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**SUBTROPICAL GRASS GROWTH. 3. EFFECTS OF
STAGE OF DEFOLIATION AND INFLORESCENCE
REMOVAL**

By L. R. HUMPHREYS, M.Sc.Agr., Ph.D.

SUMMARY

The effects of 60% defoliation at the stem elongation, heading and anthesis stages, and of inflorescence removal, on the growth of spaced plants of green panic, grown under conditions of adequate nutrition and moisture supply, were measured.

Defoliation usually depressed stem, inflorescence and total shoot growth, and usually increased leaf area/leaf weight ratio, leaf weight ratio, leaf growth and net assimilation rate. Defoliation improved net leaf expansion through a reduction in senescence, and through increases in final leaf number per shoot, maximum size attained by leaves and production of tertiary shoots.

However, increases in leaf growth were not sufficient to compensate for the large reduction in leaf surface consequent upon defoliation, which therefore reduced mean leaf area duration. Depression of shoot regrowth did not reach significance for defoliation at the anthesis stage, when residual LAI after defoliation was also greater.

Removal of young inflorescences (but not inflorescences at the post-anthesis stage) increased rate of shoot appearance and enhanced shoot growth and net assimilation rate. Effects on the leaf surface were exerted mainly *via* rate of shoot differentiation, the axillary growth of the penultimate leaf of a flowering shoot being especially affected.

Attention is directed to the manner in which components of growth operated in a compensatory, self-regulatory fashion, reducing the effects of defoliation on plant growth, and general conclusions from the three papers of this series concerning pasture defoliation practice are drawn.

I. INTRODUCTION

In a previous study (Humphreys 1966a, experiment 2), indications were obtained that the growth response to differences in LAI level induced by defoliation was complicated by flowering. It was, therefore, desirable to examine in some detail the effects of shoot removal at different developmental stages and of inflorescence removal on the pattern of green panic shoot growth, leaf expansion

and tillering. Since it was clear from previous studies that moisture and nutritional shortages limited the expression of defoliation treatments, it was preferable that these experiments should be irrigated and carried out under favourable nutritional conditions.

Other work at the "Brian Pastures" Pasture Research Station, Gayndah (Humphreys, unpublished data) had suggested that cutting swards late in autumn (April-May) affected spring regrowth more adversely than cutting in the January-March period. Hence it was desired to measure the effects of stage of defoliation on both current growth and recovery growth in the subsequent spring-summer period.

II. EXPERIMENTAL

Experiment 1: Growth of Green Panic in Relation to Defoliation at Different Developmental Stages and to Inflorescence Removal

Experiment 2: Growth of Green Panic in Relation to Defoliation and to Removal of Inflorescences of Differing Age

(i) Objective

Experiment 1 was designed to determine whether (1) the developmental stage at which defoliation was imposed and (2) the removal of inflorescences as they were exerted were significant in altering the subsequent growth pattern in green panic (*Panicum maximum* var. *trichoglume* (K. Schum.) Eyles) plants not subject to moisture or nutritional stress.

Experiment 2 was conducted under conditions somewhat similar to experiment 1 and was prompted by some questions posed by the results of experiment 1. It was desired to study the effects on green panic growth of (1) the age of inflorescence present and (2) the repeated removal of inflorescences after defoliation had been imposed. It was also desired to obtain a more detailed description of these effects on shoot and leaf rates of appearance, expansion and senescence.

In each experiment the residual effect of treatment on growth in the following spring-early summer period was recorded.

(ii) Treatments and Design

Experiment 1 had the following treatments:—

- A. Control. Uninterrupted growth during course of detailed growth study.
- B. Inflorescences removed every 2 days upon exertion (day 46–day 82).
- C. 60% of shoot material present, including the main apex, removed at the time of main stem elongation (day 39).

- D. 60% of shoot material present removed at the time of head exertion on the main shoot (day 46).
- E. 60% of shoot material present removed at the time of anthesis of the first four heads exerted (day 60).

The following harvests were made in experiment 1:

- I. A treatment at the time of C treatment application (day 39).
- II. A treatment at the time of D treatment application (day 46).
- III. A, B, C, D treatments at the time of E treatment application (day 60).
- IV. All treatments at day 82.
- V. All treatments cut at 2-cm height on September 1, 1961, and at ground level on November 30, 1961.

Treatments in experiment 2 were:

- A. Control. Uninterrupted growth.
- B. Inflorescences removed every 2 days upon exertion (day 42–day 73).
- F. Inflorescences removed every 2 days following anthesis (day 53–day 73).
- D. 60% of shoot material present removed at the time of head exertion on the main shoot (day 42).
- G. As for D, followed by inflorescence removal every 2 days upon exertion (day 53–day 73).

Harvests in experiment 2 were made as follows:

- I. A treatment at the time of D treatment application (day 42).
- II. A, B, D treatments at the time of F treatment commencement (day 53).
- III. All treatments at day 73.
- IV. All treatments cut at 2-cm height on September 11, 1962, and at ground level on January 8, 1963, when separation into the 0-2 cm and above 2 cm layers was effected.

Each experiment was arranged with nine replications as randomized blocks, with harvest series as main plots and plant treatments as subplots. Each subplot comprised two plants.

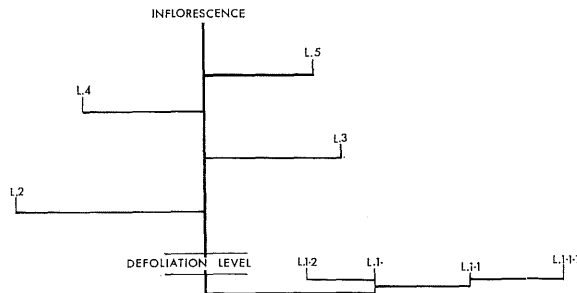
(iii) Method

Both experiments were carried out in the nursery block of the "Brian Pastures" Pasture Research Station, on a shallow chernozem soil which had been fallowed for 9 months. Green panic seeds were sown, and emergence (day 0)

occurred on February 18, 1961, in experiment 1 and on January 8, 1962, in experiment 2. The earlier sowing date in experiment 2 was chosen for reasons extraneous to the investigation. The area was watered until days 82 and 73 in experiment 1 and experiment 2 respectively. The stand was thinned to provide a plant spacing of 80 cm x 80 cm, and the area was kept free of weeds. A single guard row was left surrounding each main plot.

On each defoliation date, A treatment plants were harvested below ground level and removed to the laboratory. The fresh weight of each plant was determined, and the older whole shoots (but not necessarily including vegetative apices) severed until 60% by weight of the plant's aboveground parts had been taken. In experiment 2, the main stem was severed between the fourth and fifth last primary leaves. Similar classes of shoots were then removed from the intact plants in the field, such that the average number of shoots removed was equal to the number removed in the laboratory determination.

At each harvest date, the following determinations were made:—dry weights of leaf, stem, and inflorescence; individual leaf size; numbers of leaves, shoots, and inflorescences. The number and weight of inflorescences removed in the inter-harvest periods in treatments B, F and G were also recorded. In experiment 2 the main stem of one plant per treatment per block in harvest series IV was tagged. Nine field determinations from day 42 to day 74 were made of the size and position of individual leaves, and the number, development stage and position of individual shoots above the sixth last primary leaf of the main apex. The determinations of leaf area were made by comparison with a prepared set of leaf area standards forming a logarithmic series. The following diagram indicates the scheme of leaf numbering on the main stem, in which the leaf immediately below defoliation level was designated L.1:—



L.1. usually corresponded to the ninth or tenth leaf formed on the main apex. Floral initiation was determined by dissection; mean initiation times were day 30 in experiment 1 and day 24 in experiment 2, when an average of 11-12 leaves were externally visible and seven axillary shoots were extruded on the main stem. Rapid elongation of the stem did not occur until after floral initiation.

Table 1 indicates dry weight and leaf area immediately before and after the commencement of treatments, and Figure 1 illustrates the A and D treatments.

TABLE 1
PLANT CHARACTERISTICS IMMEDIATELY BEFORE AND AFTER TREATMENT

Treatment	Expt. 1		Expt. 2	
	Before	After	Before	After
Shoot dry weight (g/plant)				
C. Stem elongation ..	8.75	3.61
D, G. Head exertion ..	18.99	7.77	49.52	21.56
E, F. Anthesis	75.82	26.72	155.92	..
Leaf area (sq dm/plant)				
C. Apex elongation ..	8.72	2.11
D, G. Head exertion ..	13.78	4.76	45.11	14.82
E, F. Anthesis	55.81	22.06	103.93	..

Defoliation on a dry-weight basis varied from 56% in experiment 2 treatment D to 65% in experiment 1 treatment E; although in both experiments treatments were imposed at equivalent developmental stages, plants were larger in experiment 2, presumably due to better climatic conditions.

III. RESULTS

(i) Dry-weight Changes

Dry-weight changes are summarized in Table 2. The treatment comparisons form an incomplete series; basically all treatments may be compared with the control A for a growth period following treatment imposition (period I), and treatments B, C and D may also be compared for a further growth period (period II).

Absolute leaf growth rate was depressed by defoliation at heading (D) in period I, but in experiment 2 this was followed by a significant increase relative to the control. Removal of young inflorescences (B) stimulated leaf growth in experiment 1 period II. Stem growth was also depressed by defoliation at heading (D) and at stem elongation (C) in period I, while removal of young inflorescences increased stem growth in period II. Inflorescence growth was reduced by defoliation at any stage in period I, and this effect continued into period II. Removal of young inflorescences reduced total inflorescence growth in experiment 2 but increased it in experiment 1.

The summation of changes in these plant organs showed that defoliation at stem elongation or at heading reduced shoot growth in the first growth periods; this effect continued in period II of experiment 2 but was not evident in experiment 1. Over both growth periods, defoliation at stem elongation, head exertion or anthesis reduced growth by 22.6, 12.2 and 15.0 g/plant respectively. Removal of old inflorescences (F) had no effect on growth. Removing young inflorescences (B) caused a highly significant and substantial growth increase of 46% in period II of experiment 1; in experiment 2, where growth rates were higher, the increase was 10% but non-significant.

