

## SUBTROPICAL GRASS GROWTH

### 1. Relationship Between Carbohydrate Accumulation and Leaf Area in Growth

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#### SUMMARY

Green panic and buffel grass were cut at 5 cm height once or eight times per annum.

Under the normal moisture and nutritional stresses of the Gayndah (south-eastern Queensland) pastoral environment, no treatment differences in the summation of shoot growth occurred. Green panic produced more stem above 5 cm than buffel grass, and substantially less root material. Frequent defoliation reduced fluctuations in shoot growth rate, enhanced leaf growth and tillering and reduced stem, inflorescence and root growth.

Non-structural carbohydrate ("TAC") accumulated in the roots during autumn, winter and early summer, and was depleted in the spring. Buffel grass had both higher concentration and amount of TAC than green panic; frequent defoliation reduced amount of TAC.

In a further study with green panic, TAC status (and allied factors) and the leaf area remaining after defoliation were varied independently, to assess the relative importance of these two factors in the control of growth. Under conditions where moisture and nitrogen were non-limiting, residual leaf area was a greater determinant of growth rate. Thus over 20 days the presence of an additional 7.9 sq dm lamina (equivalent to 335 lb shoot dry weight per acre) resulted in increased growth of 23.8 g (equivalent to 2,010 lb/ac); the presence of an additional 0.94 g/drum of TAC in roots and crown, together with an increased root mass of 20 g (equivalent to 1,690 lb/ac) resulted in increased growth of only 5.4 g (equivalent to 445 lb/ac).

Net assimilation rates were varied substantially by treatment, but photosynthetic capacity was a more influential factor in growth. Faster leaf growth was expressed in the high TAC treatments through increased shoot differentiation, and in the high leaf area treatments through an increased rate of expansion of leaves already in existence at the commencement of the growth period.

In a subsidiary comparison, indications were obtained that under conditions of carbohydrate starvation, compounds other than TAC were involved in respiration and shoot synthesis.

In neither experiment were TAC levels simply related to shoot growth after defoliation.

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## I. INTRODUCTION

In the past decade a significant increase has occurred in the scientific knowledge on which the development of very productive pastures in tropical and subtropical regions may be based. By breeding and by plant introduction a number of suitable pasture grasses and legumes adapted to many ecological situations have been brought into commercial practice; successful establishment techniques have been developed; and considerable interest has been directed to the characterization of the nutrient responses of particular species and to the recognition of nutrient deficiencies occurring in the field.

However, less attention has been given to studies in the use of tropical pastures. With the exception of special cases where pastures are grown to stabilize yield of run-off water or to provide soil conditions favourable for subsequent crops, the productivity of pastures is assessed in terms of animal products. Hence the objective becomes not merely that of producing maximum dry-matter yields of pasture, but of securing maximum animal production through the efficient use of a sustained forage supply of optimum nutrient value.

The attainment of this objective rests partly on the understanding of animal responses to the food supply, and partly on the knowledge of pasture reaction, in terms of growth and composition, to variations in defoliation practice. The studies reported in this series of papers were conducted to describe and interpret some growth responses of subtropical grasses to defoliation, with a view to securing bases on which grass growth could be manipulated to provide greater continuity of forage supply, improvement in food quality, and increased dry-matter production.

The conventional (rather than the strict) usage of the term "defoliation", implying removal of plant shoots, has been adopted in these papers.

Defoliation may be categorized in terms of its frequency, its intensity and its timing.

Frequency of plant removal is measured by the time interval between defoliations. In field practice it is varied by the type of grazing method imposed on the pasture—e.g. continuous, rotational, strip or some system of deferred grazing—or by the frequency of cutting for hay, silage, green forage or weed control.

Intensity of defoliation is measured by the proportion of the plant removed and the characteristics and amount of plant material remaining after defoliation. It is commonly varied by the kind and number of animals grazing a unit area of pasture; it might be noted that this could also influence the time interval between successive grazings of individual plants. It is also varied by the height of cut if pasture is taken for conservation, or if pasture is slashed to control weeds or remove excess growth. The removal of plant material through cutting or by strip grazing is obviously less selective than the type of removal usually encountered in grazing

practice; cutting may produce radically different effects on sward structure and growth from those produced by grazing (Jones 1959). The dangers of extrapolation are evident.

Timing of defoliation is considered in relation to the developmental stage of the plant, the tiller population and its age, the carbohydrate status of the plant, and the nature of the environmental conditions at the time of defoliation.

Current conceptual bases for defoliation practice have been reviewed recently by Humphreys (1966c). These may be divided into those primarily concerned with meeting the particular forage requirements of animals and those essentially concerned with the control of pasture growth, flowering and botanical composition. The latter may be considered in terms of non-structural carbohydrate accumulation and maintenance, efficient use of light by the sward (by manipulation of the intercepting leaf surface), environmental modification (with reference to moisture supply, temperature regimen and nutrient status and exploitation), control of the pattern of tillering and of flowering, and the maintenance of desirable species in the sward (e.g. assuring a satisfactory legume/grass balance).

It is clear that the underlying motivation for defoliation practice in subtropical areas requires critical examination, in view of the paucity of detailed studies. Particular attention was, therefore, paid to the role of non-structural carbohydrate accumulation, the function of leaf area in determining growth, and the modifying effects of flowering on growth characteristics. Although the basic objective is the provision of satisfactory nutritional conditions for animals, the studies described were limited to some aspects of plant response.

The difficulty of interpreting defoliation experiments has been increased by the failure of some workers to record time trends in whole plant or aboveground growth, measurements being restricted to the plant yield harvested above defoliation treatment height. Accordingly, destructive harvests were made to provide accounts of both utilized yield and plant growth. These destructive harvests inevitably increased error, since time differences in plant weight were estimated from different plants or swards.

## II. EXPERIMENTAL

### (a) **Experiment 1: Growth, Development and Non-structural Carbohydrate Accumulation of Buffel Grass and Green Panic Under Two Defoliation Frequencies**

#### (i) **Objective**

The aim of this experiment was to measure the seasonal changes in dry weight and non-structural carbohydrate content of the principal plant organs, and the pattern of tillering, flowering and root initiation, of buffel grass and green panic when grown under two defoliation regimens.

**(ii) Treatments and Design**

There were four treatments:

- A. Buffel grass cv. Gayndah (*Cenchrus ciliaris* L.) cut at 5 cm height each late winter.
- B. Buffel grass cv. Gayndah cut at 5 cm height every 8 weeks.
- C. Green panic (*Panicum maximum* var. *trichoglume* (K. Schum.) Eyles) cut at 5 cm height each late winter.
- D. Green panic cut at 5 cm height every 8 weeks.

The two widely contrasting defoliation regimens were chosen to provide one in which maximum carbohydrate accumulation, root growth and winter canopy might be expected and one in which the plants would be subject to stress.

There were four absolute replications and 12 destructive harvests, making a total of 192 plots. A randomized block design was employed with harvest times as main plots and treatments as sub-plots. An additional eight plots were harvested before cutting treatments commenced, to provide further data on species differences.

Table 1 shows the sequence of events.

**TABLE 1**  
HARVEST AND CUTTING DATES IN EXPERIMENT 1

Period No.	Dates	Days	Treatments Cut on Second Date
I	23.ii.58-3.iv.58	39	..
II	3.iv.58-1.v.58	28	B, D
III	1.v.58-29.v.58	28	..
IV	29.v.58-26.vi.58	28	B, D
V	26.vi.58-21.viii.58	56	A, B, C, D
VI	21.viii.58-16.x.58	56	B, D
VII	16.x.58-10.xii.58	55	B, D
VIII	10.xii.58-5.ii.59	57	B, D
IX	5.ii.59-1.iv.59	55	B, D
X	1.iv.59-28.v.59	57	B, D
XI	28.v.59-23.vii.59	56	A, B, C, D
XII	23.vii.59-22.ix.59	61	B, D
XIII	22.ix.59-16.xi.59	55	..

**(iii) Method**

Two hundred oil drums of size 12.5 gal (average radius 18.4 cm, depth 53 cm) were cleaned and painted internally and externally with black bituminous paint. Two holes were punched beneath the rim of the open end of each drum to facilitate lifting.

A trench 60 cm deep, with bottom dimensions 41.5 m x 8.5 m, was excavated in the nursery block at "Brian Pastures" Pasture Research Station, Gayndah. Soil from the 0-23 cm and 23 cm+ horizons was kept in separate

heaps. The soil used in this and subsequent experiments was a shallow chernozem of good fertility, derived from recent basalt. River gravel was placed in the bed of the trench to a depth of 7 cm and well consolidated.

Dual screw plugs in the base of each drum were loosened to provide drainage. It had been found previously that this would permit egress of water but not of roots. River gravel was placed in the bottom of each drum to a depth of *c.* 2.5 cm. The drums were filled with subsoil to a depth of 23 cm and with top-soil to the level of the lip. The drums were then placed in the centre of plots 101 cm x 101 cm (5 lk x 5 lk) laid out in the trench. Subsoil was then filled in between the drums to the appropriate level. After a settling period of 2 months, top-soil was placed about the drums and the soil surface both inside and outside the drums levelled.

On February 17, 1958, seed was sown in each drum in a central ring *c.* 12 cm in diameter and in the plot area surrounding the drum. Satisfactory seedling emergence occurred on February 23 and plants were subsequently thinned to two per drum (= 18.9 plants per sq m or 0.77 plants per sq lk) and to an equivalent density outside the drum. Weeds were also periodically removed.

The experiment was rain grown, with the exceptions that irrigation of 7.6 cm was applied on May 7, 1958, and of 5 cm on September 4, 1959. The equivalent of 3.36 g/sq m N (= *c.* 30 lb/ac N) was applied as a 1.5% urea solution on October 15, 1958; this level of application was repeated on March 3, 1959, as sulphate of ammonia.

On each harvest occasion 16 drums (8 only at harvest 1, April 3, 1958) were removed from the plots by a chain attached to an arm lifter driven by a tractor power-take-off. The plants in the drums were cut at 5 cm height and the plant material divided into roots, green leaf below 5 cm, brown leaf below 5 cm, stem below 5 cm, stem above 5 cm, green leaf above 5 cm, brown leaf above 5 cm, and inflorescence. Leaf sheath was included in the stem fraction. Inflorescences were separated at the node bearing the flag leaf. Roots were severed from stem bases after the soil surrounding the crown of the plant had been washed away, and crown roots were counted. Drums were placed on a stand which inclined the long axis of the drum at a slight angle to the horizontal, the open lip of the drum being higher than the base, and the drum resting above a 10-mesh sieve 60 cm x 60 cm with galvanised iron sides 15 cm deep. The roots were washed free of soil with a fine spray from a conventional garden hose nozzle. The root mass in the drum was supported by hand to some extent, to minimize rupture before the bulk of the soil was removed. Broken pieces of root were picked from the sieve and all roots placed in a small container of water. By a process of agitation, the remaining soil dropped to the bottom of the container, and organic matter and dead material were skimmed from the surface. The weight was expressed on an ash-free basis to eliminate variations due to residual soil contamination.

Dry weight was estimated for each plant fraction for each drum, after holding harvested material at 100°C for 1 hr and at 70°C for 3 days subsequently.

Percentage non-structural carbohydrate, or "total available carbohydrate" (TAC), was determined on the root, stem below 5 cm, stem above 5 cm, leaf and inflorescence fractions. Duplicate determinations only for each treatment were carried out, blocks being bulked in pairs. The method of Weinmann (1947*a*), with the modifications suggested by Lindahl, Davis, and Shepherd (1949) was employed. Briefly, this involves digestion with takadiastase, acid hydrolysis using dilute HCl, neutralization, and the estimation of the total non-structural carbohydrate component as glucose with Fehling's solution. "Clarase," a purified form of takadiastase, was employed.

The number of shoots whose stems were intersected at the 5 cm cutting height (designated "main shoots") was recorded, and, on each of these the number of axillary shoots and their externally visible developmental stage were noted. Thus a quantitative account of shoot density is only available for the portion of the plant above 5 cm. The appearance externally of a leaf blade between the axil of a leaf and the stem to which it was attached was regarded as constituting the presence of a new shoot or tiller.

Soil bulk density was determined from the final 16 drums at harvest 13, on November 16, 1959, using a Jarrett 10-cm diam. soil auger. Soil was dried at 105°C to constant weight; the volume of soil was determined by measuring the average depth of the hole as successive horizons were removed; hole diameter was measured using calipers 1.7 m long with a vernier scale 0.3 m below the terminal axis pin from which could be estimated the distance between the extremities of the calipers.

The appropriate defoliation treatments were also applied throughout to the drums remaining in the plots and to the areas surrounding the drums.

Further detail is reported elsewhere (Humphreys 1965).

The experiment represented an attempt to combine some of the advantages of both pot and field experiments. Drums employed were of sufficient capacity not to restrict root growth unduly, and the use of drums facilitated the recovery of the whole root system and the reduction of soil variation. The drums were placed in such a situation that climatic and defoliation factors would simulate sward conditions encountered in the field. Plants outside the drums grew slightly better than those within the drums, where root restriction could have operated. However, these two groups of plants could not compete for moisture or minerals, and at the density employed interplant competition for light was not regarded as an important factor.

(b) **Experiment 2: Relationships Between Initial Leaf Area and Carbohydrate Status in Regrowth and the Relation of Carbohydrate Status to Regrowth Under Dark or Light Conditions**

(i) **Objective**

This short-term experiment was designed to assess—

- (1) the relative importance of the amount of residual leaf after defoliation and the non-structural carbohydrate status of the crown and roots in determining the rate of regrowth of green panic,
- (2) the relationships between
  - (i) the initial non-structural carbohydrate status of green panic,
  - (ii) growth and survival under dark conditions, and
  - (iii) growth in full light.

(ii) **Treatments and Design**

The treatments were:—

A. Light Series—Plants grown in full daylight.

(a) Harvest 1—day 0

1. Plants of low carbohydrate status, C1, 0.55 g TAC in roots + crown per drum.
2. Plants of medium carbohydrate status, C2, 1.06 g TAC in roots + crown per drum.
3. Plants of high carbohydrate status, C3, 1.49 g TAC in roots + crown per drum.

