	40
	365	33	25	32	36	33	30	37	38
signalgrass*	0	26	29	31	31	17	26	27	31
	365	21	22	24	21	14	24	25	26

*non-replicated.

Appendix Table 9. Analysis of variance of Kohala soybean under different light intensities.

Source of variation	df	Days to maturity	Pods per plant	Seeds per plant	1000 seed weight	Seed yield		%N	Total N kg/ha
						per plant	per ha		
----- mean square -----									
<u>April '76-July '76</u>									
Repli.	2	52.75	5.08	0.005	1871*	1.63	0.250	0.131*	2028
Light int.	3	121.11*	95.67*	0.014	230	23.71**	3.267	0.048	13064*
Error	6	21.86	19.42	0.005	286	2.26	0.301	0.019	1438
Total	11								
<u>November '76-February '77</u>									
Repli.	2	9.08	0.18	0.000	33	0.006		0.040	4
Light int.	3	20.67*	17.63**	0.023	562	3.705**		0.435	1616**
Error	6	2.75	0.32	0.006	122	0.121		0.072	110
Total	11								

*Significant at 5% level

**Significant at 1% level

Appendix Table 10. Analysis of variance of cowpea TVu 4557 under different light intensities.

Source of variation	df	Days to maturity	Pods per plant	Seeds per plant	1000 seed weight	Seed yield		%N	Total N kg/ha
						per plant	per ha		
					mean square				
Repli.	2	0.58	2.30	0.450	12.3	2.48	0.041	0.002	54
Treatment	3	22.97**	35.59**	1.889*	26.4	41.93**	0.716**	0.017	881**
Error	6	0.47	0.85	0.239	30.7	0.90	0.015	0.008	20
Total	11								

* Significant at 5% level.

** Significant at 1% level.

Appendix Table 11. Analysis of variance of Burpee tenderpod bushbean under different light intensities.

Source of variation	df	Days to maturity	Pods per plant	Seeds per plant	1000 seed weight	Seed yield		%N	Total N kg/ha
						per plant	per ha		
----- mean square -----									
<u>April '76-July '76</u>									
Repli.	2	1.08	3.85	0.043	274	4.3	0.235	0.024	280
Light int.	3	70.53**	7.49*	0.065	2655*	10.9	0.722	0.072	380
Error	6	0.86	0.74	0.094	517	3.3	0.208	0.030	146
Total	11								
<u>November '76-February '77</u>									
Repli.	2	81.3**	0.120	0.080	2885	4.05**	0.315**	0.038	272*
Light int.	3	160.1**	4.888**	0.171	6417*	7.08**	0.498**	0.144	277**
Error	6	3.6	0.065	0.098	890	0.33	0.024	0.019	28
Total	11								

* Significant at 5% level.