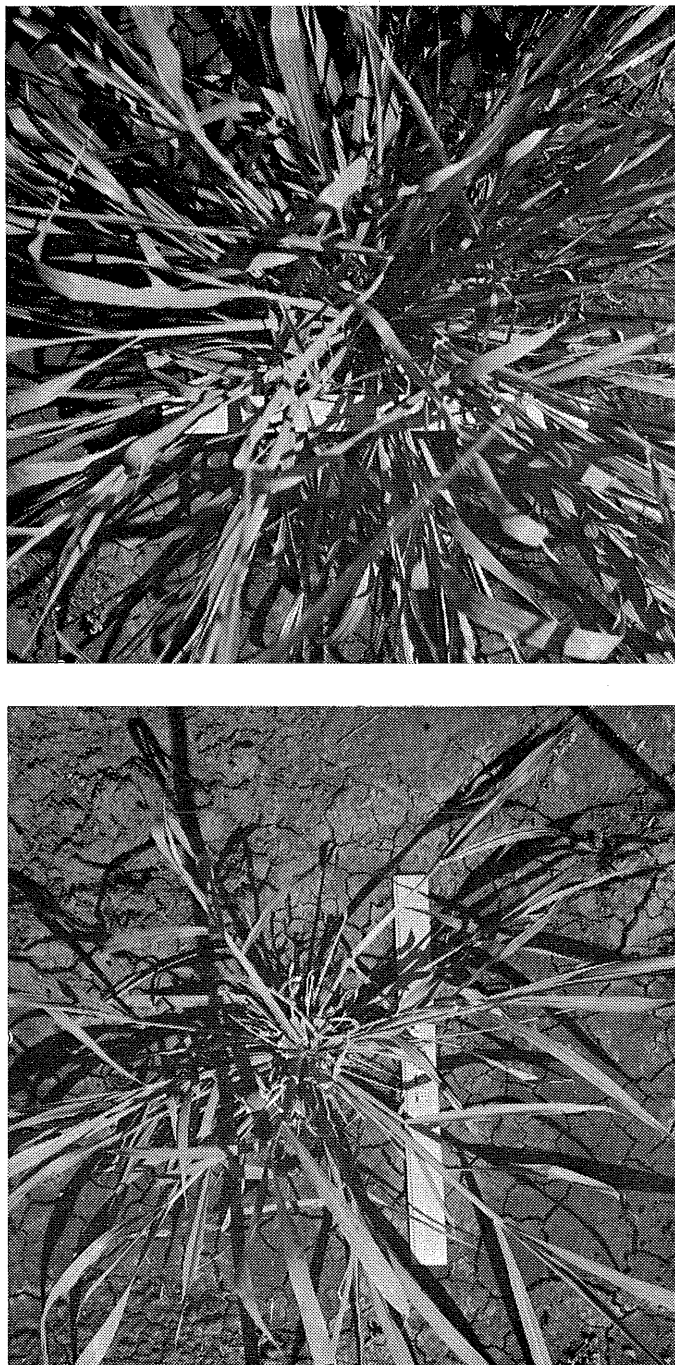


Fig. 1.—Experiment 2, Day 42: Defoliation treatments: A, control (upper); D, 60% removal at heading stage (lower).

TABLE 2
GROWTH RATES FOLLOWING DEFOLIATION OR INFLORESCENCE REMOVAL
g/plant/day

Treatment	Expt. 1			Expt. 2	
	Days 39-60	Days 46-60	Days 60-82	Days 42-53	Days 53-73
		Leaf			
A. Control	0.76	0.94	1.10	2.07	0.95
B. Removal young heads	0.91	1.56	2.28	1.13
F. Removal old heads	0.96
C. Defoliation stem elongation	0.69	..	1.06
D. Defoliation head exsertion	0.70	1.38	1.67	1.51
G. As D plus head removal	1.56
E. Defoliation anthesis	1.30
L.S.D. { 5%	N.S.	0.18	0.48	0.58	0.46
{ 1%	0.25	0.65	0.78	0.62
		Stem			
A	2.08	2.63	3.88	6.57	8.34
B	2.58	5.80	6.58	10.19
F	8.19
C	1.31	..	4.03
D	1.34	4.40	3.02	7.29
G	7.94
E	3.37
L.S.D. { 5%	0.62	0.58	1.29	2.00	1.97
{ 1%	0.90	0.81	1.73	2.68	2.64
		Inflorescence			
A	0.36	0.49	0.81	1.03	3.75
B	0.48	1.09	1.09	3.03
F	4.04
C	0.08	..	0.73
D	0.06	0.68	0.08	2.21
G	1.71
E	0.43
L.S.D. { 5%	0.16	0.35	0.28	0.31	0.52
{ 1%	0.23	0.46	0.37	0.41	0.70
		Total Shoot			
A	3.19	4.06	5.78	9.67	13.03
B	3.97	8.45	9.95	14.35
F	13.18
C	2.07	..	5.82
D	2.10	6.46	4.77	11.01
G	11.22
E	5.10
L.S.D. { 5%	0.90	0.83	1.97	2.70	2.85
{ 1%	1.31	1.14	2.64	3.62	3.81

The data relevant to persistence of treatment effects are shown in Table 3. The amount of over-wintering material present in September after defoliation showed some sympathy with the growth produced until the last harvest in the preceding autumn, but the plants defoliated at anthesis appeared to have grown more since that date than other defoliation treatments. In both experiments the greatest spring and early summer regrowth was made where young inflorescences had been removed, and the previously defoliated treatments produced less regrowth. Regrowth was positively associated with the amount of dry matter produced in the preceding season. The spring regrowth of plants defoliated previously at anthesis did not differ significantly from the control plants.

TABLE 3

RESIDUAL EFFECTS OF DEFOLIATION AND INFLORESCENCE REMOVAL TREATMENTS ON YIELD g/plant

Treatment	Expt. 1		Expt. 2		
	Above 2 cm	Above-ground	Above 2 cm	Above-ground	
				Above 2 cm	0-2 cm
A. Control	1.ix.61 233·8	30.xi.61 391·7	11.ix.62 498·1	8.i.62 217·4	8.i.62 140·2
B. Removal young heads	262·6	435·8	569·0	223·5	147·2
F. Removal old heads	462·8	206·7	129·4
C. Defoliation stem elongation	216·5	339·4
D. Defoliation head exertion	193·5	338·7	410·0	180·9	133·2
G. As D plus head removal	399·1	174·3	121·1
E. Defoliation anthesis	186·8	356·2
L.S.D. { 5%	25·6	44·9	62·6	40·3	19·1
{ 1%	33·7	59·1	84·2	54·2	25·7

(ii) Growth Analysis

Net assimilation rate and mean leaf area present over the respective growth periods are shown in Table 4. In experiment 1, net photosynthetic efficiency was significantly increased by defoliation at stem elongation or anthesis in the first growth period, and by defoliation at head exertion in the second period after defoliation. A similar trend in experiment 2 did not reach statistical significance. Removal of young heads in period II of experiment 1 increased net assimilation rate by 42%; the substantial growth advantage in this treatment was mainly due to this factor. Maximum value recorded for any treatment was 0·15 g/sq dm/day.

The reduced dry-weight increase of the defoliation treatments was occasioned by reductions in mean leaf area present. These differences persisted over both growth periods and were associated with the drastic reduction in photosynthetic capital imposed by defoliation. Absolute leaf area growth rate tended to be reduced for period I after defoliation (except for defoliation at anthesis in experiment 1); for period II it was significantly increased for defoliation at head

TABLE 4

GROWTH ANALYSIS FOLLOWING DEFOLIATION OR INFLORESCENCE REMOVAL

Treatment	Expt. 1			Expt. 2	
	Days 39-60	Days 46-60	Days 60-82	Days 42-53	Days 53-73
Net Assimilation Rate (g/sq dm/day)					
A. Control	0.125	0.134	0.079	0.142	0.106
B. Removal young heads	0.141	0.112	0.140	0.104
F. Removal old heads	0.103
C. Defoliation stem elongation	0.148	..	0.091
D. Defoliation head exsertion	0.135	0.109	0.153	0.111
G. As D plus head removal	0.116
E. Defoliation anthesis	0.120
L.S.D. { 5%	0.020	N.S.	0.024	N.S.	N.S.
{ 1%	0.028	..	0.032
Mean Leaf Area (sq dm/plant)					
A	25.01	29.80	72.45	70.1	125.0
B	28.72	77.32	72.3	137.0
F	129.7
C	14.20	..	64.16
D	15.56	60.16	32.0	98.2
G	98.6
E	43.64
L.S.D. { 5%	3.65	3.00	9.88	9.8	18.2
{ 1%	5.30	4.14	13.28	13.5	24.5
Leaf Area Growth Rate (sq dm/plant/day)					
A	2.24	3.00	1.79	5.35	2.32
B	2.77	2.60	6.04	2.81
F	2.85
C	2.15	..	1.74
D	2.33	2.47	4.32	4.32
G	4.25
E	2.56
L.S.D. { 5%	N.S.	0.46	N.S.	1.55	1.24
{ 1%	0.64	..	2.08	1.66

exsertion in experiment 2. When leaf area growth rate was considered on a relative basis, it was seen that defoliation increased leaf area growth rate at all stages, with rates of up to 0.16 sq dm/sq dm/ day being recorded.