(b) Harvest 2—day 20

4. Plants with no leaf area at day 0, L0, carbohydrate status C1.
5. Plants with no leaf area at day 0, L0, carbohydrate status C2.
6. Plants with no leaf area at day 0, L0, carbohydrate status C3.
7. Plants with LAI 0.27 at day 0, L1, carbohydrate status C1.
8. Plants with LAI 0.27 at day 0, L1, carbohydrate status C2.
9. Plants with LAI 0.27 at day 0, L1, carbohydrate status C3.
10. Plants with LAI 0.75 at day 0, L2, carbohydrate status C1.
11. Plants with LAI 0.75 at day 0, L2, carbohydrate status C2.
12. Plants with LAI 0.75 at day 0, L2, carbohydrate status C3.

LAI or leaf area index is the ratio of photosynthetic area to the soil surface supporting it.

B. Dark Series—Plants grown under light-proof shades.

13. L0, C1.

14. L0, C2.

15. L0, C3.

The experiment was designed as an incomplete factorial with six absolute replications of the 15 treatments and harvests, arranged in fully randomized blocks.

### (iii) Method

One hundred and twenty drums of 12.5 gal capacity were filled in August 1960 with 30 cm of subsoil and 22 cm of top-soil from the soil type previously described, and stood in the open. The screw plugs in the bottom of each drum were loosened to provide drainage. Green panic seed was sown in a central ring 12 cm in diameter on December 9, 1960, and the emergent plants were thinned on January 6, 1961, to three plants per drum (= 28.4 plants per sq m, based on drum surface area).

Differences in carbohydrate status were induced by varying nitrogen nutrition and defoliation frequency. On January 6, 1961, 2.82 and 11.28 g sulphate of ammonia per drum were applied to the C2 and C1 treatments respectively, using a 2% solution. These quantities were equivalent to 50 and 200 lb N per acre.

The C1 treatments were defoliated on 15 occasions at weekly intervals from January 20 to May 5, 1961, omitting March 10, 1961. The C2 treatments received five defoliations over the same period. The first defoliation was to a height of 5 cm, and plant radius was reduced to a maximum of 13 cm. All subsequent defoliations reduced individual plant crown radius to 3 cm in height and width. The C3 treatment was undefoliated over this period.

On August 28, 1961, 11.28 g sulphate of ammonia per drum was applied, and all treatments were defoliated. Thus prior to the commencement of the growth study period, 1, 6 and 16 defoliations were applied to the C3, C2 and C1 treatments respectively.

It will be appreciated that alterations in carbohydrate status were also associated with variations in root and crown size, and in crown morphology; the application of a high level of nitrogen 3 weeks prior to the commencement of the growth study period was expected to reduce the effects of previous differences in nitrogen nutrition.

Thirty drums were discarded on September 18, 1961 (day 0) to improve uniformity within each carbohydrate treatment and to ensure that each drum contained three viable plants. Plant mortality up to this date was 5% in the C1 treatments and 1% in the C2 treatments.

Differences in initial leaf area were induced on day 0. Plants were plucked, removing the older shoots preferentially to give the estimated LAI required for each treatment. The LAI values quoted are based on drum surface area. A check



on the accuracy of plucking was provided by measuring the leaf area remaining on the harvest 1 drums removed on that day and which were also hand-plucked to the estimated leaf areas required. The standard errors of the means of six samples were 5% of the means for L1 and L2 in each case.

Light-proof boxes painted black were placed over the dark series plants on day 0 following defoliation to L0. These boxes were constructed with three walls which permitted gas exchange beneath the outside and inside walls and above the middle wall, and which prevented light reaching the plants. Edwards (personal communication 1960) has indicated that diurnal temperature amplitude is slightly reduced inside these boxes, but that degree hours were 96% of those recorded in adjacent swards; relative humidity was an average of 2% higher inside the chambers. The shoot "growth" from the dark series plants was removed on days 20, 34, 48, 62, 76 and 83, and all drums in a specific carbohydrate treatment were harvested for root and crown determinations when mean plant mortality in a treatment exceeded 80%.

Natural rainfall was supplemented from January 6 to May 12, 1961, and from August 28, 1961, until the end of the experiment. In the first period, watering was carried out irregularly but sufficiently to maintain good growth; in the second period, after an initial leaching, the total water received was made up on a weekly basis to the value of  $0.8 \times$  F.W.S. evaporation thereafter.

Harvest and measurement procedures were similar to those employed in experiment 1. In the light series, dry weight and TAC content of roots, crown and shoot were determined, and leaf weight, leaf number, shoot number and individual leaf areas were recorded. In the dark series, leaf and census observations were not made.

Leaf area determinations were based on a modification of the method of Williams (1954). The areas of a considerable number of leaf outlines were determined with a planimeter. Outlines were then selected to form a logarithmic series of standards ranging from 1.0 to 56.2 sq cm, the equivalent standard numbers running from 1 to 17.5  $\log_{10}$  leaf area  $\times 10 =$  standard numbers, where leaf area is expressed as sq cm). Standard numbers rose by unity from 1 to 14, and by units of 0.5 from 14 to 17.5. The selected outlines were laid on black cloth under plate glass, and the leaf blades matched with the outlines below. Some compensation had to be made due to small variations in leaf shape, and leaves of area less than 1.0 sq cm were added to form the equivalent area of a larger leaf outline.

This method had the advantage of providing data on leaf size distribution, and was quite rapid. A team comprising two operators separating green lamina from residual plant parts, one classing the leaves and one recording the standard numbers called, could estimate the areas of 4,000–6,000 leaves in an 8-hr day.

A comparison was made between this method and that of blue-printing actual leaves; excellent agreement was recorded. The agreement between three observers using the rating method was also good, the means for any particular observer's estimates varying by not more than 1.5% of the mean of all observers.

The difficulty occasioned by the rapid wilting of leaves after cutting was overcome by harvesting all samples for leaf area determination as close to dawn as possible and placing them in plastic bags in a refrigerator.

Measurements of light intensity at the centre of each drum were made at intervals of 3 days, but these data were discarded as the raised lip of the drum prevented the photometer being placed at crown level.

The following main formulae were used in calculations:—

$$(1) \text{ Absolute growth rate, } C = \frac{W_2 - W_1}{t_2 - t_1}$$

$$(2) \text{ Net assimilation rate, } E = \frac{(W_2 - W_1) (\log_e L_2 - \log_e L_1)}{(t_2 - t_1) (L_2 - L_1)}$$

$$(3) \text{ Mean leaf area, } L = \frac{L_2 - L_1}{\log_e L_2 - \log_e L_1}$$

for a particular period.

(4) The leaf weight ratio,  $\frac{LW}{W}$ , and the leaf area leaf weight ratio  $\frac{La}{LW}$  were calculated directly on particular harvest dates.

$$(5) \text{ Leaf area growth rate} = \frac{L_2 - L_1}{t_2 - t_1}$$

$$(6) \text{ Relative leaf area growth rate} = \frac{\log_e L_2 - \log_e L_1}{t_2 - t_1}$$

where  $W_2$  and  $W_1$  are plant weights at successive harvests

where  $L_2$  and  $L_1$  are leaf areas at successive harvests

where  $t_2$  and  $t_1$  are days of successive harvests

The  $F$  and  $t$  tests applied to the analysis of variance were the principal statistical techniques employed. The bulk of the statistical computation was carried out by the C.E. 225 electronic computer at the University of Queensland, using programmes prepared by Mr. P. B. McGovern.

### III. RESULTS

#### (a) Experiment 1: Growth, Development and Non-structural Carbohydrate Accumulation of Buffel Grass and Green Panic Under Two Defoliation Frequencies

##### (i) Dry-weight Changes

(1) *Whole plant.*—The dry weights of the whole plant and its organs are shown for each harvest both before and after defoliation in Figure 1, and more detailed data are available elsewhere (Humphreys 1965). Very wide fluctuations in whole plant growth rate are evident. Rapid growth occurred in both species until May 1958, when the first defoliation was applied to the frequently cut series. Good growth responses to the abnormally heavy June rains were recorded, but subsequent frosting sharply reduced growth in period V (June 26 to August 21, 1958). Intermittently dry conditions caused slow growth in period VI, and

moderate growth rates (0.17–0.27 g/plant/day) were measured in period VII. The first highly significant effect of treatment was recorded under the favourable conditions of period VIII (December 12, 1958, to February 5, 1959), when the treatments cut only in late winter gave average growth 0.67 g/plant/day (= 113 lb/ac/day) compared with 0.37 g/plant/day in the frequently cut treatments. In period IX a significant collapse of green panic growth rate was recorded. Low or negative growth rates then occurred through the autumn, winter and early spring. In the final period XIII (September 22 to November 16, 1959) buffel grass outyielded green panic.

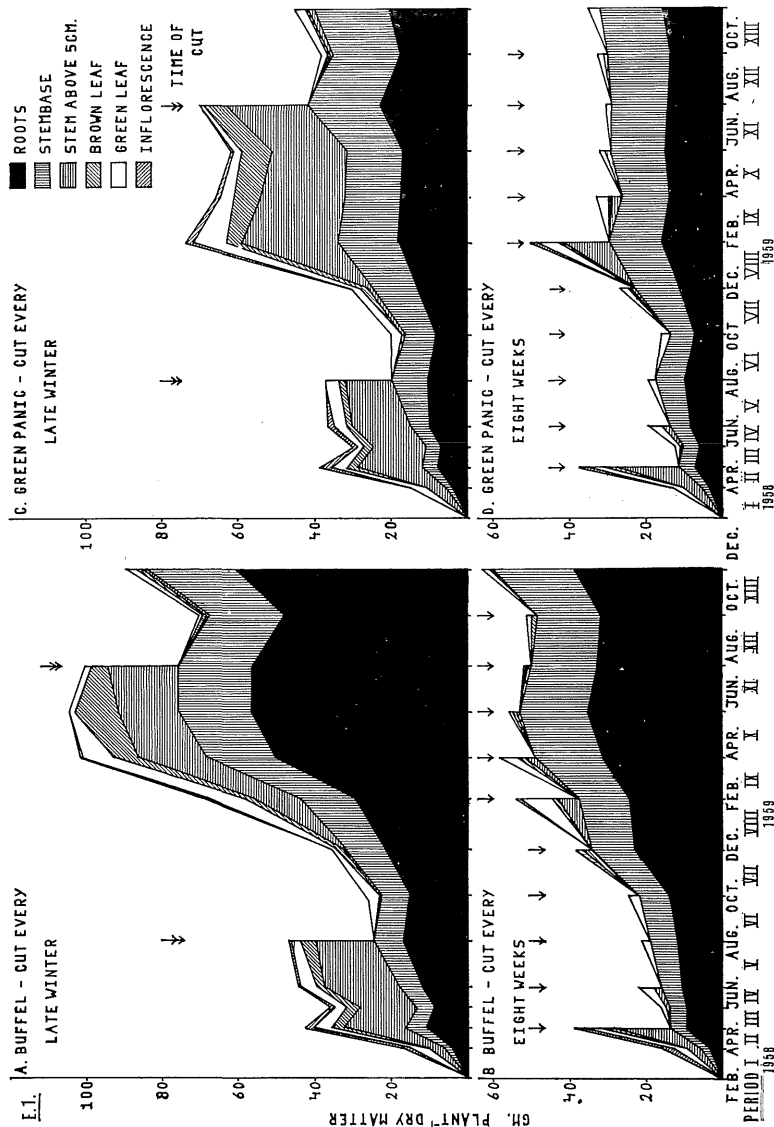


Fig. 1.—Experiment 1. Dry matter present in the various plant organs of buffel grass and of green panic grown under two cutting frequencies.

TABLE 2

EXPERIMENT 1: EFFECT OF DEFOLIATION FREQUENCY AND SPECIES ON THE CUMULATIVE POSITIVE CHANGES IN DRY WEIGHT (G/PLANT)

Plant Fraction	Buffel Grass		Green Panic		Buffel Grass (AB)	Green Panic (CD)	Infrequent (AC)	Frequent (BD)	L.S.D.			
	Infrequent (A)	Frequent (B)	Infrequent (C)	Frequent (D)					Main		Single	
									5%	1%	5%	1%
Roots .. ..	66.60*	40.59	27.72	21.59	53.60**	24.66	47.16**	31.09	9.93	14.26	14.04	20.17
Stem below 5 cm ..	21.86	23.43	23.30	20.36	22.65	21.83	22.58	21.89	N.S.	N.S.	N.S.	N.S.
Stem above 5 cm ..	25.53	13.09	33.72	19.09	19.31**	26.40	29.63**	16.09	4.18	6.00	5.91	8.49
Green leaf .. ..	14.91	22.61	13.97	23.94	18.76	18.96	14.44**	23.27	1.76	2.53	2.49	3.58
Brown leaf .. ..	14.59**	4.41	9.19	2.24	9.50**	5.71	11.89**	3.33	1.10	1.57	1.55	2.23
Total leaf .. ..	18.96	25.64	17.85	25.92	22.30	21.89	18.41**	25.78	2.00	2.87	2.83	4.06
Inflorescence ..	1.16	0.60	2.15	0.71	0.88	1.43	1.66**	0.66	0.62	0.89	0.88	1.26
Total shoots ..	62.33	58.95	67.21	60.53	60.64	63.87	64.77	59.74	N.S.	N.S.	N.S.	N.S.
Whole plant .. ..	116.01	95.64	90.32	74.39	105.82**	82.35	103.17**	85.01	12.11	17.40	17.13	24.60

L.S.D. = Least significant difference

\* = 5% level of significance

\*\* = 1% level of significance

It is difficult to assess the overall effect of treatment on growth over the whole period of the experiment. The difference between plant weights at successive harvests represents the net balance between growth and decay. Neither factor was measured in an absolute sense. In an experiment such as this, where one defoliation regimen involved a 48-wk spelling interval with consequent periods of negative growth balance, the simple summation of all dry-weight changes without regard to sign does not provide an account of the dry-matter gains occurring during the course of the experiment. The convention of considering the sum of the positive dry-weight changes has therefore been adopted, while recognizing that this index has serious conceptual limitations.

The sums of the positive growth increments from May 1, 1958, to November 16, 1959, are shown in Table 2. The whole plant growth of buffel grass was highly significantly superior to that of green panic, and more material was produced under infrequent defoliation than under frequent defoliation.

(2) *Root*.—Treatment differences in whole plant growth were primarily attributable to the root fraction.

The root weight of buffel grass significantly exceeded that of green panic at harvests 2 to 13. On May 28, 1959, 15 months after germination, the respective values for each species under lenient defoliation were 56.6 and 17.3 g/plant, which was equivalent to 9,530 and 2,920 lb/ac respectively. Striking differences in root growth rate were particularly evident in periods IX, X and XIII. Root morphology also differed. The roots of green panic were whiter, finer, more richly branched and more concentrated in the upper soil horizon than those of buffel grass. Differences in bulk density had also developed at the end of the experiment. Bulk density, which is partly a measure of soil settling, did not differ between treatments in the 0–8 cm and 8–23 cm horizons, but for the 23–50 cm horizon the value in the buffel grass drums of 0.73 g/c.c. was significantly lower than the value of 0.88 g/c.c. recorded in the green panic drums. This effect cannot be attributed simply to differences in root weight.