** Significant at 1% level.

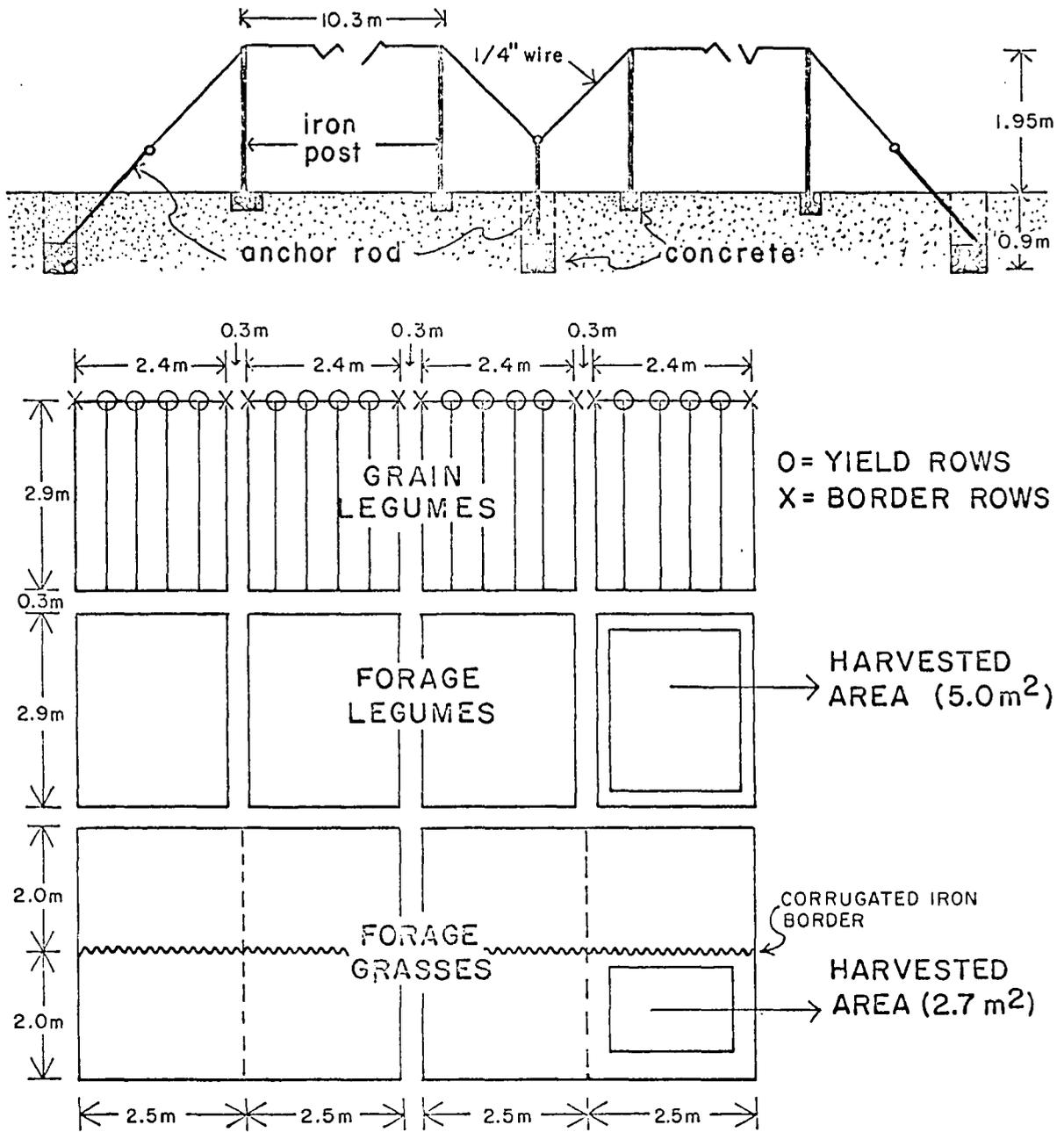
A



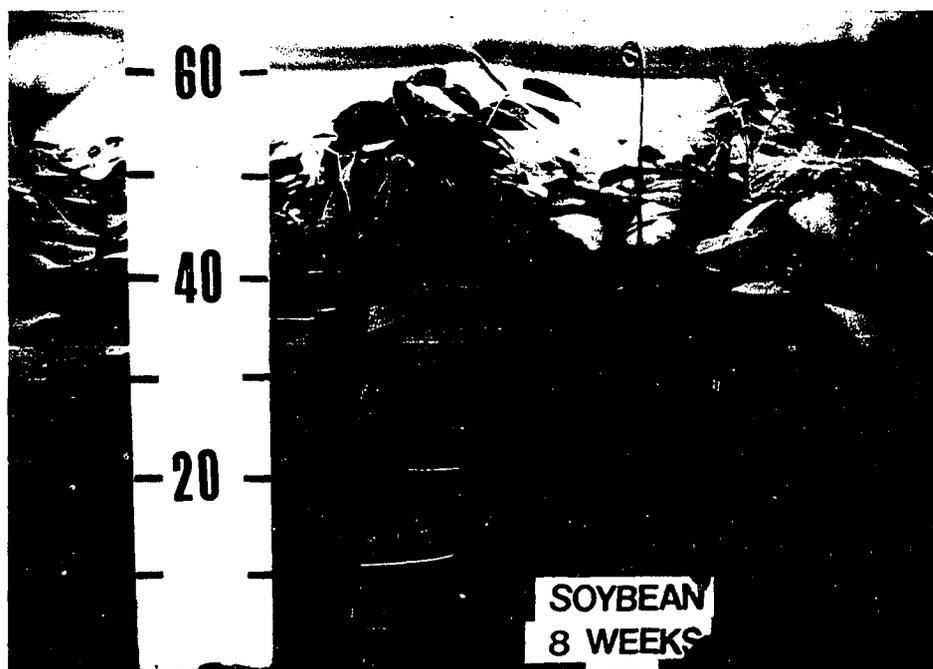
B



Appendix Figure 1. General view of the A) forage grass and legume plots and the B) grain legume plots.



Appendix Figure 2. Plot field layout showing the arrangement of treatments, plot dimensions and plot yield area. Also shown is the set up of the shaded area.



Appendix Table 3. Growth of 8 weeks old Kohala soybean at 70% daylight during the summer season.

LITERATURE CITED

- Abu-Shadra, S. and A. Bassiri. 1972. Effects of inoculation and nitrogen fertilization on nodulation, seed yield and quality of soybeans. *J. Agri. Sci.* 78:179-182.
- Abu-Shadra, S. 1975. Soil fertility and inoculation in soybean production. pp 48-53. *In* P. K. Whigman (ed.). *Proc. of Soybean Production, Protection and Utilization.* INTSOY. Urbana.
- Addison, K. B. 1956. The effect of various cultural and manurial treatments on napier fodder. *Rhod. Agr. J.* 53:491-506.
- Adedipe, N. O. and D. P. Ormrod. 1975. Effects of light intensity on growth, and on chlorophyll, carbohydrate and phosphorous contents of the cowpea (*Vigna unguiculata* L.) *Biochem. Physiol. Pflanzen.* 167:301-309.
- Alberda, T. 1957. The effects of cutting, light intensity and night temperature on growth and soluble carbohydrate content of *Lolium perenne* L. *Plant Soil.* 8:199-230.
- Allison, J. C. S. and D. J. Watson. 1966. The production and distribution of dry matter in maize after flowering. *Ann. Bot. N. S.* 30:365-381.
- de Almeida, D. L., G. G. Pessanha e A. F. Penteado. 1973. Efeito da calagem e da adubação fosfatada e nitrogenada na nodulação e produção do feijoeiro (*Phaseolus vulgaris*). *Pesq. Agropec. Bras. Ser. Agron.* 8:127-130.
- Anderson, M. 1964. Light relations of terrestrial plant communities and their measurement. *Biol. Rev.* 39:425-486.
- Anderson, M. 1971. Radiation and crop structure. pp 412-456. *In* Z. Sestak, J. Catsky, and P. G. Jarvis (eds.). *Plant Photosynthetic Production.* Junk. Hague.
- Andrew, C. S. and M. F. Robins. 1969. Effect of phosphorous on the growth and chemical composition of some tropical pasture legumes. 1. Growth and critical percentages of phosphorous. *Austr. J. Agri. Res.* 20:665-674.
- Bathurst, N. O. and K. J. Mitchell. 1958. The effect of light and temperature on the chemical composition of pasture plants. *N. Z. J. Agri. Res.* 1:540-552.
- Bergersen, F. J. 1970. The quantitative relationship between nitrogen fixation and the acetylene-reduction assay. *Austr. J. Biol. Sci.* 23:1015-1025.