The leaf area present at any point of time may be considered as the product of La/Lw, and Lw/W and W. It will be seen from Figure 2 that a pattern earlier described (Humphreys 1966a, experiment 2) was repeated. Plants previously defoliated had higher values of La/Lw subsequently. However, the La/Lw of the residual material remaining after defoliation was not reduced as in the earlier

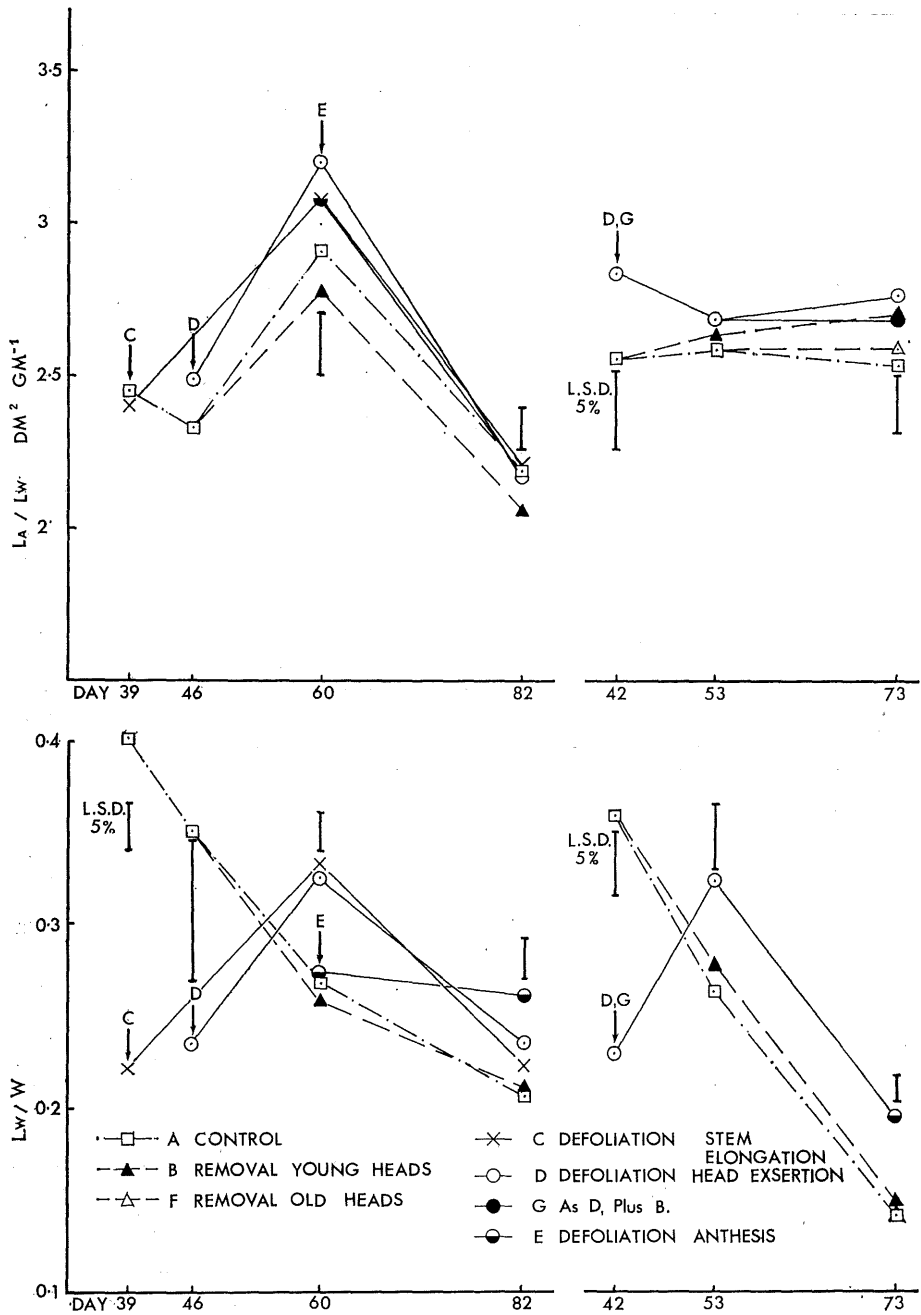


Fig. 2.—Experiments 1 (left) and 2 (right): Leaf area/leaf weight ratio (L_a/L_w) and leaf weight ratio (L_w/W) for plants defoliated at various stages or having inflorescences removed only.

TABLE 5
CENSUS DATA

Treatment	Expt. 1			Expt. 2	
	Days 39-60	Days 46-60	Days 60-82	Days 42-53	Days 53-73
Rate of Leaf Appearance (no./plant/day)					
A. Control	13·64	16·56	9·46	21·94	10·18
B. Removal young heads	17·48	13·91	21·57	15·27
F. Removal old heads	11·68
C. Defoliation stem elongation ..	14·79	..	9·20
D. Defoliation head exsertion	16·71	10·76	21·23	14·82
G. As D, plus head removal	16·02
E. Defoliation anthesis	14·31
L.S.D. { 5%	N.S.	N.S.	N.S.	N.S.	N.S.
1%
Rate of Shoot Appearance (no./plant/day)					
A	3·99	4·99	3·68	6·49	3·43
B	5·79	6·07	6·65	7·50
F	4·09
C	4·34	..	3·01
D	5·41	2·69	7·92	2·75
G	4·20
E	5·52
L.S.D. { 5%	N.S.	N.S.	1·65	N.S.	1·86
1%	2·21	..	2·48
Rate of Inflorescence Appearance (no./plant/day)					
A	0·73	0·94	2·31	1·87	5·96
B	1·30	3·92	1·77	8·27
F	5·84
C	0·17	..	2·15
D	0·12	1·71	0·19	4·16
G	4·78
E	1·10
L.S.D. { 5%	0·46	0·57	0·70	0·57	0·77
1%	0·67	0·79	0·94	0·77	1·44

work; it will be recalled that slashing was there employed, whereas whole shoots were removed in experiments 1 and 2 now being reported. Lw/W declined with time in the control plants; it was significantly reduced in the residual material after defoliation, but substantially increased in growth subsequent to defoliation. Inflorescence removal had no real effect on either parameter. It might have been

expected that this treatment would have increased the proportion of plant weight composed of leaf, but stem growth was increased and in experiment 1 inflorescence growth was also stimulated by removal of young inflorescences.

(iii) Census Data

The census data, which display changes in the rates of leaf, shoot and inflorescence appearance, are shown in Table 5. In period I, there was an apparent rise in the tillering relative to control plants following defoliation at stem elongation, head exertion and anthesis treatments. This was followed in period II by a depressed rate of shoot appearance relative to the control plants. If, however, inflorescences were continually removed after defoliation (treatment G), the rate of tiller appearance was well maintained in period II. Although this pattern was consistent for all defoliation treatments, it did not reach statistical significance in either experiment. Differences in the rate of leaf appearance also failed to reach significance, but it appeared that these did not always parallel tillering effects, due to alteration in the number of leaves per shoot.

Removal of young inflorescences significantly increased the rate of shoot appearance in period II of both experiments. This treatment also stimulated the rate of inflorescence appearance. Defoliation at all stages reduced the rate of inflorescence appearance.

(iv) Components of Leaf Area

Growth of the leaf surface will now be considered in more detail. Leaf area at any point in time is the product of the number of shoots present and the leaf area per shoot. The latter may be further considered as the product of the number of leaves differentiated per shoot and the size of the individual leaves. The characteristics of the leaf surface depend upon the previous rate at which tillers have appeared, their developmental stage (recognizing that floral initiation terminates leaf differentiation on the main axis of a particular shoot), the progress of the leaves towards their maximum size and the rate of their senescence.

Changes in leaf area per shoot are shown in Figure 3. Except for defoliation at anthesis, the average leaf area of individual shoots remaining after defoliation was smaller than that in control plants; it will be recalled that older shoots were selectively removed. The effect was due to reduction in leaf size rather than in leaf number per shoot. At the end of period I, leaf area per shoot continued to be smaller in the plants defoliated at head exertion; this was due both to reduced leaf number per shoot and to reduced leaf size. It will be recalled that this was a period when defoliation apparently increased the rate of tiller appearance; hence the shoots in this treatment had a younger age distribution. The increments in leaf number for the various leaf size classes in periods I and II are shown in Figure 4. An increased number of leaves in the smaller size classes and a reduced number in the larger size classes are evident in the defoliated plants for the period day 46-60.