Root weight was significantly reduced at harvest 4 (June 26, 1958) relative to the undefoliated plants by the imposition of a single defoliation. Significant reductions in root weight due to frequent defoliation were subsequently recorded from harvests 8 to 13. On the other hand, the loss in root weight which occurred in all treatments during period XIII (August 23 to September 22, 1959) was significantly less in the frequently defoliated series, which had a smaller root mass.

The sums of the positive changes in root weight are shown in Table 2. A treatment interaction was recorded, the absolute reduction in root growth consequent upon frequent defoliation being greater in buffel grass than in green panic.

An examination of time trends indicated highest root growth rates during summer and autumn, and a real reduction in root mass during early spring.

(3) *Shoot*.—The sum of the positive changes in shoot weight (weight of aboveground parts) over the whole period of the experiment was not significantly affected by treatment. However, some shifts in time trends were apparent. The main effects are shown in Figure 2.

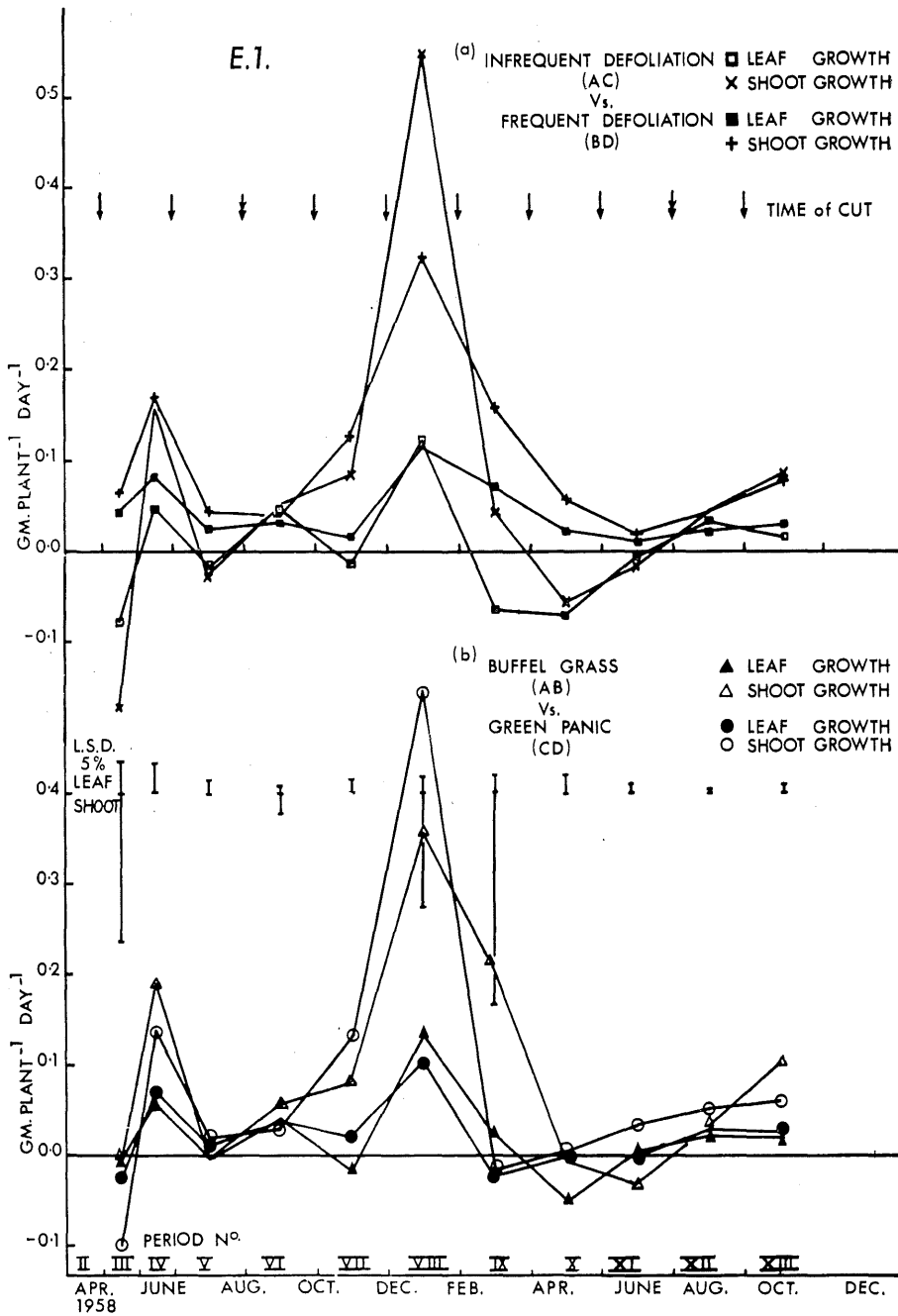


Fig. 2.—Experiment 1. Effects of (a) defoliation and (b) species on the growth of aboveground shoots and of green leaf blade.

The growth of green panic was superior to that of buffel grass under the favourable conditions of period VIII (December 10, 1958, to February 5, 1959); the reverse occurred in the early spring (August 21 to October 16, 1958) and after well advanced flowering (February 5 to April 1, 1959).

A more striking effect was attributable to defoliation frequency. Under frequent harvesting, shoot weight changes were positive for each period; under infrequent defoliation, values were negative in 4 of the 13 periods. Infrequent defoliation gave a substantially higher growth rate in midsummer (December 10, 1958, to February 5, 1959), but frequent defoliation reduced substantially time fluctuations in growth rate.

Although short-term treatment effects on aboveground shoot growth were largely balanced in summation, real treatment differences were recorded in the organs making up the shoots.

(4) *Leaf*.—It is evident from Figure 2 that the green leaf blade production of buffel was slightly superior to that of green panic in midsummer and early autumn; the situation was reversed in the early summer of both years and in the winter.

Frequent defoliation increased green leaf production most substantially; leaf growth of 23.27 g/plant was recorded, compared with 14.44 g/plant in the infrequently cut series. The effect was significant for all periods except VIII (the favourable growth period December 10, 1958, to February 5, 1959) and the periods VI and XII immediately after the defoliation of the infrequently cut series. The latter effect occurred despite a more favourable leaf status in the frequently cut plants at the beginning of the growth period. Frequent defoliation had stimulated basal branching, increasing the leaf remaining after cutting at 5 cm. The data are summarized in Table 3.

TABLE 3

EXPERIMENT 1: EFFECT OF CUTTING TREATMENT AND  
RESIDUAL LEAF WEIGHT ON LEAF GROWTH

Period	Residual Green Leaf After Defoliation (g/plant)	Green Leaf Growth (g/plant/day)
VI: 21.viii.58–16.x.58		
Infrequent defoliation ..	0.07	0.048
Frequent defoliation ..	0.53	0.033
XII: 23.vii.59–22.ix.59		
Infrequent defoliation ..	0.00	0.032
Frequent defoliation ..	0.27	0.021

Some significant interactions between species and defoliation effects occurred for particular periods, but consistent trends were absent.

The amount of senescent, brown leaf blade produced and remaining attached to the plant was greater in the infrequently cut series, and more pronounced in buffel grass than in green panic.

The low proportion of leaf blade to whole plant present at any time is illustrated in Figure 1. Variations in species and defoliation regimen altered substantially the ratio of leaf growth to whole plant growth, as shown in Table 4.

TABLE 4

EXPERIMENT 1: EFFECT OF SPECIES AND DEFOLIATION ON THE RATIO OF LEAF GROWTH TO WHOLE PLANT GROWTH, PERIODS III-XIII

—	Infrequent Defoliation	Frequent Defoliation	$\bar{x}$
Buffel grass .. ..	0.163	0.268	0.211
Green panic .. ..	0.198	0.348	0.266
$\bar{X}$ .. ..	0.178	0.303	..

(5) *Stem*.—No significant overall treatment effect was recorded for the summation of stem growth below 5 cm (Table 2) for the periods III-XIII. However, the amount present at particular harvests, which takes into account the early growth periods I and II, showed a significant advantage of buffel grass over green panic.

On the other hand, the production of stems above 5 cm was superior in green panic; this advantage derived particularly from superior green panic stem growth rates in the favourable growth period VIII (December 10, 1958, to February 5, 1959), when the bulk of upper stem production occurred.

Apart from a reduction in Period VIII, frequent defoliation was not detrimental to growth of stem below 5 cm. The production of stem above 5 cm was seriously reduced by frequent defoliation, except in the winters of 1958 and 1959.

It might be noted that reduction in weight of stem below 5 cm occurred in some treatments in both years in the early spring.

(6) *Inflorescence*.—Buffel grass flowered in advance of green panic, and produced a greater inflorescence weight by harvest 1 (April 3, 1958). Thereafter green panic appeared to produce more flowering parts, but this trend just failed to reach significance.

Frequent defoliation depressed inflorescence yield throughout.

## (ii) Carbohydrate Status

(i) *Percentage TAC*.—The percentage non-structural carbohydrate of the various plant fractions is shown in Figure 3.



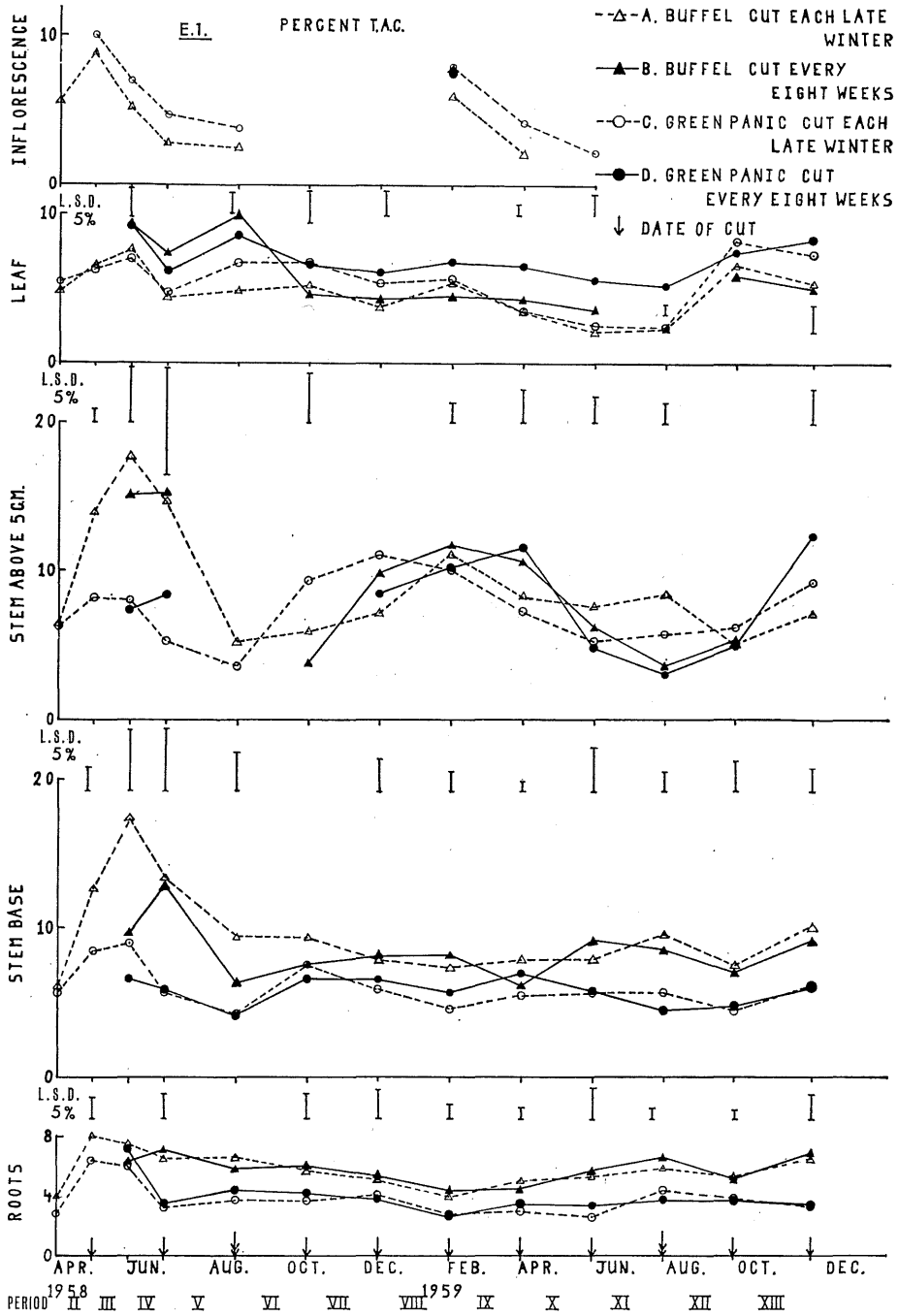


Fig. 3.—Experiment 1. Percentage non-structural carbohydrate (TAC) in the various plant organs of buffel grass and green panic grown under two cutting frequencies.

Percentage TAC of roots reached its highest value at harvest 2 (May 1, 1958), and fell steadily until harvest 8 (February 5, 1959), which occurred near the peak of inflorescence production. Values thereafter rose until the end of winter (harvest II, August 23, 1959), and then declined. The range of values was from 2.5 to 8.0. Values for buffel grass were consistently superior to those for green panic. There was no effect of defoliation regimen; however, it should be emphasized that almost all values for the frequently cut series represent carbohydrate content immediately prior to and 8 weeks subsequent to cutting at 5 cm. A fall in percentage TAC immediately after defoliation would be expected.

The time trends for stem below 5 cm were similar to those for roots, except that a depression of values occurred at harvest 5 (August 21, 1958). Values ranged from 13.4 to 4.1. Consistently higher percentages were recorded in buffel grass than in green panic. Frequent defoliation did not depress the percentages recorded, except at harvest 3 (May 29, 1958, 4 weeks after cutting), harvest 9 (April 1, 1959, for buffel grass only), and harvest 11 (July 23, 1959).