- Beuerlein, J. E. and J. W. Pendleton. 1971. Photosynthetic rates and light saturation curves of individual soybean leaves under field conditions. *Crop Sci.* 11:217-219.
- Bezdicek, D. F., R. F. Mulford, and B. H. Magee. 1974. Influence of organic nitrogen on soil nitrogen, nodulation, nitrogen fixation, and yield of soybeans. *Soil Sci. Soc. Amer. Proc.* 38:268-272.
- Bjorkman, O. 1970. Characteristics of the photosynthetic apparatus as revealed by laboratory measurements. pp 267-281. *In* Prediction and measurement of photosynthetic productivity. Proc. I.B.P/PP tech. meeting, Tribon 14-21 September 1969. N. V. Noord-Nedl. Drukkery. Wageningen.
- Black, T. N. 1963. The inter-relationship of solar radiation and leaf area index in determining the rate of dry matter production of swards of subterranean clover (*Trifolium subterraneum* L.). *Austr. J. Agri. Res.* 14:20-37.
- Blackman, G. E. and W. G. Templeman. 1938. The interaction of light intensity and nitrogen supply in the growth and metabolism of grasses and clover (*Trifolium repens*). *Ann. Bot. N. S.* 7:765-791.
- Blackman, G. E. and A. J. Rutter. 1946. Physiological and ecological studies in the analysis of plant environment. *Ann. Bot. N. S.* 10:361-390.
- Blomquist, R. V. and C. A. Kust. 1971. Translocation pattern of soybeans as affected by growth substances and maturity. *Crop Sci.* 11:390-393.
- Boardman, N. K. 1977. Comparative photosynthesis of sun and shade plants. *Ann. Rev. Plant Physiol.* 28:355-377.
- Bowes, G., W. J. Ogren, and R. H. Hageman. 1972. Light saturation, photosynthesis rate, RuDP carboxylase activity and specific leaf weight in soybeans grown under different light intensities. *Crop Sci.* 12:77-79.
- Boysen-Jensen, P. and M. L. Miller. 1929. Die maximale Ausbeute und der tagliche Verlauf der Kohlensäureassimilation. *Jahrb. Wiss. Bot.* 70:493-502.
- Brewbaker, J. L., D. L. Plucknett, and V. Gonzalez. 1972. Varietal variation and yield trials of *Leucaena leucocephala* (Koa Haole) in Hawaii. *Hawaii Agri. Exp. Sta. Bull. No.* 124.
- Brougham, R. W. 1956. Effect of intensity of defoliation on regrowth of pasture. *Austr. J. Agr. Res.* 7:377-387.
- Bryan, W. W. and T. R. Evans. 1973. Effects of soils, fertilizers and stocking rates on pastures and beef production on the Wallum of south-eastern Queensland I. Botanical composition and chemical

- effects on plants and soils. *Austr. J. Exp. Agri. Anim. Husb.* 13:516-529.
- Burris, R. H. and P. W. Wilson. 1957. Methods for measurements of nitrogen fixation. Vol. 4. pp. 355-366. In S. P. Colowick and N. O. Kaplan (eds.). *Methods in enzymology*. Academic Press, New York.
- Burton, G. W., J. E. Jackson, and F. E. Knox. 1959. Influence of light reduction upon the production, persistence and chemical composition of coastal bermuda grass (*Cynodon dactylon*). *Agron. J.* 52:537-542.
- Butler, G. W., R. M. Greenwood, and K. Soper. 1959. Effect of shading and defoliation on the turnover of root and nodule tissue of plants of *Trifolium repens*, *T. pratense* and *Lotus uliginosus*. *N. Z. J. Agri. Res.* 2:415.
- Campbell, C. M., C. W. Garcia, J. C. Nolan, Y. N. Tamimi, and H. M. Richards. 1970. Effects of a program for pasture fertilization in the subtropics of Hawaii. *West. Sect. Amer. Soc. Anim. Sci. Proc.* 21:297-302.
- Caviness, C. E. and D. A. Downey. 1969. Response of soybeans to shade and supplemental light. *Arkansas Fm. Res.* 18(3):5.
- Chomchalow, S. 1971. The effectiveness of introduced *Rhizobium* strains on "Rayong" peanut. *Thai. J. Agri. Sci.* 4:85-94.
- Chu, A. C. P. and A. G. Robertson. 1974. The effects of shading and defoliation on nodulation and nitrogen fixation by white clover. *Plant Soil.* 41:509-519.
- Coaldrake, J. E. 1964. Sub-tropical environment of eastern Australia. a) *Climat. Bull. Commonw. Bur. Past. Fld. Crops.* 47:17-26.
- Cooper, C. S. and M. Qualls. 1967. Morphology and chlorophyll content of shade and sun leaves of two legumes. *Crop Sci.* 7:672-673.
- Cooper, J. P. and N. M. Tainton. 1968. Light and temperature requirements for the growth of tropical and temperate grasses. *Herb. Abstr.* 38:167-176.
- Cunningham, R. K. and K. F. Nielsen. 1965. Cation-anion relationships in crop nutrition. The effects of soil temperature, light, and soil water tension. *J. Agri. Sci.* 64:379-386.
- Date, R. A. 1973. Nitrogen, a major limitation in the productivity of natural communities, crops and pastures in the pacific area. *Soil Bio. Biochem.* 5:5-8.

- Dart, P. J. and F. V. Mercer. 1965. The effect of growth temperature, level of ammonium nitrate, and light intensity on the growth and nodulation of cowpea (*Vigna sinensis* Endl. ex Hassk.). Austr. J. Agri. Res. 16:321-345.
- Dart, P. J. and J. M. Day. 1971. Effects of inoculation temperature and oxygen tension on nitrogenase activity of legume root-nodules. Plant Soil. Spec. Vol. pp. 167-184.
- Davis, R. G., G. M. Robertson, W. C. Johnson, and A. F. Wiese. 1966. A modified optical planimeter for measuring leaf area. Agron. J. 58:106-107.
- Deinum, B. 1966. Climate, nitrogen and grass. Research into the influence of light intensity, water supply and nitrogen on the production and chemical composition of grass. Meded. Landle. Hogesch. Wageningen. 6(11). 91 p.
- Deinum, B., A. J. H. Van Es, and P. J. Van Soest. 1968. Climate, nitrogen and grass. 2. The influence of light intensity, temperature, and nitrogen on vivo digestibility of grass and the prediction of these effects on some chemical procedures. Neth. J. Agri. Sci. 16:217-223.
- Delwiche, C. C. and J. Wijler. 1956. Non symbiotic nitrogen fixation in soil. Plant Soil. 7:113-129.
- Dilworth, M. J. 1966. Acetylene reduction by nitrogen fixing preparations from *Clostridium pasteurianum*. Biochem. Biophys. Acta. 127:285-294.
- Döbereiner, J., J. M. Day, and P. J. Dart. 1973. Rhizosphere associations between grasses and nitrogen fixing bacteria. Effect of O₂ on nitrogenase activity in the rhizosphere of *Paspalum notatum*. Soil Biol. Biochem. 5:157-160.
- Döbereiner, J. and J. M. Day. 1974. Associative symbiosis in tropical grasses: Characterization of microorganisms and dinitrogen fixing sites. International symposium on N₂ fixation - interdisciplinary discussions. June 3-7, 1974. Washington State Univ.
- Domergues, Y., J. Balandreau, G. Rinaudo, and P. Weinhard. 1973. Non symbiotic nitrogen fixation in the rhizosphere of rice, maize and different tropical grasses. Soil Biol. Biochem. 5:83-89.
- Donald, C. M. 1962. In search of yield. J. Austr. Inst. Agri. Sci. 28:171-178.
- Dore, W. G. 1958. A simple chemical light meter. Ecol. 39:151-152.