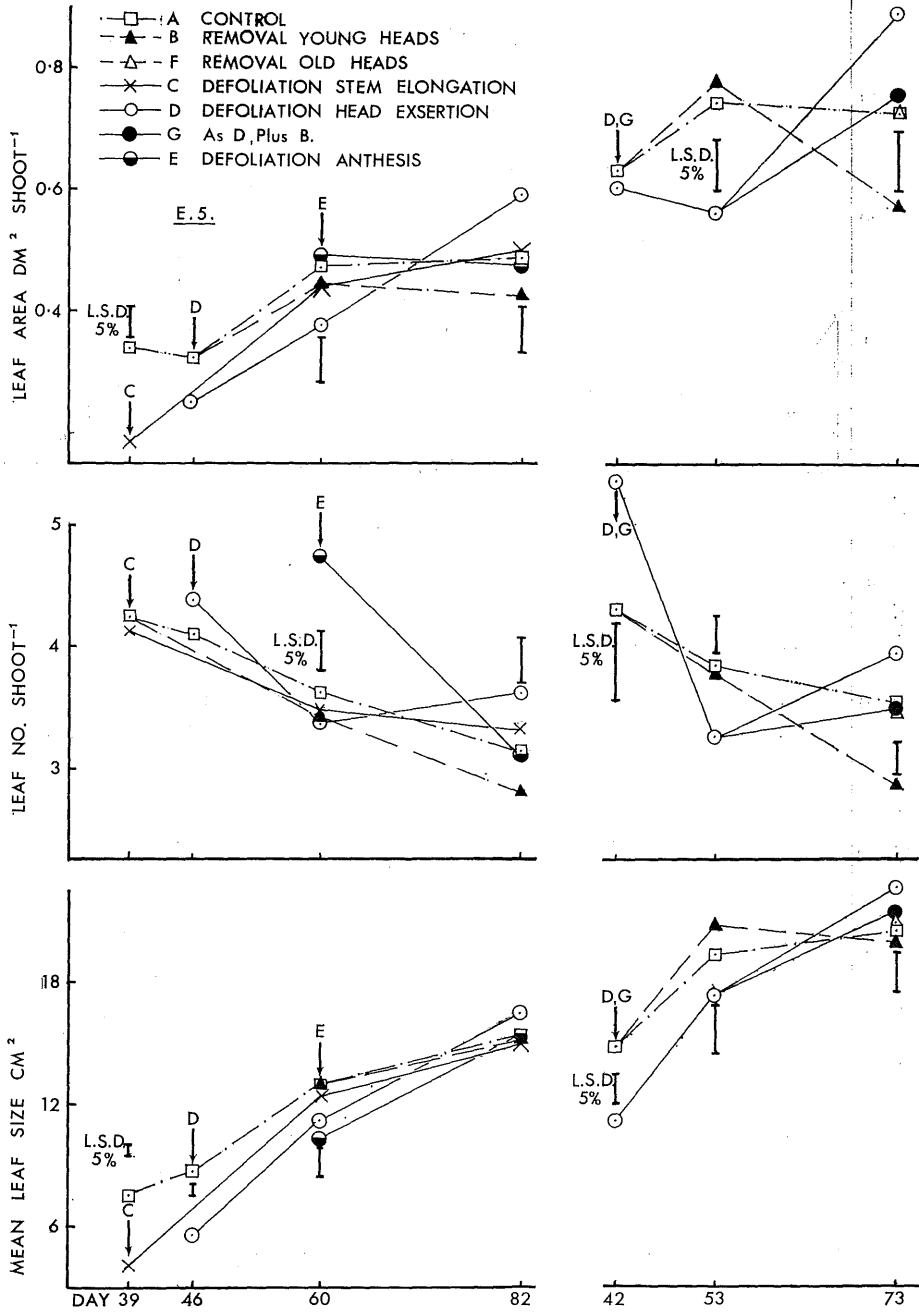


Fig. 3.—Experiments 1 (left) and 2 (right): Leaf area per shoot, leaf number per shoot and mean leaf size for plants defoliated at various stages or having inflorescences removed only.

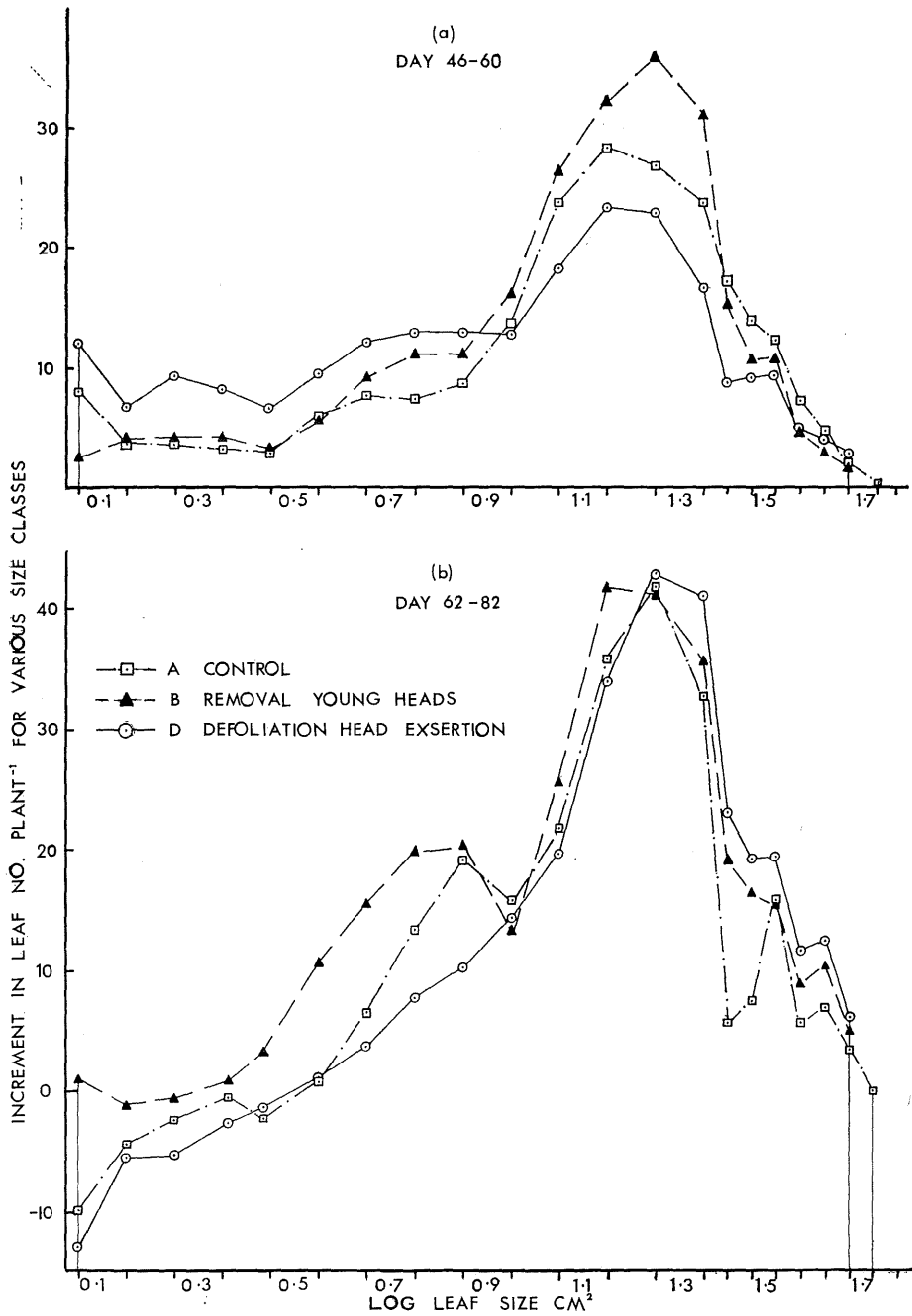


Fig. 4.—Experiment 1: Increment in leaf number per plant for various leaf size classes from (a) day 46-60, (b) 60-82, for control, head removal and defoliation treatments.

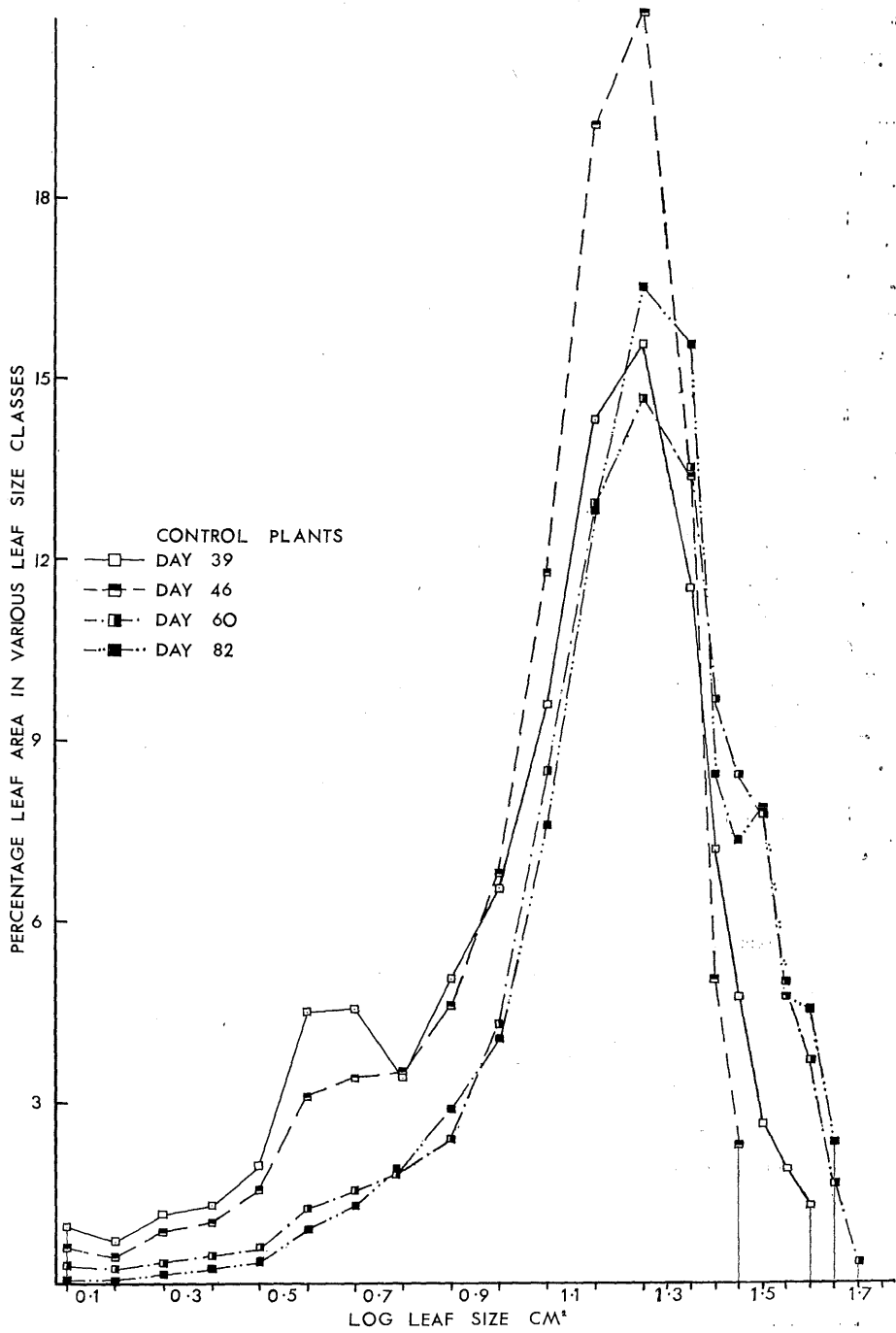


Fig. 5.—Experiment 1: Percentage leaf area in various size classes for control plants on days 39, 46, 60 and 82.