TAC percentage in the stem above 5 cm increased to a peak at harvest 3 (May 29, 1958), fell until the end of the winter, and rose again until harvest 8 or 9 (February 5 or April 1, 1959). The pattern of winter decline and spring increase was then repeated. Percentage TAC was significantly higher in buffel grass than in green panic for most harvest occasions; significant reversals occurred in the spring (October 10, 1958, and November 16, 1959). There was no consistent effect attributable to defoliation regimen.

TAC percentage in leaf was usually higher in green panic; this effect reached significance in 7 out of 12 harvests. Frequent defoliation also increased values significantly on 5 occasions.

The values for the inflorescence fraction were higher in green panic than in buffel grass.

(2) *Amount of TAC.*—The amounts of TAC present in the various organs are shown in Figure 4. Attention is directed to the root and stem below 5 cm fractions.

The generalized picture is one in which TAC accumulated in the roots during the autumn, winter and early summer, and was depleted in the spring. In the first year depletion also occurred in period III, (May 1 to May 29, 1958). Buffel grass had more TAC present in the roots at all harvests than did green panic, and differences in rate of TAC accumulation were apparent at most harvest periods. Differences in root weight, and not percentage TAC, caused gross reductions in amount of TAC present under the frequent defoliation regimen. The effect was not significant until harvest 9 (April 1, 1959), but was consistently present thereafter. On the other hand, the absolute loss of TAC in the spring of both years was significantly less in the frequently cut series.

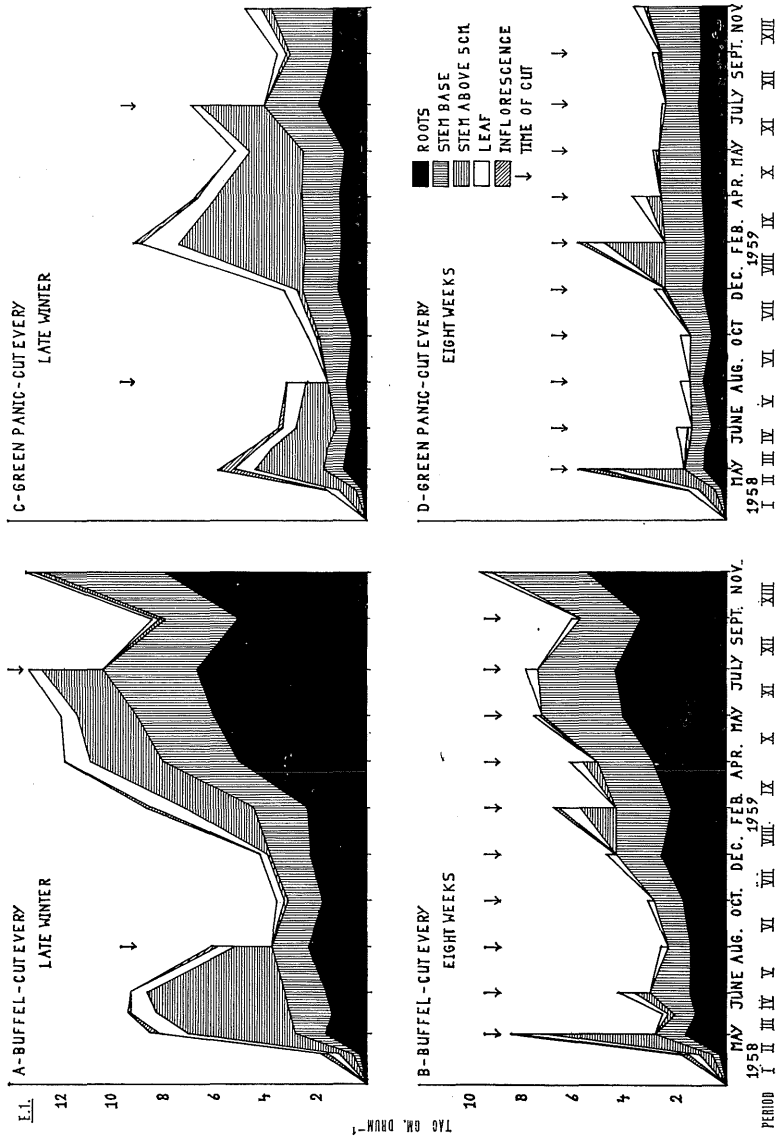


Fig. 4.—Experiment 1. Amount of non-structural carbohydrate (TAC) in the various plant organs of buffel grass and of green panic grown under two cutting frequencies.

The time trends for TAC accumulation in stem below 5 cm were somewhat similar to those in roots, with the exceptions that losses in the 1958 winter and gains in the 1958 spring were recorded. Buffel grass accumulated considerably more TAC than green panic, but had greater losses in period V (June 26 to August 21, 1958). Frequent defoliation generally reduced TAC accumulation in stem below 5 cm, but losses in the 1958 winter were greater under infrequent defoliation.

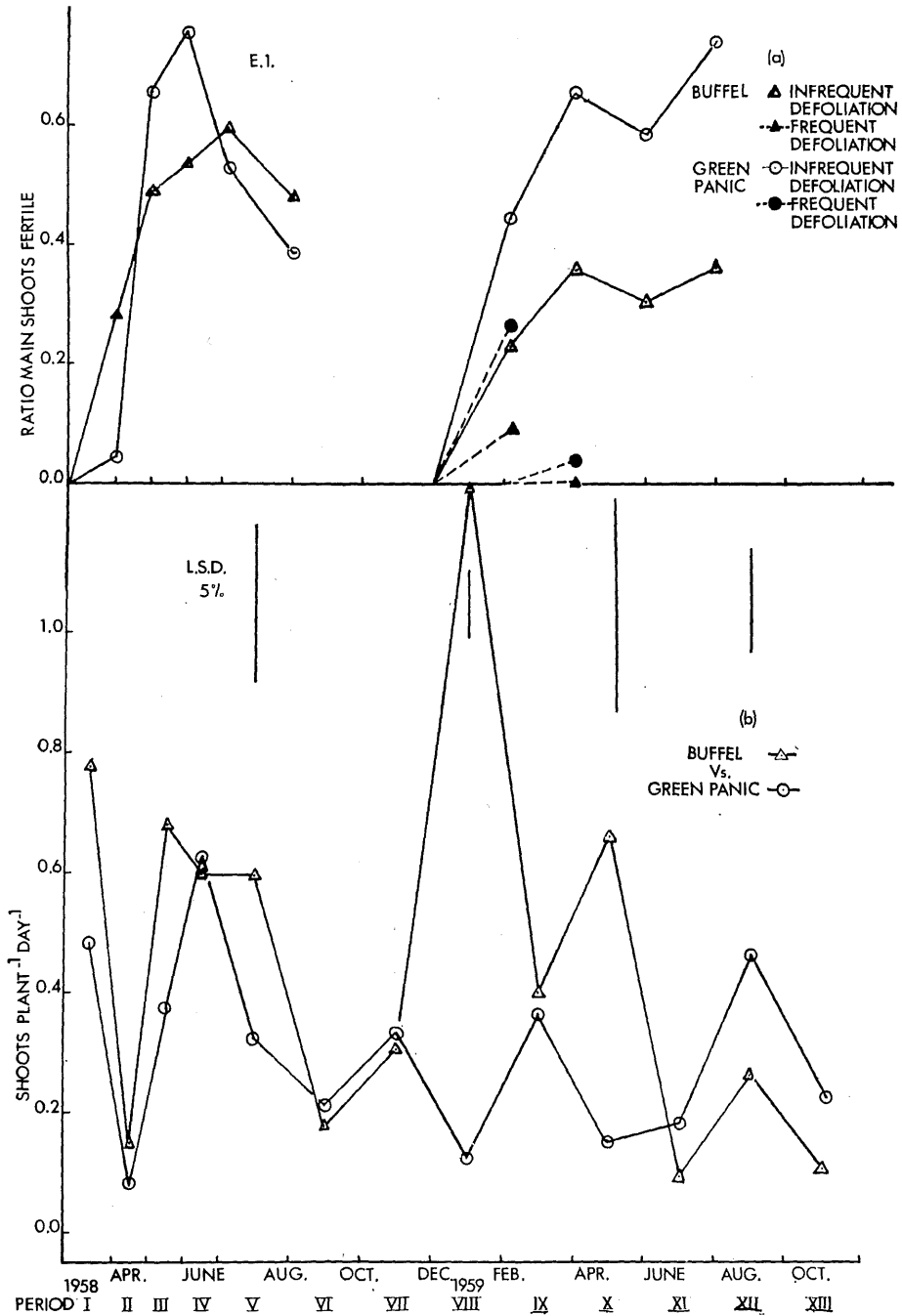


Fig. 5.—Experiment 1. Ratio of fertile main shoots to total main shoots above 5 cm in buffel grass and green panic grown under two cutting frequencies; and rate of shoot appearance above 5 cm in buffel grass and green panic.

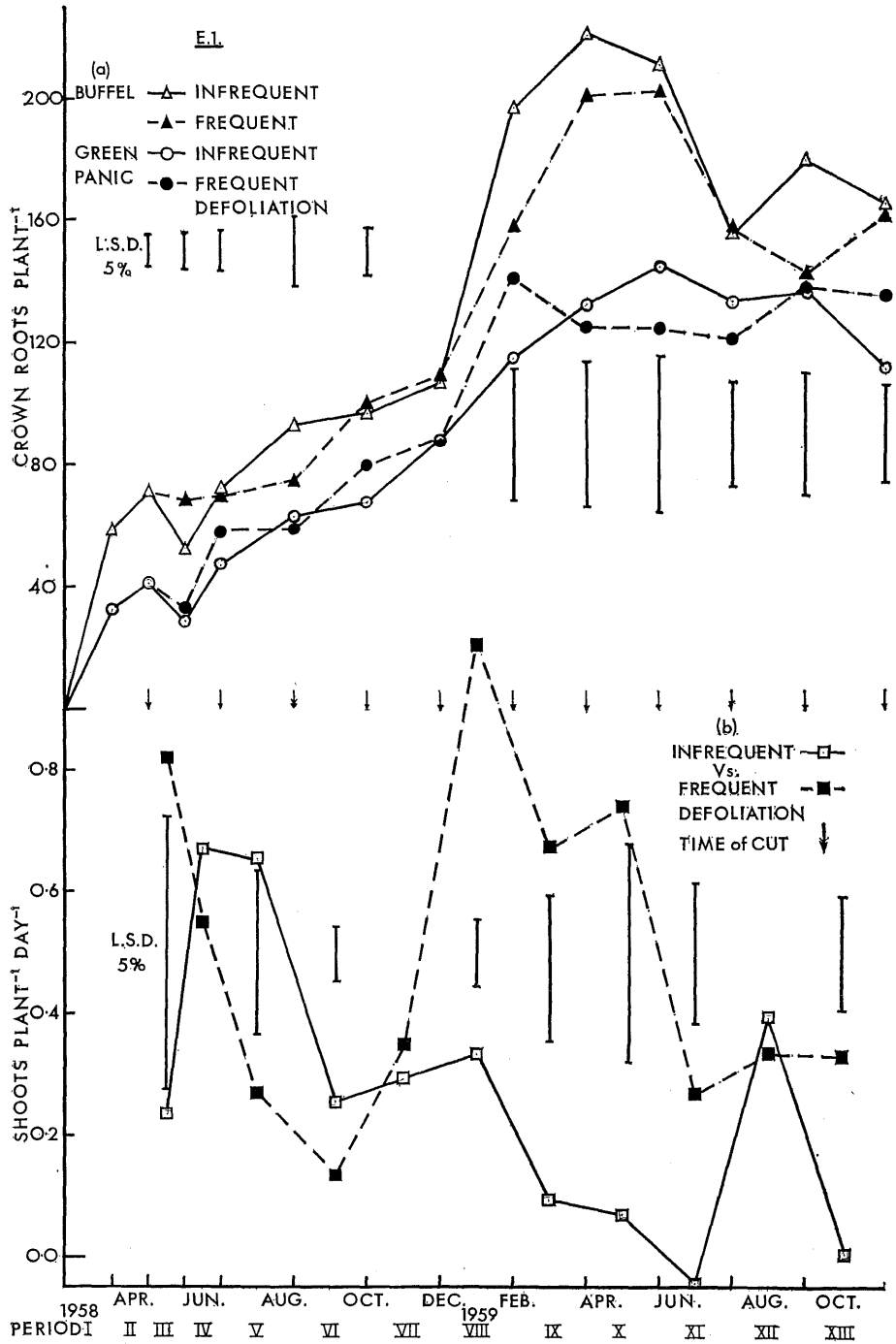


Fig. 6.—Experiment 1. Number of crown roots per plant in buffel grass and green panic grown under two cutting frequencies; and rate of shoot appearance above 5 cm under two cutting frequencies.

The summation of TAC in roots and stem bases strengthens the trends reported above. Buffel grass accumulated more TAC than green panic; frequent defoliation reduced accumulation, this effect being more pronounced in both the roots and stem below 5 cm of buffel grass; and time fluctuations were more pronounced in buffel grass than in green panic.

One aspect of the time trends requires emphasis. Although a fall in concentration of TAC in both roots and stem bases occurred in period VIII (December 10, 1958, to February 5, 1959), a concomitant reduction in amount of TAC did not occur, due to growth of root and stem bases.

### (iii) Census Data

(i) *Rate of shoot appearance.*—Changes in the number of all shoots above 5 cm are shown in Figures 5 and 6.

Buffel grass differentiated more shoots than green panic; this difference was particularly evident in midsummer and autumn, but was reversed in the spring and early summer periods. Although green panic is a taller, more erect plant, the number of secondary shoots produced per main shoot was less than in buffel grass.

Frequent defoliation stimulated shoot appearance; the effect was significant for six harvest periods, but was reversed in the winter and spring of 1958. The contrasting effects of frequent defoliation on both species are seen in Figure 7; some central crown death of green panic under frequent defoliation may be observed.

Rate of shoot appearance was not simply related either to current dry-matter production or to developmental stage. Thus high tillering rates were recorded in buffel grass in periods III, V and X when dry-weight increase was low; low tillering rate occurred in green panic in period VIII (December 10, 1958, to February 5, 1959), when extremely rapid growth occurred. The proportion of fertile main shoots is shown in Figure 5; values reached higher peaks in green panic than in buffel grass and frequent defoliation reduced flowering. A substantial increase in the rate of shoot appearance was coincident in buffel grass with full flowering in period VIII, but the length of interval between harvests is too great to establish distinct correlations.

(2) *Shoot size.*—Individual main shoot weight reached a maximum in late summer and autumn. Green panic had bigger shoots than buffel grass; this difference reached significance on 5 harvest occasions. Frequent defoliation significantly reduced shoot size on 8 of 11 sampling dates, and on 5 of these the absolute (and proportional) reduction in shoot size was greater in green panic than in buffel grass.