- Dornhoff, G. M. and R. M. Shibles. 1970. Varietal differences in net photosynthesis of soybean leaves. *Crop Sci.* 10:42-45.
- Earley, E. B., R. J. Miller, G. L. Reichert, R. H. Hageman, and R. D. Seif. 1966. Effects of shade on maize production under field conditions. *Crop Sci.* 6:1-7.
- Egli, D. G. and J. E. Leggett. 1973. Dry matter accumulation patterns in determinate and indeterminate soybeans. *Crop Sci.* 13:220-222.
- El-Beheidi, M. 1970. The effect of nitrogen status and bacteria inoculation on the yield of beans (*Phaseolus vulgaris* L.). *Beitr. Trop. Subtrop. Landwirtschaft. Tropenvet.* 8:295-301.
- Engin, M. and J. I. Sprent. 1973. Effects of water stress on growth and nitrogen-fixing activity of *Trifolium repens*. *New Phytol.* 72:117-126.
- Erdman, L. W. 1959. Legume inoculation. *USDA Farm Bull.* 2003.
- Eriksen, F. I. 1974. Grass and legume evaluation trial at Vailele coconut Plantation, Western Samoa. *FAO of U. N.* 11 p.
- Evans, G. C. 1972. *The quantitative Analysis of Plant Growth.* Blackwell Scientific Publ. Oxford.
- Ezedinma, F. O. C. 1973. Seasonal variations in vegetative growth of cowpea (*Vigna unguiculata* (L.) Walp.) in relation to insolation and ambient temperatures in Southern Nigeria. pp 138-153. *Proc. 1st Int. Inst. Trop. Agri. Grain Legume Imp. Workshop.* IITA, Ibadan, Nigeria.
- Federer, W. T. 1956. Augmented (or Hoonuiaku) designs. *Hawaiian Planters Rec.* 55:191-208.
- Friend, D. T. C. 1961. A simple method of measuring integrated light values in the field. *Ecol.* 42:577-580.
- Gabrielsen, E. K. 1948. Effects of different chlorophyll concentrations on photosynthesis in foliage leaves. *Physiol. Plant.* 1:5-37.
- Gibson, A. 1971. Factors in the physiological and biological environment affecting nodulation and nitrogen fixation by legumes. *Plant Soil. Spec. Vol.* 139-152.
- Gomide, J. A., C. H. Noller, G. O. Mott, J. H. Conrad, and D. L. Hill. 1969. Mineral composition of six tropical grasses as influenced by plant age and nitrogen fertilization. *Agron. J.* 61:120-123.
- Gordon, C. H., A. M. Decker, and H. C. Wiseman. 1962. Some effects of nitrogen fertilizer, maturity, and light on the composition of orchardgrass. *Agron. J.* 54:376-378.

- Graham, P. H. and J. C. Rosas. 1977. Growth and development of indeterminate bush and climbing cultivars of *Phaseolus vulgaris* L. inoculated with *Rhizobium*. J. Agri. Sci. Camb. 88:503-508.
- Grime, J. P. 1966. Shade avoidance and shade tolerance in flowering plants. pp 187-207. In Bainbridge, R., G. C. Evans and O. Rackham (eds.). Light as an Ecological Factor. Blackwells; Oxford.
- Groen, J. 1973. Photosynthesis of *Calendula officinalis* L. and *Impatiens parviflora* DC. As influenced by light intensity during growth and age of leaves and plants. Med. Landbouwh. Wag. 128 p.
- Grof, B. and W. A. T. Harding. 1970. Dry matter yields and animal production of guinea grass (*Panicum maximum*) on the humid tropical coast of North Queensland. Trop. Grassld. 4:85-95.
- Guss, A. and J. Döbereiner. 1972. (Effects of N fertilization and soil temperature on nitrogen fixation in *Phaseolus vulgaris*). Pesq. Agropec. Brasil Agron. 7:87-92.
- de Guzman, Jr. M. R. 1974. Pasture and fodder production under coconuts. Extn. Bull. No. 45. ASPAC, FFTC, . 29 pp.
- Halliday, J. and J. S. Pate. 1976. The acetylene-reduction assay as a means of studying nitrogen fixation in white clover under sward and laboratory conditions. J. Brit. Grassld. Soc. 31:29-35.
- Hanway, J. J. and C. R. Weber. 1971. Dry matter accumulation in eight soybean (*Glycine max* (L.) Merrill) varieties. Agron. J. 63:227-230.
- Harder, R. 1930. Ueber die Assimilation der Kohlen säure bei konstaten Aussenbedin-gungen. Planta. 11:263-293.
- Hardy, R. W. F. and E. Knight. 1968 a. The biochemistry and postulated mechanisms of N₂ fixation. Vol. 1. pp 407-489. In L. Reinheld and J. Liwschitz (eds.). Progress in phytochemistry. Wiley, London.
- Hardy, R. W. F., R. D. Holsten, E. K. Jackson, and R. C. Burns. 1968 b. The acetylene-ethylene assay for N₂ fixation; laboratory and field evaluation. Plant Physiol. 43:1185-1207.
- Hardy, R. W. F., R. C. Burns, and G. W. Parshall. 1971 a. The biochemistry of N₂ fixation. Adv. Chem. Ser. 110:219-247.
- Hardy, R. W. F., R. C. Burns, R. R. Hebert, R. D. Holsten, and E. K. Jackson. 1971 b. Biological nitrogen fixation: a key to world protein. Plant Soil Spec. Vol. 561-590.
- Hardy, R. W. F. and U. D. Havelka. 1973. Symbiotic N₂ fixation multifold enhancement by CO₂ enrichment of field-grown soybeans. Plant Physiol. 51 (Suppl.), 35.