However, by the end of period II leaf area per shoot was greater than in the control plants, due primarily to increased leaf number per shoot; this followed a period when tillering was apparently reduced relative to the controls. If head removal was continued after defoliation (treatment G) this effect was not evident, since the rate of tiller appearance was maintained in period II. There is some evidence in Figure 4 (b) that fewer small leaves and more large leaves were produced in this period in the defoliation (D) treatment.

Removal of young inflorescences had no effect in period I, but in period II, when both tillering and inflorescence exertion were stimulated radically, leaf area per shoot was reduced; this was caused by a reduction in leaf number per shoot, mean leaf size being relatively unaffected. There is, however, a suggestion in Figure 4 (b) that increased numbers occurred in the smaller size classes in this period.

In the control plants, leaf area per shoot rose in the first half of the study, and was relatively static in the second. Leaf number per shoot fell steadily with time, associated with earlier floral initiation on individual shoots, while mean leaf size increased with time. The changing leaf size distribution with advancing development is shown in Figure 5.

The greater leaf area produced in experiment 2 was due mainly to the production of larger leaves than occurred in experiment 1.

Consideration of mean values has obvious limitations, since the leaf surface is the summation of leaves on individual tillers, all varying in status and life history. Examination of the more detailed data available for the last five leaves on the main apex in experiment 2 will assist in this respect. Since the data are voluminous, only the more important aspects are presented.

In experiment 2 the main shoot was severed above the fifth last leaf, designated L.1. The average situation at day 42 is shown in Table 6.

TABLE 6

EXPERIMENT 2: LEAVES PRESENT ON DATUM SECTION OF PLANTS AT HEAD EXERTION, DAY 42

Treatment	First Order	Second Order
All treatments (A, B, F, D, G)	L.1.	L.1.1. L.1.2. L.1.3. (?)
Plus, undefoliated treatments (A, B, F)	L.2. L.3. L.4. L.5. (flag leaf)	L.2.1. L.2.2. L.3.1.

The defoliated plants were, therefore, left with four leaves externally visible on the datum section of the plant and three bud sites externally visible, while the remaining treatments had 11 leaves remaining and seven unexploited bud sites.

The course of net leaf expansion for leaves including and above L.1. is shown in Figure 6. Net leaf increment was similar in all treatments, but for the control plants and those having aged inflorescences removed, this showed a steep decline after day 65. On the other hand, removal of young inflorescences,

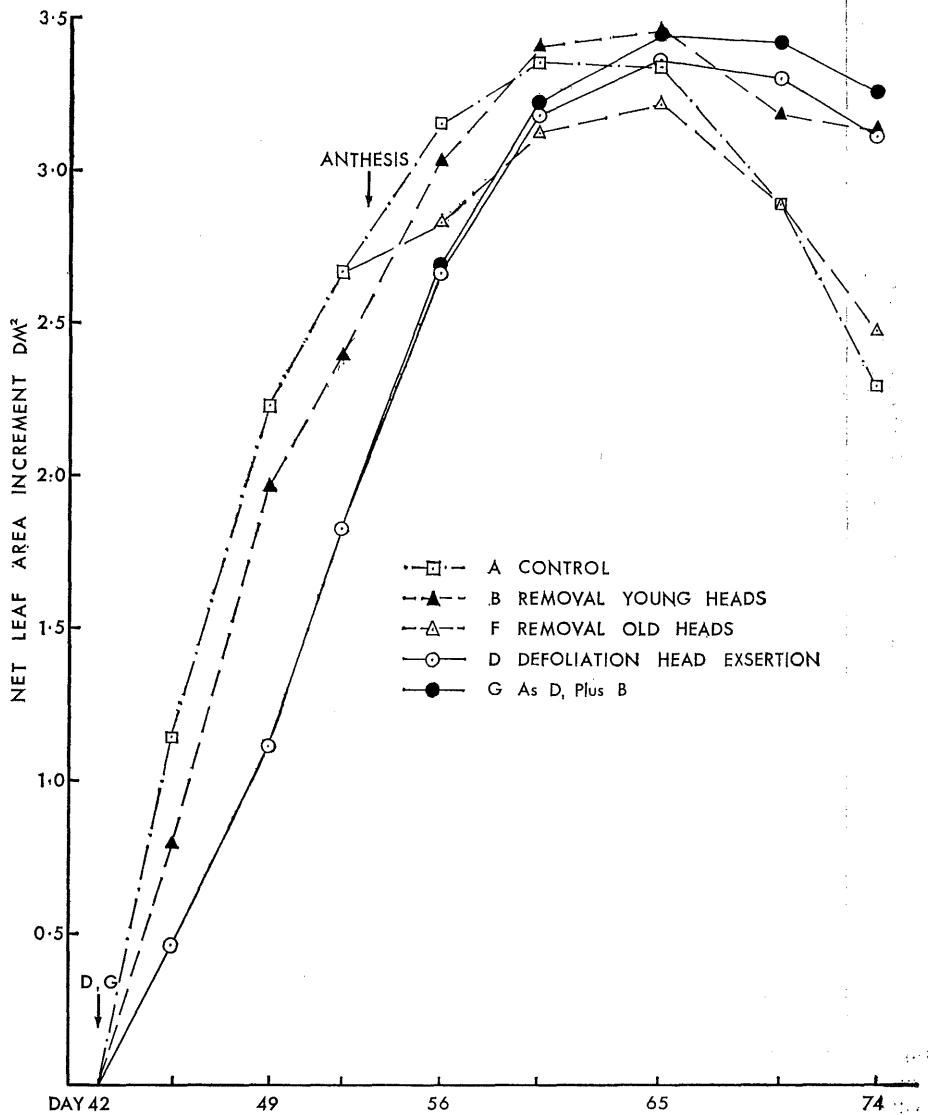


Fig. 6.—Experiment 2: Cumulative net leaf area increment after defoliation (for last leaf on main axis and its axillary growth) or after inflorescence removal (for last five leaves on main axis and their axillary growth).

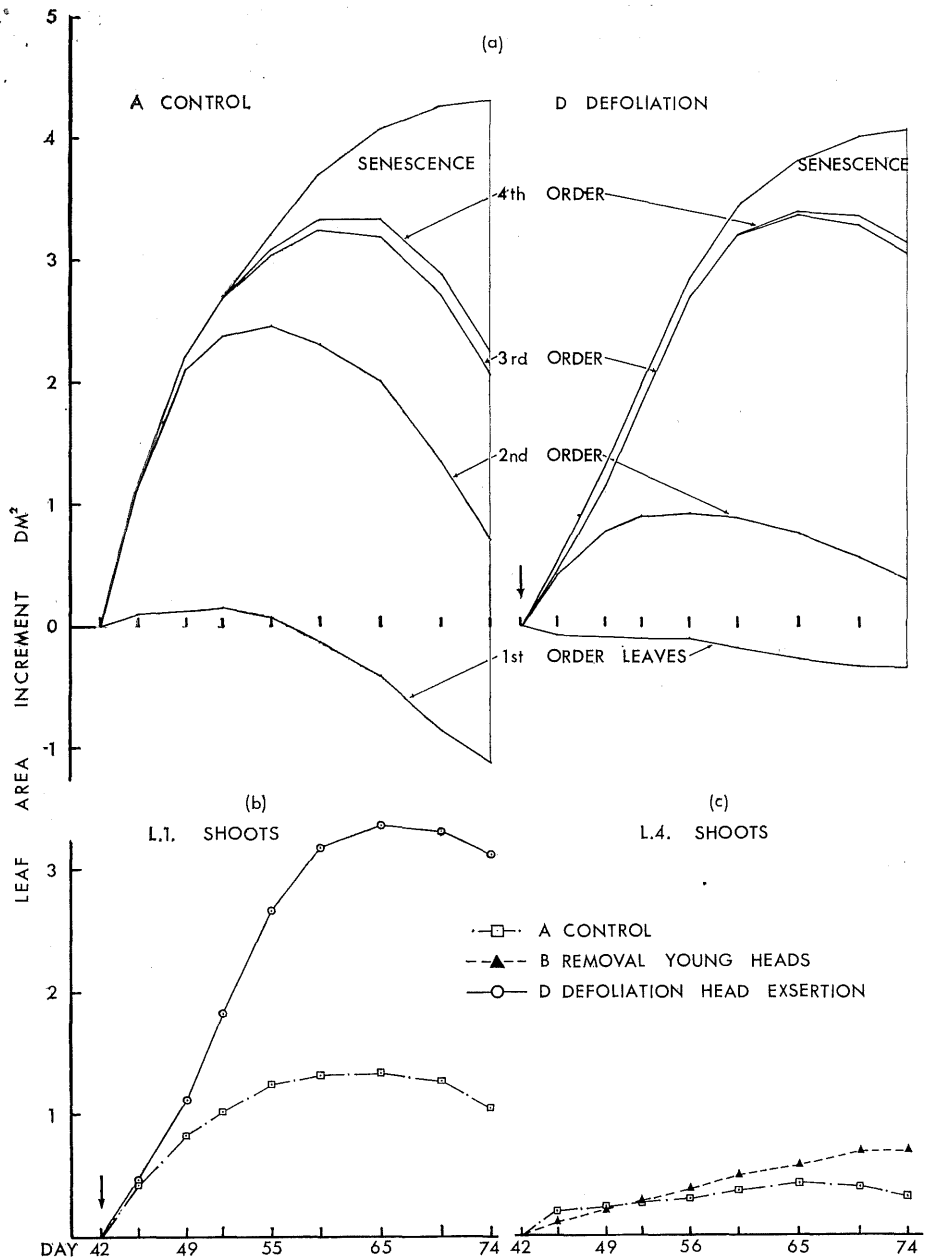


Fig. 7.—Experiment 2: (a) Net leaf area increment for first, second, third and fourth order leaves, and total senescence, for control plants (for last five leaves on main axis and their axillary growth) and for defoliated plants (for last remaining leaf L.1 on main axis and its axillary growth). Net leaf area increment (b) for L.1 shoots and (c) L.4 shoots (for leaf below flag leaf L.4 and its axillary growth).

defoliation, or a combination of these two treatments, sustained the leaf surface area at a higher value towards the close of the datum period. The depressing effect of the younger leaves and shoots on the axillary growth of the leaves below them is clearly shown in Figure 7 (b), where the leaf area of the L.1. shoots is contrasted for the control plants (A) and the defoliated plants (D); maximum net increments were 1.3 and 3.4 sq dm respectively.