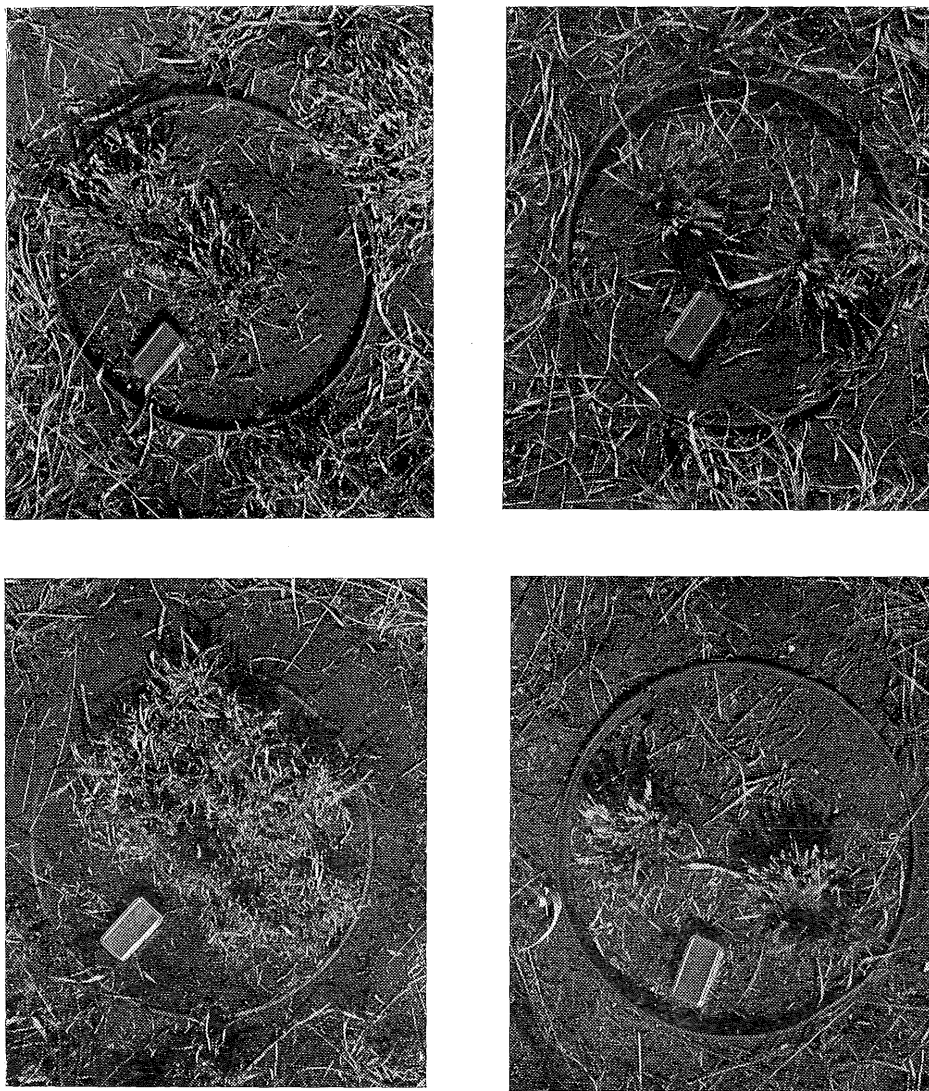


Fig. 7.—Experiment 1. Effects of defoliation treatments on plant crowns (28.viii.59, 5 days after all treatments defoliated). L, buffel grass; R, green panic; upper, cut once per annum; lower, cut every 8 weeks.

Treatment differences in the time trends of dry-weight changes reported in section (a) (i) (3) may now be described further. The superiority of green panic shoot growth in period VIII (December 10, 1958, to February 5, 1958) is seen to be wholly associated with larger increases in individual shoot size; a similar situation accounted for superior buffel growth in periods VI and IX (August 2 to October 16, 1959, and February 5 to April 1, 1959). The

better growth under infrequent defoliation in period VIII was due to increased shoot size, and occurred despite a substantially greater rate of tillering in the frequently defoliated series. On the other hand, the inferior growth of the infrequently defoliated plants in period III (May 1 to May 29, 1958) was due both to a reduced rate of tillering and to a fall in shoot size.

(3) *Crown root number*.—The number of roots arising from the crown recorded at each harvest occasion is shown in Figure 6. Buffel grass produced significantly more roots than green panic, but a sharp decline in root number occurred in the winter of 1959. Frequent defoliation did not depress root number significantly; hence the observed depression in root weight was associated with size of crown root.

The rate of crown root initiation could not be related simply to rate of shoot appearance.

**(b) Experiment 2: Relationships Between Initial Leaf Area and Carbohydrate Status in Regrowth, and the Relation of Carbohydrate Status to Regrowth Under Dark or Light Conditions**

Table 5 summarizes characteristics of the treatments at the commencement of the growth study period on September 18, 1961 (day 0). The treatments are illustrated in Figure 8.

**TABLE 5**  
EXPERIMENT 2: TREATMENT CHARACTERISTICS AT DAY 0

	Carbohydrate Status				
	C1	C2	C3	L.S.D.	
				5%	1%
No. of previous defoliations	16	6	1		
Percentage TAC—					
Roots .. .. .	1.53	2.28	2.75	0.45	0.63
Crown .. .. .	1.63	1.75	2.17	0.38	0.53
Amount TAC (g/drum)—					
Roots .. .. .	0.223	0.507	0.966	0.226	0.322
Crown .. .. .	0.331	0.555	0.527	0.132	0.188
Roots plus crown ..	0.554	1.062	1.493		
Dry weight (g/drum)—					
Roots .. .. .	14.31	21.97	34.35	6.93	9.59
Crown .. .. .	20.34	27.14	24.40	4.03	5.58

INITIAL LEAF AREA

	L0	L1	L2
Initial leaf area (sq dm/drum) ..	0.0	2.89 ± 0.14	7.88 ± 0.37
LAI .. .. .	0.0	0.27	0.75
Shoot weight above crown (g/drum)	0.0	1.75 ± 0.13	3.97 ± 0.24
Leaf no./drum .. .. .	0.0	175 ± 8.8	382 ± 18.0



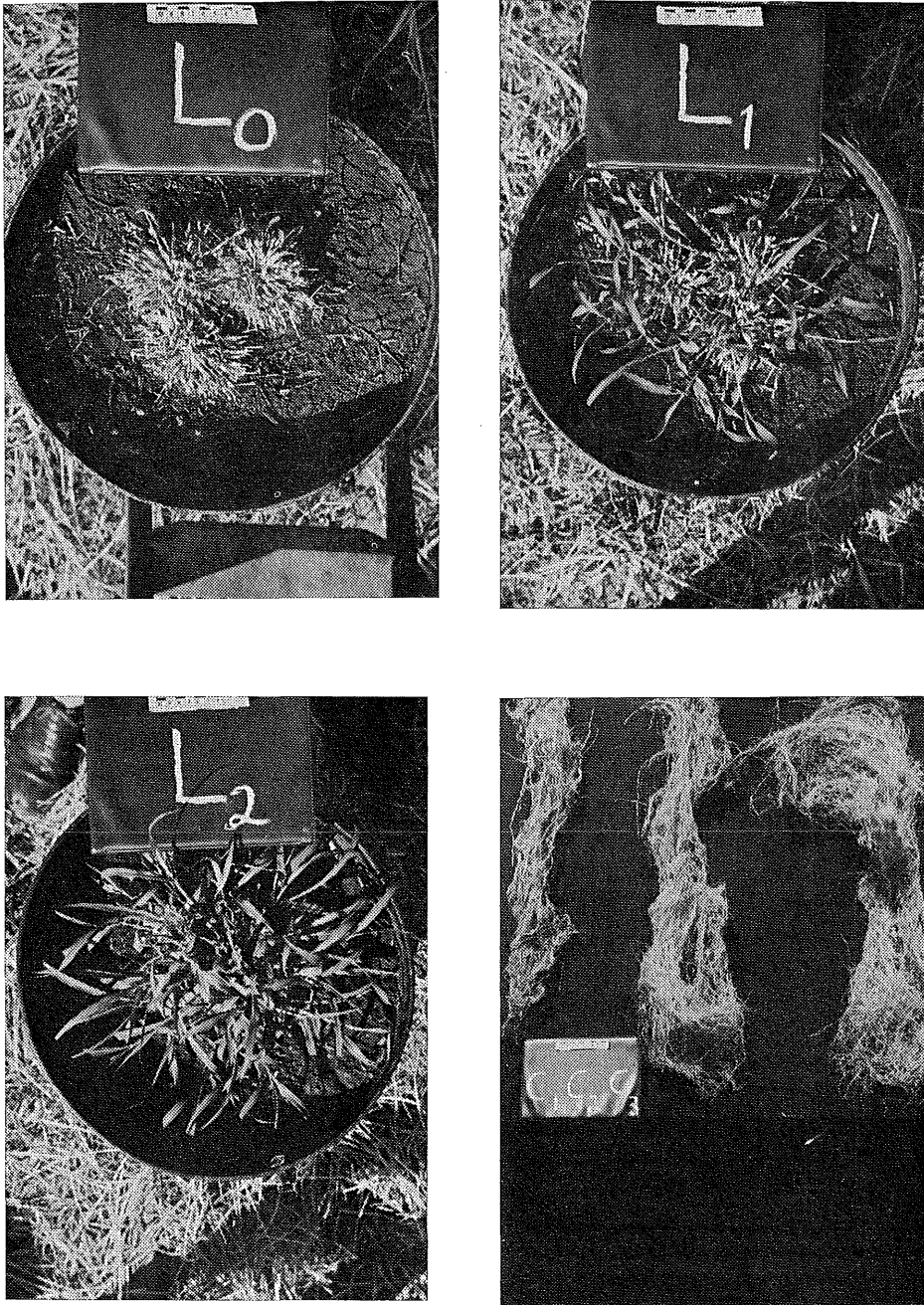


Fig. 8.—Experiment 2. Residual leaf area of treatments at day 1, and root systems of carbohydrate treatments at day 0 (lower right).

(i) **Growth in Full Daylight**

(i) *Dry-weight changes.*—Rapid growth occurred over the period day 0-20 in all treatments, and plant apices remained vegetative. Whole plant growth rates are shown in Table 6.

**TABLE 6**  
EXPERIMENT 2: EFFECT OF PREVIOUS CARBOHYDRATE STATUS AND LEAF AREA ON WHOLE PLANT GROWTH (g/drum/day)

Initial Leaf Area	Carbohydrate Status			$\bar{X}$
	C1	C2	C3	
L0	1.213	1.021	1.653	1.296
L1	1.950	1.769	2.146	1.955
L2	2.715	1.869	2.886	2.490
$\bar{X}$	1.959	1.553	2.228	1.913
	L.S.D.	5%	1%	
	C**,L**	0.280	0.375	
	C x L	0.485	0.649	

It will be seen from Table 6 that the amount of leaf area present at the start of the growth period was a greater determinant of growth rate than the carbohydrate status of the roots and crown. Comparing main effects, the difference between the growth rates of the L0 and L2 treatments was 1.2 g/drum/day. Thus in 20 days the presence of an additional 7.9 sq dm lamina (equivalent to 335 lb shoot dry weight per acre) resulted in increased growth of 23.8 g (equivalent to 2,010 lb/ac). Over the same period, the presence of an additional 0.94 g/TAC/drum in roots and crown, together with an increased root mass of 20.0 g (equivalent to 1,690 lb/ac), resulted in increased growth of only 5.4 g (equivalent to 455 lb/ac).

It will be noted that plants which had been previously heavily defoliated but allowed to develop leaf canopy grew faster than plants leniently treated in the past but which entered the growth period with little leaf canopy (e.g. L2 C1 > L0 C3, L1 C3).

The behaviour of the C2 treatment was aberrant, in that growth was less than in the C1 treatment.

Whereas initial carbohydrate status had little effect on the distribution of growth between roots, crown and shoots, initial leaf area had a profound influence. The percentage of whole plant growth appearing in shoots was 66.2, 51.1 and 47.7 for the L0, L1 and L2 treatments, respectively (L.S.D. 5% = 8.8). However, in absolute terms the growth of each organ followed the trends for whole plant dry-weight changes.

(2) *Growth analysis.*—The absolute growth rate is the product of net assimilation rate (E) and mean leaf area (L). These parameters are plotted for each treatment combination for the period day 0-20 in Figure 9.

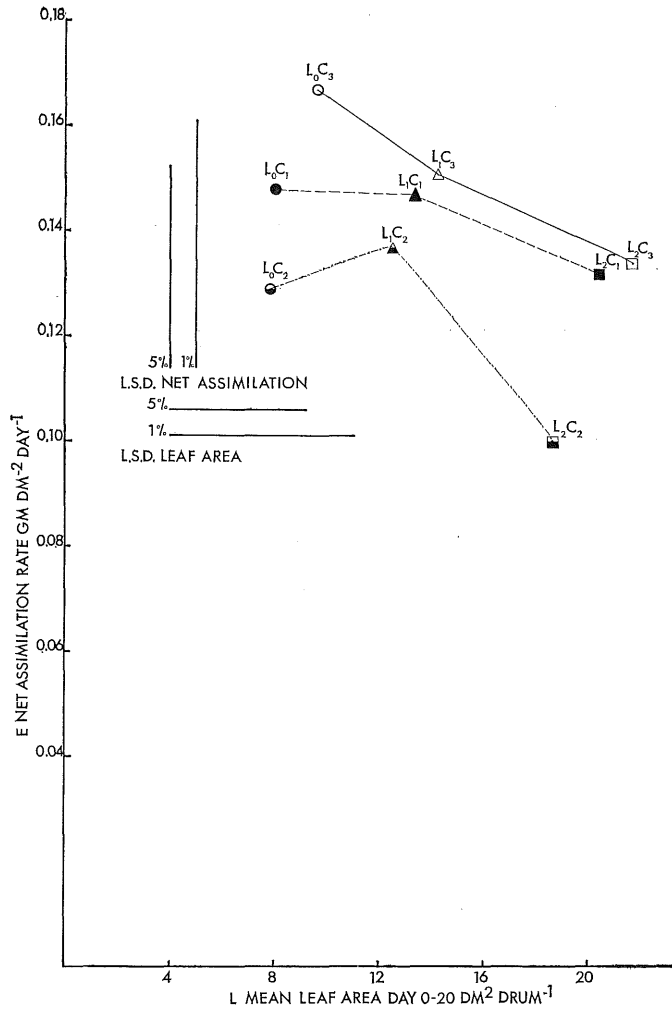


Fig. 9.—Experiment 2. Relationships of net assimilation rate and mean leaf area for treatment combinations of three levels of initial leaf area (L<sub>0</sub>, L<sub>1</sub>, L<sub>2</sub>) and three variations in previous history affecting carbohydrate status (C<sub>1</sub>, C<sub>2</sub>, C<sub>3</sub>).