- Hardy, R. W. F., R. C. Burns, and R. D. Holsten. 1973. Applications of the acetylene-ethylene assay for measurement of nitrogen fixation. *Soil Biol. Biochem.* 5:57-81.
- Harper, J. E. and R. H. Hageman. 1972. Canopy and seasonal profiles of nitrate reductase in soybeans (*Glycine max* L. Merr.). *Plant Physiol.* 49:146-154.
- Harris, D. and P. J. Dart. 1973. Nitrogenase activity in the rhizosphere of *Stachys sylvatica* and some other dicot plants. *Soil Biol. Biochem.* 5:277-279.
- Henzell, E. F. and D. O. Norris. 1962. Processes by which nitrogen is added to the soil/plant system. *In* A review of nitrogen in the tropics with particular reference to pastures. *Bull. Commonw. Bur. Past. Fld. Crops.* 46:1-18.
- Hight, G. K., D. P. Sinclair, and R. J. Lancaster. 1968. Some effects of shading and nitrogen fertilizer on the chemical composition of freeze-dried and oven-dried herbage fed to sheep. *N. Z. J. Agri. Res.* 11:286-302.
- Hittle, C. N. 1975. Soybeans around the world. pp 6-15. *In* D. K. Whigham (ed.). *Proc. of Soybean Production, Protection and Utilization.* INTSOY, Urbana.
- Horrocks, R. D. and J. B. Washko. 1971. Studies of tiller formation in reed canarygrass (*Phalaris arundinacea* L.) and 'Climax' timothy (*Phleum pratense* L.). *Crop Sci.* 11:41-44.
- Hugh, E. I. 1972. Regional seminar on pastures and cattle under coconuts, Western Samoa, 30 Aug.-12 Sept. *South Pac. Comm.*, Noumea, New Caledonia. 156 p.
- Hughes, A. P. 1966. The importance of light compared with other factors affecting plant growth. pp 121-146. *In* R. Bainbridge, G. C. Evans and O. Rackham (eds.). *Light as an Ecological Factor.* Blackwells; Oxford.
- Hutton, E. M. and I. A. Bonner. 1960. Dry matter and protein yields in four strains of *Leucaena glauca* Benth. *J. Austr. Inst. Agr. Sci.* 26:276-277.
- Hume, D. J. and J. G. Criswell. 1972. Translocation and respiration losses in soybean after assimilation of $^{14}\text{CO}_2$ at various growth stages. *Agron. Abstr.* 35.
- Janssen, K. A. and M. L. Vitosh. 1974. Effect of lime, sulphur and molybdenum on nitrogen fixation and yield in dark red kidney beans. *Agron. J.* 6:736-740.
- Javier, E. Q. 1974. Improved varieties for pastures under coconuts. *Extn. Bull. No. 37.* ASPAC, FFTC. 12 pp.

- Kanemasu, E. T., K. C. Feltner and, J. F. Vesecky. 1971. Light interception and reflectance measurements with ozalid paper. *Crop Sci.* 11:931-933.
- Kasanaga, H. and M. Monsi. 1954. On the light-transmission of leaves, and its meaning for the production of matter in plant communities. *Jap. Bot.* 14:301-324.
- Khein, *et al.* 1971. Changes in the properties of the photosynthetic apparatus of *Vicia faba* plants during a change in the light system. *Doki. Akad. Nauk. SSSR.* 200:244-247.
- King, R. W. and L. T. Evans. 1967. Photosynthesis in artificial communities of wheat, lucerne, and subterranean clover plants. *Austr. J. Biol. Sci.* 20:623-635.
- Koch, B. and H. J. Evans. 1966. Reduction of acetylene to ethylene by soybean root nodules. *Plant Physiol.* 41:1748-1750.
- Koch, B., H. J. Evans, and S. Russell. 1967. Reduction of acetylene and nitrogen gas by breis and cell-free extracts of soybean root nodules. *Plant Physiol.* 42:466-468.
- Kry, T. 1976. The effect of shading and root temperature on growth, nodulation and symbiotic nitrogen fixation by soybeans. (Ph.D. dissertation, Univ. of Georgia). 83 p.
- Langer, R. H. M. 1963. Tillering in herbage grasses. *Herb. Abstr.* 33:141-148.
- Lawn, R. J. and W. A. Brun. 1974. Symbiotic nitrogen fixation in soybeans. I. Effect of photosynthetic source-sink manipulations. *Crop Sci.* 14:11-16.
- Lawn, R. J., K. S. Ficher, and W. A. Brun. 1974. Symbiotic nitrogen fixation in soybeans. II. Interrelationship between carbon and nitrogen assimilation. *Crop Sci.* 14:17-21.
- Lawrie, A. C. and C. T. Wheeler. 1975. Nitrogen fixation in the root nodules of *Vicia faba* L. in relation to the assimilation of carbon. *New Phytol.* 74:429-436.
- Loach, K. 1970. Shade tolerance in tree seedlings. II Growth analysis of plants raised under artificial shade. *New Phytol.* 69:273-286.
- Lucas, R. E. and J. F. Davis. 1961. Relationship between pH values of organic soils and availability of twelve plant nutrients. *Soil Sci.* 92:177-182.