Removal of young inflorescences did not cause a large difference in leaf expansion, and while differences were recorded in the axillary growth of the L.1, L.2, L.3 and L.4 leaves, the main effect was exerted in the axillary growth of the leaf below the flag leaf, L.4 (see Figure 7 (c)). Removal of inflorescences at anthesis slightly increased leaf growth at this site also. Both treatments increased the rate of senescence of the flag leaf; this may have been caused by damage during inflorescence removal.

The change in leaf area of leaves of differing morphological status is shown for the control and defoliated plants in Figure 7 (a). First-order leaves (i.e. leaves on main stem) declined in area, and the senescence of second-order leaves (i.e. leaves produced in the axils of first-order leaves) exceeded their expansion by day 65 in both treatments. Secondary leaves could be produced from four sites in a control plant and from one site in a defoliated plant; maximum net expansion was 2.3 times as great as in the former. It was in the tertiary leaf class that the defoliated plants produced substantially greater leaf area than the control plants; leaf area increment was greater by a factor of 2. Removal of young inflorescences enhanced the leaf area of the tertiary and quaternary leaf classes only.

The total senescence for leaves including the above L.1. is also shown in Figure 7 (a). True leaf expansion is seen to be greater in the control plants than in the defoliated plants, but the greater senescence in the former reduced maximum net leaf area increment to similar levels in both treatments, and to a much lower level at the end of the measurement period. By day 74, senescence represented 48% of accumulated true leaf expansion in the control plants, but only 23% in the defoliated plants.

For the datum section of the plant, defoliation reduced the total number of shoots produced, but increased it in L.1. (Figure 8 (c)). Removal of young inflorescences, with or without defoliation, also increased shoot appearance in L.1. Removal of young inflorescences alone stimulated the rate of shoot appearance at all sites.

As indicated earlier, the average number of leaves present per shoot is influenced by both the shoot age distribution and the final number of leaves differentiated on any shoot. Final leaf number per shoot for selected sites which had ceased to differentiate leaves may be seen in Table 7. It will be noted that this parameter was slightly increased by defoliation. For the leaf axil (L.1.4) below the flag leaf of the L.1. secondary shoot, removal of the young inflorescence increased the number of leaves differentiated.

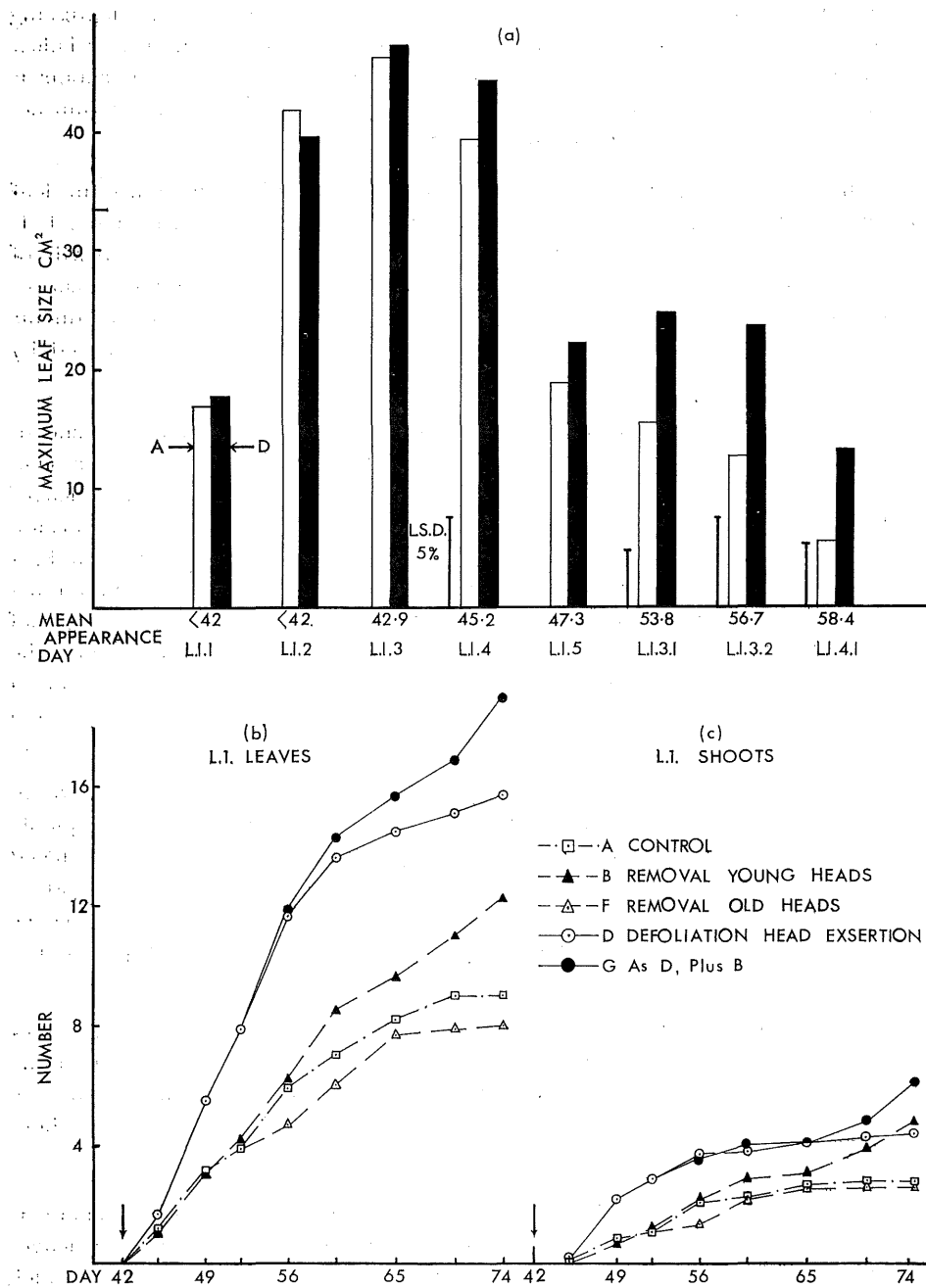


Fig. 8.—Experiment 2: (a) Effect of defoliation (D) on maximum size of leaves of varying age; number of (b) leaves and (c) shoots appearing after defoliation, or inflorescence removal, in the axillary growth of leaf L.1.

TABLE 7

EXPERIMENT 2: FINAL LEAF NUMBER/SHOOT

Leaf Axil Designation	L.1.2.	L.1.3.	L.1.4.
Treatment			
A. Control	2.9	2.7	1.6
B. Removal young heads ..	2.8	2.8	2.2
F. Removal old heads ..	2.0	2.3	2.0
D. Defoliation head exsertion	4.2	2.8	1.9
G. As D, plus B	3.8	3.0	2.2
L.S.D. { 5%	1.5	N.S.	0.6
{ 1%	2.0	..	0.8

The maximum size recorded for selected leaves of successive appearance date is shown in Figure 8 (a) for the control of (A) and defoliation (D) treatments. Leaves externally visible after defoliation on day 42, and which were still actively growing, grew to the same maximum size as their counterparts in the control plants. Leaves appearing after day 45 on the defoliated plants grew to a larger size than leaves on the control plants. It should be noted, however, that external environmental conditions for this comparison were not identical for the last three leaves shown in Figure 8 (a), since date of appearance was from 2 to 6 days earlier in the defoliated plants.

Maximum size of individual leaves on L.1. progressively increased from the first to the third leaf and diminished gradually in subsequently formed leaves. The nature of the sequence varied with the status of the shoot.

The period and frequency of measurement were not sufficient to establish the complete life history of individual leaves. Mean maximum size for specific leaves was usually recorded from 3 to 9 days after leaf exsertion; previous defoliation did not appear to reduce time taken to reach maximum size in subsequently formed leaves. Leaves appearing after day 42 retained some green lamina on day 74. An average of four leaves disappeared from the datum section of a control plant in 32 days. Leaves on the main axis appeared to have a life of 40-50 days.

Thus the principal conclusions are that defoliation improved net leaf expansion through a reduction in senescence and increases in final leaf number per shoot, maximum leaf size and production of tertiary shoots; the effects due to removal of young inflorescences were exerted mainly *via* rate of shoot differentiation, the axillary growth of the penultimate leaf of a flowering shoot being especially affected.

IV. DISCUSSION

(a) Growth Analysis

In these spaced plant experiments, where moisture and nutrients were in adequate supply, reduction of the leaf surface by defoliation caused a concomitant reduction in shoot growth rate. Although defoliation stimulated relative leaf growth rate, and in some instances increased absolute leaf growth rate, differences in residual leaf area after defoliation exerted a decisive control. The smaller reduction in growth rate occurring when 60% defoliation was delayed until anthesis is explicable in these terms. It is also in agreement with the emphasis of Teel (1956), Jones (1959) and Davies (1960) on the advantages of defoliating when residual basal shoots have commenced expansion. At the conclusion of experiments 1 and 2 the control plants had LAI values of only 1.5 and 2.3 respectively, and complete light saturation was not recorded.

On the other hand, net assimilation rate (E) was enhanced by defoliation or by the removal of young inflorescences. In the case of the former, this confirms the finding of previous experiments and may be understood in terms of increased LAR (reduced respiratory load) and of better illuminated foliage.