The values of E generally declined with increasing leaf area but the relationship was not a simple one. They were higher in C<sub>3</sub> than in C<sub>1</sub>, but lower in C<sub>2</sub> than C<sub>1</sub>. E exhibited a substantial variation of from 0.10 to 0.17 g/sq dm/day for treatment means, but this variation was less influential than the variation in L in inducing changes in growth rate. However, the depressed growth of the intermediate carbohydrate treatment (C<sub>2</sub>) was due more to low values of E than of L.

The values of the leaf area:leaf weight ratio for day 20 also declined with increasing leaf area (see Table 7); high values were recorded for treatment C<sub>2</sub>.

TABLE 7

EXPERIMENT 2: EFFECT OF PREVIOUS CARBOHYDRATE STATUS AND LEAF AREA  
ON LEAF  
AREA/LEAF WEIGHT RATIO, DAY 20 (sq dm/g)

Initial Leaf Area	Carbohydrate Status			$\bar{X}$
	C1	C2	C3	
L0	2.91	2.98	2.86	2.92
L1	2.63	2.82	2.75	2.73
L2	2.42	2.63	2.59	2.55
$\bar{X}$	2.66	2.81	2.73	—
	L.S.D.	5%	1%	
	C*,L**	0.12	0.15	
	C x L	0.20	0.26	

On the other hand, differences in leaf area ratio (which ranged from 0.47 to 0.38 sq dm/g for C1 and C3, respectively) did not reach statistical significance.

(3) *Components of leaf area.*—The mean leaf area present over the growth period is obviously greatly under the influence of the amount of leaf present at the commencement of the period. Under the favourable growing conditions of this experiment, the rate of leaf area increase was also strongly influenced by initial leaf area (Table 8). This rate was also highly significantly greater in C3 than in C2 and C1; the value for L2 C2 was abnormally low.

TABLE 8

EXPERIMENT 2: EFFECT OF PREVIOUS CARBOHYDRATE STATUS AND LEAF AREA  
ON LEAF AREA INCREASE, DAY 0-20 (sq dm/drum/day)

Initial Leaf Area	Carbohydrate Status			$\bar{X}$
	C1	C2	C3	
L0	1.35	1.28	1.70	1.44
L1	1.64	1.61	1.87	1.71
L2	1.73	1.44	1.92	1.70
$\bar{X}$	1.57	1.44	1.83	—
	L.S.D.	5%	1%	
	C**,L**	0.15	0.20	
	C x L	0.26	0.35	

Leaf area is the product of leaf number and leaf size. The rates of change in these two parameters were influenced in opposite directions by treatment. The presence of leaves at the start of the growth period strikingly inhibited the rate of appearance of new leaves, which varied from 34.5 to 19.9 leaves/drum/day for treatments L0 and L2, respectively. Superior leaf area increase in L2 and L1 was thus associated with a more rapid increase in leaf size, and occurred despite reduced rates of leaf appearance, as shown in Table 9.

TABLE 9

EXPERIMENT 2: EFFECT OF PREVIOUS CARBOHYDRATE STATUS AND LEAF AREA ON LEAF EXERTION AND LEAF SIZE

(a) Rate of Leaf Exsertion, Day 0-20 (no./drum/day)

Initial Leaf Area	Carbohydrate Status			$\bar{X}$
	C1	C2	C3	
L0	35.7	31.5	36.4	34.5
L1	29.6	25.2	29.5	28.1
L2	21.7	16.8	21.2	19.9
$\bar{X}$	29.0	24.5	29.0	—
	L.S.D.	5%	1%	
	L**,C*	4.17	5.58	
	L x C	7.22	9.66	

(b) Mean Leaf Size, Day 20 (sq cm)

Initial Leaf Area	Carbohydrate Status			$\bar{X}$
	C1	C2	C3	
L0	3.79	4.10	4.70	4.19
L1	4.86	5.22	5.29	5.12
L2	6.15	5.14	5.86	5.71
$\bar{X}$	4.93	4.82	5.28	5.01
	L.S.D.	5%	1%	
	L***	0.58	0.78	
	C x L	1.01	1.35	

Rate of leaf appearance was equal for the C3 and C1 treatments, but was depressed in C2. Differences in mean leaf size between C treatments did not reach significance but some suggestive effects are apparent in the more detailed analysis of leaf size distribution shown in Figure 10. For the L0 series, smaller leaves were more abundant in C1 than C3, and C2 occupied an intermediate position. For the L2 series, the C2 curve was displaced towards smaller leaf size classes. The distributions show double peaks about the leaf size classes 6-7 and 11-12. The peak at the larger size class became increasingly accentuated with increasing initial leaf area, and it is reasonable to assume that this is also associated with an older leaf age distribution. However, this effect is not only a function of a greater number of old leaves being present at day 0, but is also an expression of a reduced rate of leaf appearance, which would decrease the proportion of young, small leaves.

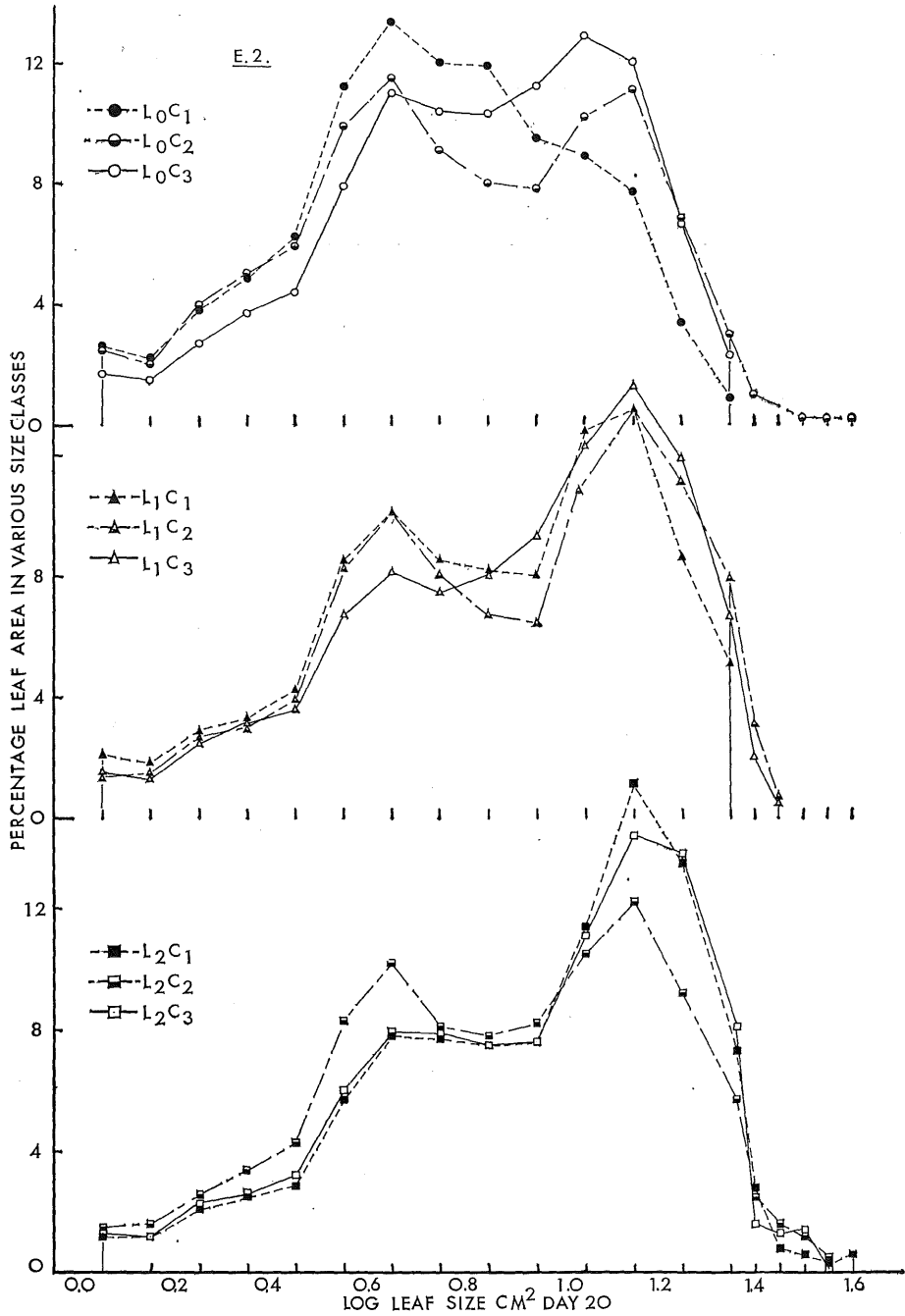


Fig. 10.—Experiment 2. Percentage of leaf area at day 20 contributed by various leaf size classes (calculated as running means of two size classes) for treatment combinations of three levels of initial leaf area (L<sub>0</sub>, L<sub>1</sub>, L<sub>2</sub>) and three variations in previous history affecting carbohydrate status (C<sub>1</sub>, C<sub>2</sub>, C<sub>3</sub>).

The rate of leaf differentiation may be further considered in terms of number of leaves produced per shoot, and number of shoots produced, as shown in Table 10.

**TABLE 10**

EXPERIMENT 2: EFFECT OF PREVIOUS CARBOHYDRATE STATUS AND LEAF AREA ON SHOOT CHARACTERISTICS

(a) Leaf No./Shoot, Day 20

Initial Leaf Area	Carbohydrate Status			$\bar{X}$
	C1	C2	C3	
L0	3.71	3.31	3.18	3.40
L1	3.76	3.22	3.42	3.47
L2	4.12	4.08	3.88	4.03
$\bar{X}$	3.86	3.54	3.49	—
	L.S.D. L**,C	5% 0.35	1% 0.47	

(b) Shoot No./Drum, Day 20

Initial Leaf Area	Carbohydrate Status			$\bar{X}$
	C1	C2	C3	
L0	193.8	190.5	230.0	204.8
L1	205.8	211.3	226.3	214.5
L2	174.8	176.6	208.2	186.6
$\bar{X}$	191.5	192.8	221.5	—
	L.S.D. C**,L*	5% 19.4	1% 25.9	
	C x L	33.6	44.9	

(c) Leaf Area/Shoot, Day 20 (sq dm)

Initial Leaf Area	Carbohydrate Status			$\bar{X}$
	C1	C2	C3	
L0	0.141	0.135	0.147	0.141
L1	0.176	0.168	0.181	0.175
L2	0.254	0.208	0.224	0.228
$\bar{X}$	0.190	0.170	0.184	—
	L.S.D. L*,C	5% 0.019	1% 0.025	
	C x L	0.032	0.043	

The number of leaves produced per shoot by day 20 was positively associated with initial leaf area, and negatively associated with initial carbohydrate status. In the former case this is due to the leaves already present at day 0; rate of leaf appearance was reduced with increasing initial leaf area. In the latter case the net effect of the two opposing factors of leaf number per shoot and leaf size is that leaf area per shoot was equal at the carbohydrate levels C1 and C3.

The greater number of shoots present at day 20 in LO (which had none at day 0) than in L2 indicates that the presence of shoots inhibited the differentiation of other shoots. The C3 treatment produced more shoots than the C1 and C2 treatments. This difference was not evident at day 2, although differences in shoot extension were then apparent.

Thus the main conclusions are that faster leaf growth was expressed in the high carbohydrate treatments through increased shoot differentiation, and in the higher leaf area treatments through an increased rate of expansion of leaves already in existence.

(4) *Carbohydrate status*.—During the period day 0-20, percentage TAC in roots declined in all treatments. This percentage decline was less in the L2 treatments and directly proportional to initial TAC. On the other hand, percentage TAC in crown rose in all treatments, the increase being proportional to the initial leaf area present. The increase was less in C3.

The change in absolute amounts of TAC are shown in Table 11. The amount of TAC present in the roots fell between day 0 and day 20 in all treatments except L1 C1 and L2 C1. The amount of reduction was directly proportional to initial TAC level, and inversely proportional to initial leaf area. There was a significant interaction between the two factors; the reduction in TAC amount due to LO relative to L2 followed the order  $C3 > C1 > C2$ . The amount of TAC in plant crown increased in all treatments. This increase was highest in C3 and lowest in C2.

TABLE 11  
EXPERIMENT 2: EFFECT OF PREVIOUS CARBOHYDRATE STATUS AND LEAF AREA  
ON CHANGE IN TAC, DAY 0-20 (g/drum)  
(a) Roots

Initial Leaf Area	Carbohydrate Status			$\bar{x}$
	C1	C2	C3	
L0	- 0.038	- 0.200	- 0.398	- 0.212
L1	+ 0.017	- 0.141	- 0.341	- 0.155
L2	+ 0.131	- 0.146	- 0.067	- 0.027
$\bar{x}$	+ 0.036	- 0.163	- 0.269	—

L.S.D.	5%	1%
C** <sub>1</sub> L**	0.078	0.104
C x L* means	0.135	0.180
C x L cross differences	0.095	0.127



(b) Crowns

Initial Leaf Area	Carbohydrate Status			$\bar{X}$
	C1	C2	C3	
L0	+ 0.197	+ 0.048	+ 0.445	+ 0.230
L1	+ 0.429	+ 0.228	+ 0.691	+ 0.449
L2	+ 0.785	+ 0.325	+ 0.977	+ 0.695
$\bar{X}$	+ 0.470	+ 0.200	+ 0.704	—

L.S.D.            5%            1%  
 C\*\*,L\*\*        0.101        0.135  
 C x L            0.175        0.234

(c) Roots plus Crowns

Initial Leaf Area	Carbohydrate Status			$\bar{X}$
	C1	C2	C3	
L0	+ 0.159	- 0.153	+ 0.047	+ 0.018
L1	+ 0.445	+ 0.088	+ 0.350	+ 0.294
L2	+ 0.915	+ 0.179	+ 0.909	+ 0.668
$\bar{X}$	+ 0.507	+ 0.038	+ 0.435	—

L.S.D.            5%            1%  
 C\*\*,L\*\*        0.144        0.193  
 C x L\* means 0.249        0.334  
 C x L cross  
           differences 0.176        0.236

The summation of the changes in amount of TAC in roots and crown indicated net increments in all treatments except L0 C2. The individual treatment values for absolute growth rate are plotted against the values for change in amount of TAC in Figure 11. A regression analysis for growth rate on TAC change showed that variations in growth rate could not account for treatment differences in TAC change; significant residual treatment effects on TAC change occurred independently of growth rate, as shown in Table 12.