- Ludlow, M. M., G. L. Wilson, and M. R. Heslehurst. 1974. Studies on the productivity of tropical pasture plants. Effect of shading on growth photosynthesis and respiration in two grasses and two legumes. *Austr. J. Agr. Res.* 25:425-433.
- MacEvoy, M. G. 1974. Establishment and management of pastures in coconut plantations. *Extn. Bull. No. 38, ASPAC, FFTC.* 16 p.
- Mague, T. H. and R. H. Burris. 1972. Reduction of acetylene and nitrogen by field-grown soybeans. *New Phytol.* 71:275-286.
- t'Mannetje, L. 1969. *Rhizobium* affinities and phenetic relationship with the genus *Stylosanthes*. *Austr. J. Bot.* 17:553-564.
- Mayaki, W. C., I. D. Teare, and L. R. Stone. 1976. Top and root growth, of irrigated and non-irrigated soybeans. *Crop Sci.* 16:92-94.
- Mayland, H. F. and D. L. Grunes. 1974. Shade induced grass-tetany-prone chemical changes in *Agropyron desertorum* and *Elymus cinereus*. *J. Range Mgmt.* 27:198-201.
- McCree, K. J. and J. M. Troughton. 1966. Prediction of growth rate at different light levels from measured photosynthesis and respiration rates. *Plant Physiol.* 41:559-566.
- McKee, G. W. 1962. Effects of shading and plant competition on seedling growth and nodulation in birds-foot trefoil. *Pa. Agro. Exp. Sta. Bull. No. 689.*
- Mellenberger, R. W., L. D. Satter, M. A. Millett, and A. J. Baker. 1970. An in vitro technique for estimating digestibility of treated and untreated wood. *J. Anim. Sci.* 30:1005-1011.
- Melville, J. and P. D. Sears. 1953. Pasture growth and soil fertility. II. The influence of red and white clovers, super-phosphate lime and dung and urine on the chemical composition of pastures. *N. Z. J. Sci. Tech.* 35A Suppl. 1:30-41.
- Mitchell, K. J. 1953. Influence of light and temperature on the growth of ryegrass (*Lolium* spp.). 1. Pattern of vegetative development. *Physiol. Plant.* 6:21-46.
- Monteith, J. L. 1969. Light interception and radiative exchange in crop stands. pp 89-109. *In* Eastin, Heskins, Sullivan, and van Bavel (eds.). *Physiological aspects of crop yield.* Am. Soc. Agron. Crop Sci. Am. Madison, Wisconsin.
- Moustafa, E., R. Ball and T. R. O. Field. 1969. The use of acetylene reduction to study the effect of nitrogen fertilizer and defoliation on nitrogen fixation by field grown white clover. *N. Z. J. Agr. Res.* 12:691-696.

- Munns, D. N. and R. L. Fox. 1975. Comparative lime requirements of tropical and temperate legumes. (In press).
- Munns, D. N. 1975. Mineral nutrition and the legume symbiosis. In Dinitrogen Fixation (R. W. Hardy, (ed.)). In press.
- Myhr, K. and S. Saebo. 1969. Veerknaden av skygging på vekst, utvekling og kjemisk samensetning hos nokre grasarter. (The effects of shade on growth, development and chemical composition in some grass-species.). Forskn. Förs. Landor. 20:297-315.
- Niilisk, H., T. Nilson, and J. Ross. 1970. Radiation in plant canopies and its measurement of photosynthetic productivity. pp 165-176. Proc. of the IBP/PP technical meeting, Trebon, 14-21 Sept. 1969. N. V. Noord-Nederlandse Drukkerij, Meppel, Wagen.
- Nitis, I. M., K. Rika, M. Supardjata, K. D. Nurbudhi, and L. R. Humphreys. 1976. Productivity of improved pastures grazed by Bali cattle under coconuts: A preliminary report. Dept. Anim. Husb. Prov. Bali. 18 p.
- Ng, T. T. 1972. Comparative response of some tropical grasses to fertilizer nitrogen in Sarawak, E. Malaysia. Trop. Grassld. 6:229-236.
- Ng, T. T. and T. H. Wong. 1976. Comparative productivity of two tropical grasses as influenced by fertilizer nitrogen and pasture legumes. Trop. Grassld. 10:179-185.
- Nomoto, N., H. Iwaki, and M. Monsi. 1961. Physiological and ecological analysis of shade tolerance of plants. 1. Growth of green-grass under varying light intensities. Bot. Mag. Tokyo. 74:386-394.
- Norris, D. O. 1959. Legume bacteriology in the tropics. J. Austr. Inst. Agri. Sci. 25:202-207.
- Olsen, F. J. and P. G. Moe. 1971. The effect of phosphate and lime on the establishment, productivity, nodulation and persistence of *Desmodium intortum*, *Medicago sativa* and *Stylosanthes gracilis*. E. Afr. Agr. Forest. J. 37:29-37.
- Olsen, F. J. 1972. Effect of large applications of nitrogen fertilizer on the productivity and protein content of four tropical grasses in Uganda. Trop. Agr. (Trin.). 49:251-259.
- Paulsen, G. P. M. and D. Smith. 1969. Organic reserves, axillary bud activity, and herbage yields of smooth brome grass as influenced by time of cutting, nitrogen fertilization, and shading. Crop Sci. 9:529-534.