However, these explanations are not relevant to increases in E occasioned by inflorescence removal. This treatment increased stem growth, while inflorescence growth was increased in experiment 1 and reduced in experiment 2 (phase differences being operative between the two experiments); the net result was that LAR was virtually unchanged. The possible shading effect of the inflorescences of green panic is not considered of great moment. Alterations in the age distribution of leaves might be expected to change assimilatory activity (Gabrielson 1948; Clendenning and Gorham 1950); although in period II the increment in leaf numbers was apparently greater, this had a very small effect in altering the percentage of total leaf area occurring in the various leaf size classes, since young leaves make a proportionately insignificant contribution to total area. Reductions in the rate of senescence were not recorded. Obvious changes in spatial arrangement and dispersion of leaves were not observed; new leaves appeared at all sites. It is conceivable that the enhanced rates of inflorescence appearance and stem growth may have been associated with increased internode length, but no measurements of this parameter were made.

Moss (1962) has demonstrated that CO₂ uptake is restricted by removal of the ear in maize, and of the fruit in the tomato plant. This was associated with a higher sugar content in barren stems, i.e. carbohydrate accumulation reduced assimilation. However, in green panic, a perennial, removal of young inflorescences increased the number of sinks available by stimulating inflorescence and shoot appearance. This is regarded as the most probable explanation of the rise in E (cf. Humphries 1963; Humphries and Thorne 1964; Thorn and Evans 1964).

The increased growth rate of the plants having their young inflorescences removed suggests that more attention should be paid to the use of late or non-flowering grasses (cf. Cooper and Saeed 1949) as an avenue by which growth rate and length of growing season may be increased.

(b) Tillering

Inductive conditions for flowering operated for the duration of both experiments; although treatments were applied at the commencement of stem elongation, inflorescence exertion or anthesis, these developmental stages occurred subsequently on later initiated tillers. It has been reported that the inhibition of axillary bud expansion by the flowering heads commonly ceases at anthesis or post-anthesis stage (e.g. Lamp 1952; Langer 1956; Eastin, Teel, and Langston 1964; Anslow 1965), and in experiment 2 the apparent stimulation of tillering by the removal of inflorescences only occurred if these were removed at the pre-anthesis stage. It might be argued that the experimental period was not sufficient to permit a true assessment of the effect of aged inflorescence removal, but the influence of removal of young inflorescences on shoot and leaf number was clearly evident 18 days after the commencement of treatment. In both experiments the rate of shoot appearance in the seedling control plants progressively increased until anthesis of the first four inflorescences and decreased thereafter. This decrease is not associated with the particular developmental stage of the main tillers, but is attributable to the increased rate of inflorescence appearance during the "post-anthesis" phase (see Table 5).

Defoliation caused an apparent increase in the rate of shoot differentiation; this was followed by an apparent decrease relative to the control plants. The removal of young inflorescences from the defoliated plants in the second phase counteracted this decrease. In this situation the control of tillering is still not clear. In both periods there were fewer unexploited bud sites (leaf number minus shoot number) on the defoliated plants. The rate of inflorescence appearance was reduced in the defoliated plants relative to the controls; hence young inflorescences inhibited tillering more strongly in the defoliated plants.

The inhibition of axillary bud expansion by reproductive structures is well known in agricultural practice and has been reported for both annual and perennial plants (e.g. Mattiolo 1899; Murneek 1926; Cooper and Saeed 1949; Lamp 1952; Langer 1958*a*, 1958*b*; Dale 1959; Leopold, Niedergang-Kamien, and Janick 1959; Lockhart and Gottschall 1961; Sax 1962). The mechanisms involved in this process and in apical dominance are complex. It is known that auxin will substitute for the apex in some respects (e.g. Leopold 1949), and in *Pisum sativum* kinetin will oppose the effect of I.A.A. and maintain viability in an otherwise dominated bud (Sachs and Thimann 1964). The inhibition is sometimes interpreted in terms of competition for nutrients (Aspinall 1961), and Gregory and Veale (1957) have attempted a reconciliation of the two viewpoints by suggesting that auxin retards the differentiation of vascular connections to the buds and therefore retards nutrient translocation. However, Goodwin (1963) points out that this should provide a slow rate of growth rather than an absence

of growth, and that previous investigations have shown that one component of the inhibition complex can diffuse through an aqueous layer. It is known that the growth of the inflorescence depends very largely upon the current assimilation of the flag leaf and the inflorescence itself (Archbold and Mukerjee 1942; Archbold and Datta 1944; Quinlan and Sagar 1962; Evans and Wardlaw 1964; Williams 1964) and less upon assimilate produced or accumulated in other parts of the plant; hence removal would not by simple subtraction greatly increase nutrient availability to other sites. In experiment 2 the stimulation of tillering was evident at all sites but was most influential in the axil of the penultimate leaf.

Shoot removal not only creates conditions for the establishment of new dominances, but has the immediate effect of increasing the light intensity at the residual leaf surface. In previously reported experiments (Humphreys and Robinson 1966), rates of shoot appearance were significantly in sympathy with the frequency and the intensity of defoliation. In the seedling experiments 1 and 2, tillering was stimulated, but it diminished unless inflorescences were continually removed. This experience finds a parallel in the literature, where defoliation stimulated tillering under many established sward conditions (e.g. Harrison 1931; Cook and Stoddard 1953; Baker 1957; Langer 1958*a*, 1959; Lambert 1962; Langer, Ryle, and Jewiss 1964) and reduced it under pot conditions, where restriction on available bud site number and absence of light limitations would be more apparent (e.g. Mitchell 1954, 1955; Mitchell and Coles 1955). Very severe defoliation, which implies excessive bud site removal, may also reduce tillering (Holscher 1945).

(c) Leaf Growth

As indicated previously, leaf growth is a function of the rate of shoot appearance and the leaf area of individual shoots; the latter may be considered as a function of the rate and duration of leaf appearance on specific shoots, the rate of individual leaf size expansion and its duration, and the rate of leaf senescence. The extent of intra-plant competition may be gauged from figure 7(b) where the growth of a particular shoot was varied by a factor of 2.6 by the removal of other shoots.

Defoliation effects on meristematic activity were evident within 3 days of defoliation, both shoot and leaf number being stimulated. The main defoliation effect on net leaf expansion occurred in the tertiary leaf class. The effect was delayed longer in the case of the removal of young inflorescences, but it was clear that any additional expansion of the leaf surface in this treatment was occasioned almost entirely by an increased number of shoots. On the other hand, the defoliation effects were exerted in several ways.

Leaves on individual shoots were in some instances differentiated earlier and more leaves were produced on an individual shoot, i.e. greater activity occurred at each terminal meristem until floral initiation. Brougham (1958) reported that leaf differentiation rose and then fell following defoliation; light saturation was involved.

Maximum size of individual leaves was increased by defoliation; this was mainly associated with rate of leaf expansion rather than with increased duration of expansion. Fernando (1958) noted that removal of leaves in sugar beet increased the size of residual leaves; this contrasts with the reduced leaf size reported by Mitchell (1954, 1955) in paspalum, cocksfoot and perennial and short-rotation ryegrasses, and by Langer (1954) in timothy. In experiment 2, increased maximum leaf size was only recorded in leaves appearing at least 3 days after defoliation; residual leaves which were still expanding at the time of defoliation were unaffected. It is tempting to implicate increased cell number, but measurements of cell number and cell size were not made. Morton and Watson (1948) defoliated sugar beet; increased cell size (but not cell number) was recorded in neighbouring leaves. Defoliation of *Ipomoea* (Ashby 1948) promoted both cell number and cell size; cell division could be stimulated at an advanced stage of leaf expansion.

Senescence played an important role in determining net leaf area increment even in these well-grown, spaced seedling plants 10 weeks after emergence. In the datum section of the experiment 2 plants, senescence was equal to net leaf area increment by day 73 in undefoliated plants, whereas senescence amounted to one-third of net leaf area increment in defoliated plants. This difference was due principally to the change in age distribution of leaves rather than to effects of treatment on senescence *per se*. Bean (1964) and Hunt (1965) have drawn attention to the difficulty of interpreting growth data which do not take account of senescence. The individual leaf duration of 40-50 days recorded for green panic in experiment 2 may be contrasted with the values of 56-70 days for cocksfoot (Bean 1964), 40 days for white clover (Brougham 1958) and 42 days for subterranean clover (Stern 1960). Obviously the position, nutrition and light environment of the individual leaf will affect leaf duration; it might also be noted that in experiment 2 leaves were handled in the course of measurement.

Although the magnitude of the effects on growth varied according to stage of defoliation, and the comparisons are to some extent incomplete, the basic pattern of response was similar at the three stages investigated. It was clear that under the favourable growing conditions of the experiments, reduction of the leaf surface by defoliation in flowering plants had little detrimental effect on subsequent leaf growth and in some circumstances increased it, while considerable reductions in stem and inflorescence growth were recorded.

V. GENERAL CONCLUSIONS

A consistent pattern in the experiments reported in this series of papers was the manner in which components of growth operated in a compensatory, self-regulatory fashion, reducing the effects of defoliation on plant growth.

Compensatory relationships were recorded between photosynthetic capacity and efficiency, leaf and stem growth, leaf area/leaf weight ratio and shoot weight, shoot differentiation and leaf number per shoot, leaf number per shoot and leaf size, leaf expansion and leaf senescence, inflorescence removal and rate of appearance

and carbohydrate accumulation and carbohydrate use. This equilibration was well illustrated in experiment 1 of Humphreys and Robinson (1966), where two species of differing habit and management reputation were grown under two extreme defoliation frequencies. Between treatments, root mass varied by a factor of 3.8, non-structural carbohydrate in roots and crown by a factor of 4.0, green leaf growth by a factor of 1.7, and gross treatment differences in rate of tillering were recorded, yet the summation of shoot growth over the period of the experiment varied by only 8% between the four treatments.