TABLE 12

EXPERIMENT 2: MEAN TAC ACCUMULATION, ADJUSTED FOR GROWTH RATE,  
FOR TREATMENTS VARYING IN INITIAL LEAF AREA AND CARBOHYDRATE  
STATUS (g/drum)

Initial Leaf Area	Initial Carbohydrate Status			$\bar{X}$
	C1	C2	C3	
L0	0.363	0.108	0.123	0.198
L1	0.435	0.130	0.282	0.282
L2	0.682	0.192	0.625	0.499
$\bar{X}$	0.493	0.143	0.344	—
	L.S.D.	5%	1%	
	L**	0.137	0.183	
	C**	0.167	0.224	
	L x C*	0.240	0.321	

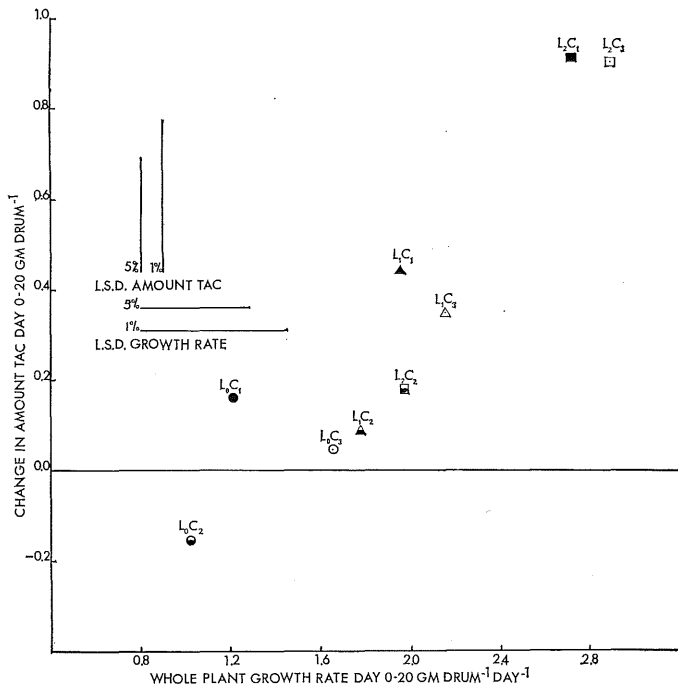


Fig. 11.—Experiment 2. Change in amount of TAC in roots plus crown, and whole plant growth rate for day 0-20 for treatment combinations of three levels of initial leaf area (L0, L1, L2) and three variations in previous history affecting carbohydrate status (C1, C2, C3).

The net increment in TAC, adjusted for growth rate, was highest at L2, and C1>C3>C2. The superiority of the lowest carbohydrate level over the highest carbohydrate level was greater at low initial leaf area than at high initial leaf area.

(ii) "Growth" Under Dark Conditions

Table 13 summarizes the pertinent data from this section of the experiment.

TABLE 13

EXPERIMENT 2: EFFECT OF VARIATIONS IN PREVIOUS HISTORY AFFECTING CARBOHYDRATE STATUS ON CHANGES IN DRY WEIGHT, TAC, AND PLANT MORTALITY UNDER DARK CONDITIONS

	Carbohydrate Status			L.S.D.	
	C1	C2	C3	5%	1%
Percentage loss in weight day 0—final harvest					
Roots .. .. .	54.1	46.6	24.7	10.5	15.0
Crown .. .. .	13.5	23.1	10.9	N.S.	
Roots minus crown .. .. .	40.6	23.3	13.8	9.7	13.8
Shoot growth (g/drum) .. .. .	0.65	2.22	3.88	**	
Ratio, shoot growth/loss in weight, roots plus crown .. .. .	0.07	0.14	0.63 <sup>1</sup>	N.S.	
Percentage TAC, final harvest					
Roots .. .. .	1.02	0.48	0.53	0.22	0.31
Crown .. .. .	1.13	0.85	0.93	N.S.	
Amount TAC, final harvest (g/drum)					
Roots .. .. .	0.068	0.056	0.139	0.040	0.056
Crown .. .. .	0.198	0.177	0.206	N.S.	
Ratio, loss in TAC, roots plus crown/shoot growth .. .. .	0.45	0.40	0.34	N.S.	
Days to > 80% mortality .. .. .	48	83	83	**	

<sup>1</sup>This ratio was calculated as the mean of individual plot ratios. If calculated as the ratio of mean shoot growth/mean loss in weight, the value for C3 is 0.35.

(1) *Dry-weight changes.*—The absolute and proportional losses in weight until death point were significantly greater from roots than from crowns; the percentage loss in weight was inversely proportional to initial carbohydrate status and to root mass.

The amount of shoot "growth" made in the dark followed the same order as the initial carbohydrate status of the plants (see Figure 12). The amount of shoot material translocated varied from 0.65 g/drum in C1 (equivalent to 55 lb/ac) to 3.88 g/drum in C3 (equivalent to 330 lb/ac). C2 was intermediate in yield, in contrast to its behaviour in the light series.

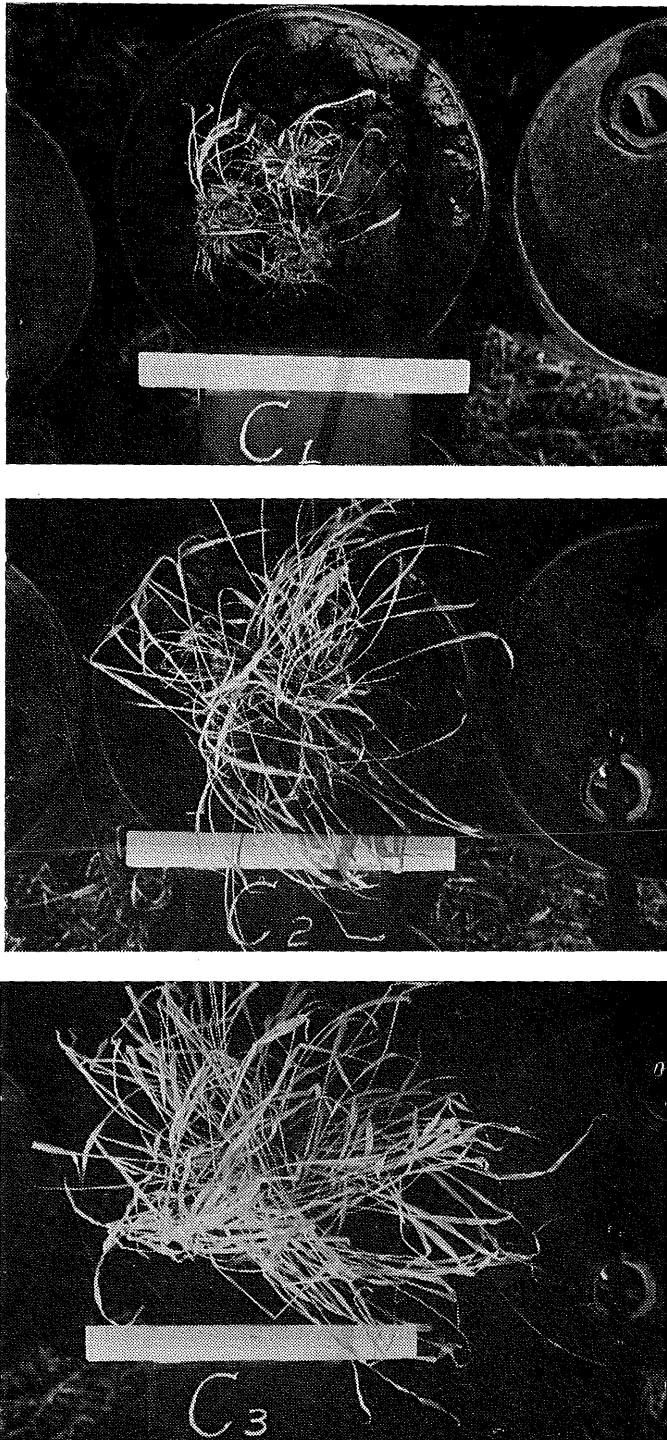


Fig. 12.—Experiment 2. Dark “regrowth” from carbohydrate treatments, day 20.

The efficiency of shoot synthesis in the absence of light, as measured by the ratio of shoot weight to loss of weight in roots and crowns, appeared to be greater at the high carbohydrate level, but this effect did not reach significance.

(2) *Carbohydrate changes*.—Percentage TAC (Table 13) declined to death point, but death occurred at a lower percentage TAC in C2 and C3 than C1. The percentage decline was proportional to initial TAC. The loss in amount of TAC was higher from roots than from crown, and least in the lowest carbohydrate treatment. Neither percentage nor amount of TAC was constant between treatments at death.

The ratio of loss of amount of TAC in roots plus crown to shoot weight produced in the dark varied from 0.45 in C1 to 0.34 in C3; thus loss of TAC could account neither for the weight of material translocated nor for the respiratory losses. The ratio of loss of TAC to loss of weight ranged from 0.03 in C1 to 0.10 in C3; thus translocation and respiration depended more on sources of material other than TAC in C1 than in C3.

(3) *Plant mortality*.—Under dark conditions, the time to reach more than 80% mortality was 46 days in the C1 treatment, and 83 days in both C2 and C3. Thus time to "exhaustion" did not successfully distinguish the C2 and C3 treatments, despite the fact that their initial levels of TAC differed by a factor of c. 1.5.

#### IV. DISCUSSION

##### (a) Treatment Effects on Growth Rhythm and Growth of Plant Organs

The self-regulatory pattern of growth is well demonstrated in experiment 1, where the total shoot dry-weight production of two species of differing growth form, each grown under two widely contrasted defoliation frequencies, did not vary more than 8% from the mean of all four treatments. It is usual for increasing defoliation frequency to reduce shoot yield; this has been recorded for tropical or subtropical grasses by Paterson 1933; Louw 1938; Wilsie, Akamine, and Takahashi 1940; Lander 1942; Lovvorn 1944; Schofield 1944; Anon. 1953, pp. 33-4; Smith 1961; Beaty *et al.* 1963; and Bryan and Sharpe 1965. However, instances have been reported where a very long interval between defoliations has reduced yield (e.g. Burton, Jackson, and Hart 1963; Shaw *et al.* 1965) or where yield has not been very responsive to defoliation treatment (Holt and McDaniel 1963). The lack of an overall favourable response in the plants cut once only per annum compared to those cut every 8 weeks is attributed to the following:—

- (a) The higher respiratory load of plant material present, and the inevitable decay of the material when not utilized, reduced the growth balance.
- (b) Notwithstanding the greater leaf surface developed in midsummer by the infrequently defoliated swards, further expansion and satisfactory assimilatory activity were impeded by the limits imposed by nitrogen and moisture supply.

- (c) Although a higher plant carbohydrate status was induced in the infrequently defoliated swards, the influence of carbohydrate status on growth was less than expected.

On the other hand, very striking effects of defoliation frequency on the seasonal distribution of growth were recorded. Reference has been made to the need for sustained plant growth to meet animal requirements; frequent defoliation substantially reduced time fluctuations in shoot growth rate. Growth increments in this series were positive for all harvest intervals (Figure 2), and the only serious growth depression relative to the infrequently defoliated series was recorded in midsummer, a time of feed surplus. On the two occasions in late winter when both series were defoliated on the same date, the shoot growth advantage of the infrequently cut series was small and non-significant, although a minor advantage in leaf growth was evident. Thus the loss in utilization and reduced feed quality implicit in the infrequent defoliation series was not counterbalanced by superior vigour or persistence. It must be recognized that more pasture was present throughout in this treatment, but this occurred under the extreme circumstance of utilization in late winter only. It is, of course, conceivable that a different choice of defoliation treatments or a longer duration of experimental treatments may have produced different conclusions; it might be recalled (Figure 7) that central crown death was present in frequently defoliated green panic at the end of the experiment.

Under the favourable conditions of experiment 2 and the midsummer conditions (period VIII) of experiment 1, the amount of growth produced was related in a strongly positive fashion to the amount of leaf surface present. In experiment 2 this factor was much more important than the non-structural carbohydrate status of the sward; even the lowest carbohydrate plants which had been close to death point, when allowed to develop some leaf canopy, produced more growth than high carbohydrate plants with a smaller leaf canopy. This suggests that under good growing conditions, management directed to the maintenance of adequate leaf canopy will produce greater yields, that heavily utilized swards of green panic will recover productive capacity rapidly if spelled from use, and that the amount of material grazed off should be determined in the light of the need for supra-minimum canopy, rather than the need to accumulate carbohydrate and grow a large root system. However, it should be noted that competitive factors, e.g. susceptibility to weed invasion, were not studied.

In experiment 2 a real growth response to high carbohydrate status was recorded; for the L0 treatments increases in C3 series of 37% over the C1 series and 63% over the C2 series were measured. No explanation can be offered for the aberrant behaviour of the intermediate C2 series, which yielded less than the low C1 series. It must be recognized that differing non-structural carbohydrate levels were induced by varying previous nitrogen nutrition and defoliation history, which also altered root mass, crown size and structure, and previous developmental history; thus many factors are confounded.

The dark shoot "growth" of the C2 series swards was intermediate between the C1 and C3 swards, as were their root mass and initial TAC concentration. The low growth rate of the C2 swards was expressed principally through a low net assimilation rate; this factor was of greater importance than reduced leaf expansion. It was also associated with high values of leaf area/leaf weight ratio, and there is a possibility that thinner leaves with less depth of chlorophyll bearing cells may be less productive of assimilate. However, Blackman and Wilson (1954) found *E* to be independent of  $L_a/L_w$ , and a more probable explanation is that the slower rate of shoot appearance, resulting in fewer sinks, reduced photosynthesis. Reduced leaf expansion resulted primarily from reduced shoot number appearance, and for the C2 L2 treatment, in smaller leaf size. Nitrogen uptake in the plant crown was also impaired. The following hypotheses might be considered:—

- (a) There may have been a residual response from the previous differential nitrogen fertilizing, which was not masked by the leaching given on August 28, 1961, followed by the addition of the heavy nitrogen dressing applied to all treatments at this time. However, nitrogen uptake was less in C2 than in C3, which had received less nitrogen initially.
- (b) The C2 treatment may have produced more growth from January 20 to May 5, 1961, than the C1 or C3 treatments, thereby inducing a subsequent nutrient deficiency. Other nutrition work with this soil makes this hypothesis unlikely.
- (c) The pattern of defoliation of the C2 plants may have developed elevated apices and a crown with fewer bud sites present in the spring. It was noted on day 2 that of the L0 series, the C2 swards had the fewest expanded shoots. Whatever the explanation of the phenomenon, it should be noted that the treatment order for dry-weight increase did not parallel exactly the initial TAC status.