- Perkins, A. T. 1924. The effect of several mineral fertilizers upon nodulation of Virginian soybeans. *Soil Sci.* 17:439-447.
- Plucknett, D. L. and R. L. Fox 1965. Effects of phosphorous fertilization on yields and composition of pangola grass and *Desmodium intortum*. *Proc. 9th Int. Grassld. Cong.* 1525-1529.
- Pyon, J. Y. 1975. Studies on the biology of sourgrass (*Trichachne insularis* (L.) Nees) and its competition with buffelgrass (*Cenchrus ciliaris* L.) and guineagrass (*Panicum maximum* Jacq.). (Ph.D. Dissertation. University of Hawaii). 133 p.
- Ranacou, E. 1972. Pasture species under coconuts. pp 95-103. In E. Hugh (ed.). *Regional Seminar on Pastures and Cattle under coconuts. 30 Aug.-12 Sept., 1972.* South Pac. Comm. Noumea, New Caledonia.
- Richards, B. N. and D. I. Bevege. 1969. The productivity and N economy of artificial ecosystems comprising various combinations of perennial legume and conifer tree species. *Austr. J. Bot.* 15:467-480.
- Richardson, D. A., D. C. Jordon, and E. H. Garrard. 1957. The influence of combined nitrogen on nodulation and nitrogen fixation by *Rhizobium meliloti* Dangeard. *Can. J. Plant Sci.* 37:205-214.
- Rocha, H. M., P. D. T. Alvin, J. Döbereiner. 1970. Influencia da intensidade de radiação solar sobre o crescimento e a fixação simbiótica de nitrogênio pela soja (*Glycine max*). *Turrialba, Rev. Interam. Ciencias Agr.* 20:293-298.
- Rodrigues, S. J., C. Rivera-Lopez, and A. Santiago. 1973. Variation in chemical composition of *Dracaena sandariana* leaves as influenced by leaf maturity and shade intensity. *J. Agr. (Puerto Rico)*. 57:136-148.
- Rotar, P. P., U. Urata, and A. Bromdep. 1967. Effectiveness of nodulation on growth and nitrogen content of legumes grown on several Hawaiian soils with and without the use of proper *Rhizobium* strains. *Hawaii Agr. Exp. Sta. Bull.* No. 158.
- Rotar, P. P., Y. N. Tamimi, O. R. Younge, and T. Izuno. 1976. Forage legume production trials at the volcano research station, island of Hawaii. *Hawaii Agri. Exp. Sta. Bull.* No. 206.
- Ryle, G. J. A. 1961. Effects of light intensity on reproduction of 548 timothy (*Phleum pratense* L.). *Nature Land.* 191:196-197.
- Salisbury, F. G. and C. Ross. 1969. *Plant Physiology.* Wadsworth Publ. Co. Inc. Belmont, Calif. 747 p.

- Sampaio, I. B. M. and J. Döbereiner. 1968. Efeito do sombreamento e caledrio na taxa relativa de fixacao de nitrogenio e na eficiencia dos nodules da soja (*Glycine max*). (Shading and lime effects on rate of N-fixation and efficiency of soybean nodules). *Pesq. Agropec. Brasil.* 3:250-256.
- Santhirasegaram, K., J. E. Coaldrake, and M. H. M. Salih. 1966. Yield of mixed sub-tropical pasture in relation to frequency and height of cutting and leaf-area index. *Proc. 10th Int. Grassld. Cong:*125-129.
- Sathirasegaram, K. and D. E. F. Fernandez. 1967. Yield and comparative relationship between two species of *Brachiaria* in association. *Trop. Agr. (Trin.)*. 44:229-234.
- Schank, S. C. and J. M. Day. 1977. Nitrogenase activity, nitrogen content, in vitro digestibility and yield of 30 tropical forage grasses in Brazil. *Trop. Agr. (Trin.)*. 54:119-125.
- Schollhorn, R. and R. H. Burris. 1967. Acetylene as a competitive inhibitor of N-fixation. *Natl. Acad. Sci. U.S. Proc.* 58:213-216.
- Schou, J. B., D. L. Jeffers, and J. G. Streeter. 1974. Effects of light enrichment on yield of soybeans. *Ohio Agri. Res. Dev. Agron.* 1974-1976.
- Scott, D., D. M. Menalda, and R. W. Brougham. 1968. Spectral analysis of radiation transmitted and reflected by different vegetations. *N. Z. J. Bot.* 427-449.
- Silisbury, J. H. 1970. Leaf growth in pasture grasses. *Trop. Grassld.* 4:17-35.
- Silver, W. S. and T. Mague. 1970. Assessment of nitrogen fixation in terrestrial environments in field conditions. *Nature.* 227:378-379.
- Sinclair, A. G. 1973. Non-destructive acetylene reduction assay of nitrogen fixation applied to white clover plants growing in soil. *N. Z. J. Agri. Res.* 16:263-270.
- Singh, M. W., L. Ogren, and J. M. Widholm. 1974. Photosynthetic characteristics of several C₃ and C₄ plant species grown under different light intensities. *Crop Sci.* 14:563-566.
- Sistachs, E. 1970. Effect of N fertilization and inoculation on yield and N content of black beans (*Phaseolus vulgaris*). *Rev. Cubana Cienc. Agri.* 4:227-230.
- Sivakumar, M. V. K., H. M. Taylor, and R. H. Shaw. 1977. Top and root relations of field-grown soybeans. *Agron. J.* 69:470-473.

- Sloger, C. 1969. Symbiotic effectiveness and N_2 fixation in nodulated soybean. *Plant Physiol.* 44:1666-1668.
- Sloger, C., D. Bezdicek, R. Milberg and N. Boonkerd. 1975. Seasonal and diurnal variations in $N_2(C_2H_2)$ -fixing activity in field soybeans. pp 271-284. *In* W. D. P. Stewart (ed.). Nitrogen fixation by free-living micro-organisms.
- Souto, S. M. and J. Döbereiner. 1970. (Effects of soil temperature on N-fixation by *Stylosanthes gracilis* and *Pueraria javanica*.) *Pesq. Agropec. Brasil.* 5:365-371.
- Sprent, M. 1971. The effect of water stress on N-fixing root nodules. I. Effects on the physiology of detached soybean nodules. *New Phytol.* 70:9-17.
- Sprent, J. I. 1973. Growth and nitrogen fixation in *Lupinus arboreus* as affected by shading and water supply. *New Phytol.* 27:1005-1022.
- Sprent, J. I. 1976. Nitrogen fixation by legumes subjected to water and light stresses. pp 405-420. *In* P. S. Nutman (ed.). Symbiotic Nitrogen Fixation in Plants. Cambridge Univ. Press.
- Sprent, J. I. and A. M. Bradford. 1977. Nitrogen fixation in field beans (*Vicia faba*) as affected by population density, shading and its relationship with soil moisture. *J. Agri. Sci. Camb.* 88:303-310.
- Stern, W. R. 1962. Light measurements in pastures. *Herb. Abstr.* 32:91-96.
- Stewart, W. D. P. 1966. Nitrogen fixation in plants. The Athlone Press, London.
- Stewart, W. D. P., G. P. Fitzgerald, and R. H. Burris. 1967. *In* studies in N_2 fixation using the acetylene-reduction technique. *Natl. Acad. Sci. U. S. Proc.* 58:2071-2078.
- Straley, C. S. and C. S. Cooper. 1972. Effect of shading mature leaves of alfalfa and sainfoin plants on specific leaf weight of leaves formed in sunlight. *Crop Sci.* 12:703-704.
- Straley, C. S., C. S. Cooper, and A. E. Carlton. 1972. Environmental influence on specific leaf weight and its in sainfoin (*Onobrychis viciaefolia* Scop.). *Crop Sci.* 12:474-475.
- Tamimi, Y. N., L. B. Sherrod, S. M. Ishizaki, and T. Izuno. 1968. The effect of levels of nitrogen, phosphorous and potassium fertilization upon beef production on kikuyugrass. *Hawaii Agr. Exp. Sta. Tech. Bull.* No. 76.