Advances in defoliation practice therefore depend upon:

- (a) creating conditions for growth where compensatory checks and balances are less influential;
- (b) recognizing situations where particular growth components predominate;
- (c) promoting the growth of plant organs which are consumed more readily or converted more efficiently by the grazing animal;
- (d) reducing short-term fluctuations in the forage supply; and
- (e) synchronizing more nearly grazing pressure and pasture growth.

Each of these will be discussed in turn.

(a) There is indirect evidence to suggest that the limitations to growth imposed by environmental stresses, such as shortages of nitrogen and of moisture, reduced the effect of differences in the extent of the leaf surface in subsequent shoot growth. This type of effect has been reported in the literature; for instance Bryan and Sharpe (1965) found in pangola grass that the growth response to extension of defoliation interval was enhanced by nitrogen application. In experiment 2 of Humphreys and Robinson (1966) and in experiments 1 and 2 of this paper, where nutrients and moisture were adequate, growth was positively related to residual leaf area. In experiment 1 of Humphreys and Robinson (1966), this relationship was observed during a favourable growth period but was not evident when environmental limitations were apparent. In experiment 2 of Humphreys (1966a), this positive relationship was transitory and disappeared during intermittent checks to growth; the leaf surface did not reach critical LAI.

The climate is capable of sustaining higher growth rates than those recorded in this region under current nutritional conditions; LAI values of up to 7.3 and yields up to 1,320 gm/sq m (11,800 lb/ac) were reported 8 weeks after defoliation in experiment 1 of Humphreys (1966a) following adequate nitrogen and sulphur fertilizer application. It is apparent that the environment is not being exploited under current pasture practice to the point where all light is intercepted by foliage. The scope for improved production from efficient manipulation of the leaf surface will increase when fertility levels have been raised or when irrigation is more commonly employed.

(b) Certain circumstances occurred where specific growth components preponderated. Thus removal of young inflorescences in experiment 1 promoted a real increase in growth, which was attributable to improved net assimilation rate; the use of non-flowering and late flowering grasses, and mechanical topping

of pasture to improve and extend the duration of growth, require further exploration. It should also be noted that net assimilation rate was found to be an influential variable in these experiments, and that high values were recorded.

Reference has already been made to the positive effect of residual leaf area on growth when conditions favourable for growth occurred. As indicated in experiment 2 of Humphreys and Robinson (1966), judicious deferment in these circumstances promoted excellent recovery in plants subjected previously to excessive defoliation stress.

In general, the studies of tillering were not very productive in terms of field application. A better description of plant growth was obtained, but this usually revealed balancing trends; e.g. in experiment 2 of Humphreys and Robinson (1966), heavy defoliation stimulated shoot appearance but individual leaf size was greater on leniently treated plants. In their experiment 1, short-term treatment differences in growth were mainly expressed *via* tiller size rather than tiller number. Particular vulnerabilities to defoliation according to developmental stage and tiller population were not encountered; stage of defoliation effects were largely explicable in terms of residual leaf area.

(c) Although substantial differences in total shoot growth were not recorded in the experiments where intermittent checks to growth occurred, leaf growth was very considerably increased by frequent or severe defoliation. Leaf weight increase was enhanced by a factor of 1.7 in both experiment 1 of Humphreys and Robinson (1966) and experiment 2 of Humphreys (1966a). Leaf area ratios were low; leaf area/leaf weight ratio had values equivalent to those reported for temperate grasses, but leaf weight ratios were comparatively less. The improvement of this factor could lead to production benefits. The relationship of leaf weight ratio to tropical grass quality requires greater study in view of the strictures of Milford (1965). It should, however, be noted that increases in nitrogen content were positively associated with leaf weight ratio and with defoliation intensity in experiment 2 of Humphreys (1966a). The long-term effects require confirmation because of the alternating arrangement of treatments and the common grazing imposed in this experiment, but more efficient cycling of nitrogen under heavy stocking is generally accepted (Davidson 1964).

The magnitude of leaf senescence recorded even in the young, rapidly growing plants in experiment 2 points to the need for frequent defoliation if pasture quality is to be maintained and leaf growth rates maximized. Frequent defoliation is primarily associated with the intensity of grazing pressure, i.e. number of animals carried per unit of land area; it is also associated with grazing method. Rotational grazing, if based on a long interval between grazings, or deferred grazing to meet particular animal needs, must inevitably result in the presentation of forage of reduced quality unless compensating effects on sward botanical compositions occur. Rotational grazing also implies restricted opportunity for the improvement of stock diet through selective grazing of leaf; the higher nutritional status of the leaf fraction was clearly demonstrated in experiment 2 of Humphreys (1966a). Although the evidence

of these studies is indirect, the pertinent information points to more satisfactory utilization occurring under continuous grazing of green panic and buffel grass pastures. On native pasture at "Brian Pastures", Humphreys (unpublished data) recorded that rotational grazing (2 weeks' grazing, 6 weeks' deferment) significantly depressed animal growth compared with continuous grazing.

Increased growth of the root system and the accumulation of additional non-structural carbohydrate had little effect on shoot growth or persistence in experiment 1 of Humphreys and Robinson (1966). The cycle of spring TAC loss and autumn accumulation was accentuated under infrequent defoliation and the midsummer decline in TAC percentage was shown not to represent a reduction in the amount of TAC present. The view is therefore accepted that most of this material is lost in respiration or decay. Under the satisfactory conditions for growth in experiment 2 of Humphreys and Robinson (1966), superior non-structural carbohydrate accumulation (with which was allied other plant factors) stimulated regrowth; however, residual leaf area was of more decisive import, and ranking for carbohydrate status did not parallel exactly the ranking for subsequent growth. Data were also presented which suggested that substrates other than non-structural carbohydrate were involved in shoot synthesis in the absence of light. No evidence was adduced to indicate that stock concentration or pasture cutting may be especially deleterious at a particular stage of plant development or of "reserve" decline.

Attention has often been directed to the importance of an extensive root system and the maintenance of a large crown below defoliation height (Weinmann 1948; Troughton 1957). The wide differences in these factors according to species and defoliation frequency in experiment 1 of Humphreys and Robinson (1966) were not related to shoot growth. Obviously root growth should be sufficient to ensure plant persistence and the adequate absorption of water and minerals, but attention to the maintenance of the leaf canopy is the overriding management objective.

(d) Continuity of the forage supply depends partly upon the maintenance of growth rate and partly upon under-utilization to provide forage reserves for periods of slow growth or of pasture deterioration. In experiment 1 of Humphreys and Robinson (1966), frequent defoliation diminished fluctuations in growth rate and extended the duration of growth; in experiment 2 of Humphreys (1966a), there were no consistent effects of defoliation intensity on the extension of the growing season, although short-term extensions in the duration of plant turgor were noted. In both experiments greater pasture use was obtained without detriment to total shoot growth. Within the limits of these experimental conditions, the evidence therefore favoured a policy of heavy stocking. Under the restricted fertility and moisture regimen common in pastoral practice, the studies suggest that pasture may be cut for conservation quite close to the ground without detriment to aftermath growth. In these experiments and in experiments 1 and 2, leaf growth was increased later into the autumn by heavy defoliation.

Heavy use of pasture renders the stock-raiser more vulnerable to drought and the land more susceptible to erosion. In assessing these hazards, it should be recognized that deterioration of pasture quality and substantial losses in dry matter attributable to senescence are implicit in lenient grazing systems. Sown pastures in southern and central Queensland have shown good performance under abnormal drought conditions when heavily stocked. Young, Fox, and Burns (1959) recorded that cattle grazing sown pastures at "Brian Pastures" at double the normal stocking rate of native pastures survived the severe 1958 drought without loss; excellent persistence of green panic and of buffel grass also occurred. Similarly, sown pastures at Rodds Bay, on the central Queensland coast (Anon. 1964) have given high stock production and persistence under heavy grazing regimens during drought.

(e) The more effective synchronization of grazing pressure and pasture growth is fraught with practical difficulties. These are mainly related to the lack of flexibility in animal numbers on a property basis, the inability accurately to predict pasture growth rate, and the seasonal nature of pasture growth. On the majority of subtropical cattle properties, stocking rate is primarily determined by the quality of the native pasture in the cool season, as this limits the number of animals which can be grazed on a year-round basis. This results in extreme under-utilization of pasture growth; it is difficult to influence pasture growth under these conditions (Moore, Barrie, and Kipps 1946). The wide variation between seasons in pasture growth was illustrated in the two long-term experiments reported in this series.

The following management practices can result in improved utilization of summer growth:

- (1) The restriction of calving to the late winter-early spring period.
- (2) The sale of non-pregnant cows and other dry stock in autumn.
- (3) The purchase of cattle in early summer and their sale in autumn.
- (4) The provision of protein supplements when pasture quality is low, thereby enabling more effective use of stand-over pasture and the overall raising of stocking rate.
- (5) The provision of alternative feed sources for periods of pasture scarcity, e.g. grazing oats grown on summer fallow, feedlot finishing of cattle using grain and/or conserved pasture, irrigated pasture.
- (6) The utilization of faster responding pastures on lighter soils earlier in the growing season than slower growing swards on heavier soils.
- (7) The establishment of pasture legumes and the use of fertilizer to improve herbage quality.

The literature on defoliation was reviewed elsewhere (Humphreys 1966b) in terms of six conceptual bases for management practice, and the relevance of some aspects of five of those to grass management in a sub-coastal southern Queensland area has been investigated. It has been shown that the concepts of maintenance of plant carbohydrate status, efficient use of light, and control of

plant tillering have very limited applicability under current pasture productivity levels and management intensity. On the other hand, some modifications to the environment in terms of nitrogen and moisture use are possible, and animal requirements for sustained pasture growth of better quality may in part be met by the substantial improvement in leaf growth occasioned by defoliation of sufficient frequency and intensity. These aspects are undergoing further study.

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(The work reported here was conducted while the author was an officer of the Agriculture Branch, Division of Plant Industry, Department of Primary Industries. His present address is Department of Agriculture, University of Queensland.)