A study of relevance to this investigation is that of Ward and Blaser (1961), who measured the effects of two levels of carbohydrate status (8 and 2% "reserve carbohydrate") induced by short-term shading, and two residual leaf area treatments (nil and 3.3 sq cm/tiller) on the regrowth of cocksfoot tillers. These authors state that the regrowth of the apex blades was influenced both by carbohydrate status and leaf area; the former predominated until day 25 and the latter was more influential from day 25 to day 35. They suggest that the importance of residual leaf area is greater for plants of low carbohydrate status; however, it would appear from their published data that the response to higher leaf area, in terms of dry-matter production by apex blades and new tillers, and increase in length of apex blades, was greater at the higher carbohydrate treatment than at the lower. Jewiss, Powell, and Woledge (1963) have reported superior growth from cocksfoot swards having higher residual LAI but lower water-soluble carbohydrate content than swards having a previously more lenient defoliation history. The converse result was shown in experiment 1 (Table 3). Jewiss and Powell

(1964) also reported no effect of treatments similar to the above on dry-weight production 4 weeks after defoliation, and a temporary depression of dry-weight production following short-term shading. The relative importance of the leaf area and carbohydrate factors seems to vary widely with experimental conditions.

In both experiments, defoliation radically changed the distribution of dry-weight increase between the various plant organs. The sensitivity of root growth to defoliation, which has been recognized so widely (Troughton 1957), was well demonstrated. Although gross differences in total shoot growth were not induced in experiment 1, root growth varied by a factor of 4. In experiment 2 root growth varied by a factor of 2.4 at the commencement of the growth study period. It is of interest that in experiment 1 differences in root weight were almost wholly accounted for by variation in individual crown root size. Jacques and Edmond (1952) reported that in cocksfoot and perennial ryegrass root number was much reduced by defoliation; Albertson, Riegel, and Launchbaugh (1953) noted that heavy clipping reduced the root number in Kansas short grasses, but that moderate clipping increased root initiation. Baker (1957a) observed that cutting perennial ryegrass increased root number per tiller; however, total root number was reduced. Although no simple relationship between root initiation and tillering was evident in experiment 1, the effect of frequent defoliation in stimulating tillering may have helped to keep the root system in a more juvenile condition and to maintain root numbers.

The growth rate of roots relative to that of shoots did not fall in the first season with the onset of flowering (Figure 7); this has been confirmed in some detail for several buffel grass varieties (Humphreys, unpublished data). This finding is in contrast to that of Troughton (1956, 1960), working with temperate grasses. An implication is that the timing of the first grazing in the establishment year of a tropical grass sward, insofar as this timing is influenced by the degree of rooting, may be determined on the basis of plant size rather than by development stage. Root growth was fastest during summer and autumn. A decline in root mass occurred in the spring; root mass represents the current balance between growth and decay, and rising spring temperatures could be associated with an increased rate of decomposition.

Buffel grass is known as a species having a high proportion of plant weight in the roots and good root growth (Edye *et al.* 1964). Buffel grass whole plant growth significantly exceeded that of green panic in experiment 1 by some 25%; shoot growth was not significantly different. A higher proportion of the root system is located in the deeper soil horizons than is the case with green panic (Humphreys and Cull, unpublished data), and this was reflected in experiment 1 in significantly reduced soil bulk density figures for the 23–50 cm horizon. However, this beneficial structural effect does not necessarily improve following crop yields; at "Brian Pastures" Pasture Research Station, first-year crops of sorghum and of oats were poorer following buffel grass than following green panic or Rhodes grass. It is thought that this may be associated with an increased amount of nutrients immobilized in the root system or required for its decay, and with the more effective moisture exploitation by buffel grass swards.



The weight of plant crown was relatively insensitive to treatment, but the proportion of leaf, stem above 5 cm, and inflorescence was influenced markedly. Green panic produced more stem than buffel grass; no evidence was forthcoming to support the common belief that green panic, with its large prominent leaves, is leafier than buffel grass.

Frequent defoliation significantly improved leaf production and reduced stem and inflorescence growth. It is assumed that this arises mainly from the continual removal of shoots before their development is well advanced; plant material present is thereby always in a more juvenile condition. Apical dominance and the inhibition of axillary shoots by flowering stems is also associated with the more stemmy nature of the infrequently cut plants. A positive relationship of leaf weight percentage to defoliation frequency has been commonly reported (Stapledon 1924; Cashmore 1934; Prine and Burton 1956; Smith 1961; Beaty *et al.* 1963; Burton, Jackson, and Hart 1963; Jones 1963; Begg and Wright 1964); in some studies, yield of leaf was increased by frequent defoliation, as occurred in experiment 1. The relevance of plant age, leafiness and development stage to pasture quality requires further study.

#### (b) Accumulation and Use of Non-structural Carbohydrate

The pattern displayed in experiment 1 of declining percentage non-structural carbohydrate in the roots and plant crown during winter, spring, and early and midsummer, and increasing percentage values from after mid-flowering until the late autumn, is commonly reported in the literature; with minor variations these seasonal and developmental changes are illustrated by McCarty (1938); Weinmann (1940a, 1940b, 1947b, 1961); Weinmann and Goldsmith (1948); McCarty and Price (1942); Mackenzie and Wylam (1957); Couchman (1959); Barnes (1960); Reynolds and Smith (1962); Eastin, Teel, and Langston (1964); and Okazima and Smith (1964). However, there have been few long-term whole plant studies, and some workers have assumed that a low percentage TAC of roots at flowering time indicates a net loss in amount of TAC and a time of vulnerability. In experiment 1 the amount of TAC in the roots and crown was not reduced at the February harvest 8 (Figure 4), since increased root and crown weight compensated for the fall in percentage TAC. Weinmann and Goldsmith (1948) noted that the amount of TAC in the roots of *Cynodon dactylon* rose during the summer months; Barnes (1956) reported a similar trend, and also the converse in a further investigation (Barnes 1960). Depletion of TAC was only evident in the spring in experiment 1.

In the absence of labelled carbon studies, it was not possible to define in detail the movement of TAC between organs in the two experiments reported; the amount of TAC present at any time in any organ represents the current balance between accumulation on the one hand, and, on the other hand, respiration and decay.

The values recorded for non-structural carbohydrate were generally low, but were of the same order as those recorded for summer growing grasses in southern Africa (Weinmann 1944; Weinmann and Reinhold 1946; Barnes 1960). Catchpoole (1965) recorded midsummer harvest values of only 4.6-6.1% water-soluble sugars in the shoots of *Setaria sphacelata*, and 3.0-3.5% in *Chloris gayana*. Buffel grass had a higher percentage TAC in roots, crown, and stem above 5 cm than green panic; the converse applied for the leaf and inflorescence fractions. It might be recalled that despite the fact that the amount of TAC in the roots and crown differed between species by a factor of 3 in the latter part of the experiment, green panic and buffel grass shoot growth rates were similar.

Frequent defoliation had no persistent effect on percentage TAC in roots and crown in experiment 1, as measured 8 weeks after each defoliation; small but consistent differences were recorded, however, in experiment 2, where differences in defoliation frequency were also allied with differences in nitrogen nutrition. In both experiments, differences in amount of TAC were induced more by alterations in root mass. Weinmann (1944) reported an instance where frequent defoliation reduced root mass but increased percentage non-structural carbohydrate.

The changes in TAC amount 20 days after defoliation (Table 11) show an interesting balance between the effects of residual leaf area and of initial TAC concentration and amount. Loss of TAC from the roots was least if initial leaf area was high or if initial TAC was low. Similarly, the increase of TAC in plant crown was greater with high initial photosynthetic capital, but was also greater with higher initial TAC status. When TAC accumulation in roots plus crown was adjusted for growth rate, it was again higher in the high leaf area treatments, but was also higher in the treatments having a low initial TAC concentration, i.e. a tendency to establish equilibrium was shown. The latter effect disappeared if high leaf area was allied with low initial TAC status. Treatments of intermediate carbohydrate status did not fit these trends. It might be noted that Sprague and Sullivan (1950) found that the decrease in water-soluble carbohydrate after defoliation was proportional to the initial concentration. It is difficult to interpret these results in the absence of information concerning photosynthetic rate, transport from leaves and from roots, respiration, and intermediate time trends.

The loss of TAC from roots results from respiration and possibly from transport to other organs. The figures for dark "growth" also suggest that roots were more important than crown in providing mobilized material; the decline in percentage TAC, amount of TAC, dry weight and percentage loss in weight were all greater from roots than from crown (Table 13). This finding contrasts with the emphasis of some other workers (Sullivan and Sprague 1943; Sprague and Sullivan 1950; Baker 1957*b*; May and Davidson 1958; Wardlow and Williams 1964) on the greater importance of the plant crown or the shoot base.

The loss of TAC in the roots and crown could not account for the dry weight of "growth" produced in the dark, and setting aside the possibility of weaknesses in technique (e.g. possible losses of soluble carbohydrate during root washing), it would appear that under conditions of carbohydrate starvation, other substances must be involved both in translocation to the shoot meristems and in respiration. Yemm (1935, 1949) has noted the breakdown of protein under carbohydrate starvation. Turner (1949) has referred to the steady decrease of the alcohol insoluble residues (probably celluloses and pectic components) during apple storage, while James (1953, p 110) noted that "hemicelluloses . . . are mobilised only in extreme starvation when irreversible degradations are far advanced". Davidson (1963) found that the loss in carbohydrate amount after severe defoliation of cocksfoot was less than that expected from CO<sub>2</sub> gas exchange measurements; he suggests that other materials such as protein may be broken down. It might be noted (Table 13) that the translocation of materials to dark shoot "growth" depended less on sources of material other than TAC and was a more efficient process in the high carbohydrate treatment than in the low. This is in agreement with the results of Davidson and Milthorpe (1965); in one experiment these workers found that the contribution to new growth and to respiration from protein and other labile fractions was four times that from carbohydrate reserves.

The possible applicability of the light-proof box as an experimental tool in pasture management studies is weakened by the discrepancies in treatment rank for "growth" in dark and in light conditions (which was also recorded by Weinmann (1947*b*)), and the failure of survival time to distinguish between the intermediate and high carbohydrate treatments. Percentage TAC at death also varied between treatments.

### (c) Growth Analysis

Absolute growth rate may be considered broadly as the product of photosynthetic efficiency (E) and photosynthetic capacity (L). Although variation in L was a more potent source of variation in growth rate than variation in E, a substantial range in treatment means for E of from 0.10 to 0.17 g/sq dm/day was recorded in experiment 2. The earlier view of Gregory (1938) that E was relatively constant for different environments, species and nutritional conditions has been discounted as more evidence accumulated (Watson 1958; Watson and Wits 1959; Black and Watson 1960; Rees 1962). The maximum value of E recorded (0.17 g/sq dm/day) is high relative to most values reported from temperate climates (Blackman and Black 1959; Black and Watson 1960); higher values of up to 0.25 g/sq dm/day have been recorded at Gayndah with buffel grass seedlings (Humphreys, unpublished data).

The positive association between defoliation intensity and E which was noted in experiment 2 has been previously reported (Brougham 1956*a*; Davidson and Donald 1958; Alexander and McCloud 1959; Maggs 1964); this may be reasonably expected from consideration of the effect of defoliation on leaf illumination, leaf area ratio and respiratory load. The dependence of E on L

was linear for the C3 treatments (Figure 9); this is in agreement with Watson (1958) and Watson, Thorne, and French (1963). However, a curved relationship was noted for the C1 and C2 treatments. The effect of high carbohydrate status in increasing E is interesting; the higher carbohydrate percentage could conceivably inhibit photosynthesis (Went 1958) and the larger root system of the plants would increase respiratory losses, but it appears that these factors were outweighed by the larger root system and the more rapid rate of tillering which provided better sinks for assimilates (Moss 1962; Humphries and Thorne 1964; Thorne and Evans 1964).

Under the favourable growing conditions of experiment 2, the rate of leaf area increase was proportional to initial L. The measurements of light values at the base of the plants were discarded because of a weakness in technique, but it appeared that these light values at the end of the experiment did not fall below 0.2 daylight. The effect of high L in increasing leaf area growth rate was due wholly to an increased rate of expansion of individual leaves which were also of larger average size at the start of the growth period (*cf.* Langer 1954; Brougham 1958*b*), since high L strongly inhibited the rate of leaf appearance (see Davidson and Donald 1958).

The stimulation of leaf appearance by defoliation may occur through the production of more leaves per shoot and/or more shoots per plant; the latter factor was more important in experiment 2. The number of leaves per shoot at any given time is strongly influenced by time shifts in rate of shoot appearance, and evidence in Table 10 suggests that high carbohydrate status reduced the number of leaves per shoot; however, leaf area per shoot was insensitive to carbohydrate status, since there were compensating effects *via* leaf size. Superior leaf growth rate in the high carbohydrate treatment was therefore due to improved rate of shoot appearance (contrast Beinhart 1963). Due to the absence of repeated cutting it would be expected that fewer bud sites would be initially available in the C3 plants, and, in fact, shoot appearance in the L0 series at day 2 shows no advantage of C3 over C1.

The function of leaf area in determining growth under field conditions is further considered elsewhere (Humphreys 1965*a*).

#### (d) Effects on Tillering

Increased frequency of defoliation (experiment 1) and intensity of defoliation (experiment 2) increased tillering; some contrasting reports have been mentioned previously. Buffel grass produced more shoots than green panic, and there is a suggestion in the data that the inhibition of axillary shoots by flowering stems was less important in buffel grass than in green panic. Despite these differences in tillering, total shoot growth did not differ between treatments in experiment 1. The significant short-term treatment differences in growth were occasioned more by variation in shoot size than in shoot number. This finding is in agreement with Langer (1958*b*, 1959, 1963). Tillering effects are discussed in more detail in a subsequent paper (Humphreys 1966*b*).

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