- Tarila, A. G. I., D. P. Ormrod, and N. O. Adedipe. 1977. Effects of phosphorous and light intensity on growth and development of the cowpea (*Vigna unguiculata* L.). *Ann. Bot.* 41:75-83.
- Thaine, R., S.L. Ovenden, and J. S. Turner. 1959. Translocation of labelled assimilates in the soybean. *Austr. J. Biol. Sci.* 12:349-372.
- Virtanen, A. I., T. Moisio, and R. N. Burris. 1955. Fixation of nitrogen by nodules excised from illuminated and darkened pea plants. *Acta. Chem. Scan.* 9:184-186.
- Watson, G. A. 1957. Nitrogen fixation by *Centrosema pubescens*. *J. Rubber Res. Inst. Malaya.* 15:168-176.
- Watson, G. A. 1963. Cover plants in Malayan rubber plantations. *World crops.* 15:48-52.
- Weber, C. R. 1966. Nodulating and non-nodulating soybean isolines. II. Response to applied nitrogen and modified soil conditions. *Agron. J.* 58:46-49.
- Weber, D. F., B. E. Caldwell, C. Sloger, and H. G. Vest. 1971. Some USDA studies on the soybean-*Rhizobium* symbiosis. *Plant Soil. Spec. Vol.* pp 293-304.
- Vincente-Chandler, J., F. Abruna, R. Caro-Costas, J. Figarella, S. Silva, and R. W. Pearson. 1974. Intensive grassland management in the humid tropics of Puerto Rico. *Bull.* 233. Univ. Puerto Rico, Mayaguez Campus, Rio Piedras, Puerto Rico. 163 p.
- Whiteman, P. C. 1970. Seasonal changes in growth and nodulation of perennial tropical pasture legumes in the field. II. Effects of controlled defoliation levels on nodulation of *Desmodium intortum* and *Phaseolus atropurpureus*. *Austr. J. Agri. Res.* 21:207-214.
- Whiteman, P. C. and A. Lulham. 1970. Seasonal changes in growth and nodulation of perennial tropical pasture legumes in the field I. The influence of planting date and grazing and cutting on *Desmodium incinatum* and *Phaseolus atropurpureus*. *Austr. J. Agri. Res.* 21:195-206.
- Whitney, A. S., Y. Kanehiro, and G. D. Sherman. 1967. Nitrogen relationships of three tropical forage legumes in pure stands and in grass mixtures. *Agron. J.* 59:47-50.
- Whitney, A. S. and R. E. Green. 1969. Legume contributions to yields and compositions of *Desmodium* spp.- pangolagrass mixtures. *Agron. J.* 61:741-746.

- Whitney, A. S. 1970. Effects of harvesting interval, height of cut, and nitrogen fertilization on the performance of *Desmodium intortum* mixtures in Hawaii. Proc. 11th Int. Grassld. Cong: pp 631-636.
- Whitney, A. S. 1974. Growth of kikuyugrass (*Pennisetum clandestinum*) under clipping. I. Effects of nitrogen fertilization, cutting interval, and season on yields and forage characteristics. Agron. J. 66:281-287.
- Whitney, A. S. 1975. Symbiotic and non-symbiotic N-fixation. Hawaii Agr. Exp. Sta. (In press).
- Williams, W. A., R. S. Loomis, and C. R. Hepley. 1965. Vegetative growth of corn as affected by population density. I. Productivity in relation to interception of solar radiation. Crop Sci. 5:211-215.
- Woledge, J. 1971. The effect of light intensity during growth on the subsequent rate of photosynthesis of leaves of tall fescue (*Festuca arundinacea* Schreb.). Ann. Bot. 35:311-322.
- Wolf, D. D. and R. E. Blaser. 1972. Growth rate and physiology of alfalfa and influenced by canopy and light. Crop Sci. 12:23-26.
- Younge, D. R. and J. C. Ripperton. 1960. Nitrogen fertilization of pasture and forage grasses in Hawaii. Hawaii Agr. Exp. Sta. Bull. No. 124.
- Younge, O. R. and D. L. Plucknett. 1966. Quenching the high phosphorous fixation of Hawaiian latosols. Proc. Soil Sci. Soc. Am. 30:653-655.
- Younge, O. R., D. L. Plucknett, and P. P. Rotar. 1964. Culture and yield performance of *Desmodium intortum* and *D. canum* in Hawaii. Hawaii Agri. Expt. Sta. Bull. No. 59.
- Yoshida, S. 1973. The influence of shading on nodulation and nitrogen fixation of soybean. Proc. Crop. Sci. Soc. Japan. 42:135-136.
- Yoshida, T. and R. R. Ancajas. 1973. The fixation of atmospheric nitrogen in the rice rhizosphere. Soil Biol. Biochem. 5:153-156.
- Yoshihara, T. and P. C. Ekern. 1977. Solar radiation measurements in Hawaii. Hawaii Nat. Energy Inst. Univ. of Hawaii. 43 p.