QUEENSLAND DEPARTMENT OF PRIMARY INDUSTRIES
DIVISION OF PLANT INDUSTRY BULLETIN No. 363

SUBTROPICAL GRASS GROWTH. 2. EFFECTS OF VARIATION IN LEAF AREA INDEX IN THE FIELD

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SUMMARY

Swards of green panic whose growth had been varied by fertilizer application exhibited critical LAI values of 3·5–4·0 at shoot yields of 700–820 g/m^2 at Gayndah, south-eastern Queensland. Leaf area/leaf weight and leaf weight ratio were respectively positively and negatively related to yield.

In a subsequent experiment, the residual leaf area remaining after defoliation of green panic was varied, and growth characteristics recorded in the 6 weeks following each of a series of 12 defoliations. Under the normal moisture and nutritional stresses of this environment, leaf growth was insufficient to intercept all light and residual LAI was poorly related to shoot growth. On the other hand, leaf growth and shoot nitrogen content were negatively related to residual LAI.

I. INTRODUCTION

In the first paper of this series (Humphreys and Robinson 1966), a positive relationship between residual LAI after defoliation and growth rate was recorded for green panic (*Panicum maximum* var. *trichoglume* (K. Schum.) Eyles) grown in large drums under conditions of adequate moisture and nitrogen supply. This paper reports the results of growth studies of green panic which were carried out under sward conditions, to determine whether relationships between LAI, light interception and growth could be established in order to secure bases for defoliation practice. The literature on this question has been reviewed elsewhere (Humphreys 1966*b*).

"Queensland Journal of Agricultural and Animal Sciences", Vol. 23, 1966.

II. EXPERIMENTAL

(a) Experiment 1: Inter-relations of Yield, Leaf Area and Light Interception in Green Panic Swards

The objective of this study was to determine the inter-relations of yield, leaf area and light interception in green panic swards, by measuring these parameters on plots whose growth had been varied by fertilizer application.

A fertilizer experiment was established on a green panic sward sown in March 1954 in the B.P.I. reserve paddock of the "Brian Pastures" Pasture Research Station, Gayndah. An opportunity was taken to collect subordinate data on leaf area and yield from this experiment. A factorial design of eight nitrogen treatments involving levels of nil to 210 lb nitrogen per acre in equal 30-lb increments as urea and of four sulphur levels of nil to 60 lb sulphur per acre in equal 20-lb increments was laid down with two absolute replications as a confounded arrangement in blocks of 16 plots.

Plot size was 2·12 m x 3·18 m and fertilizer was applied on March 2, 1959. The area was mown on October 29, 1959. On January 8, 1960, 26 plots were selected which would provide a range of swards whose light values 2 cm above ground level varied from 0·01 to 0·65 daylight. Yield was estimated by cutting three 1·01 m x 0·40 m quadrats per plot; leaf weight ratio was determined from a subsample from each plot. Leaf area/leaf weight ratio was only determined from 16 plots. The area was again mown on January 8, 1960, and regrowth yield determined on 48 plots on March 23, 1960. Leaf weight ratio was estimated on 48 plots and leaf area/leaf weight ratio on 24 plots.

Leaf area per unit ground surface (LAI) was then calculated from the formula $\text{LAI} = \frac{\text{La}}{\text{Lw}} \times \frac{\text{Lw}}{\text{W}} \times \text{W}$, where La and Lw are leaf areas and leaf weights respectively and W is the plant weight. The time involved in leaf area determinations being greater than that involved in weight determinations, a higher order of sampling intensity was possible with the latter parameter. Care was necessary to obtain representative subsamples; the total plant sample was spread thinly on the laboratory bench and random "grab" samples of whole tillers taken. These were then divided into green lamina and residual plant parts, and the area of green lamina was determined.

Leaf area was determined by blueprinting leaf outlines with "Pherax medium" blueprint paper. The leaf outlines were then cut out with scissors, bulked, weighed, and leaf area determined using the ratio of paper area/paper weight. Large plant samples were air-dried in coarse-mesh hessian bags suspended just below the roof of an open building. Small samples were air-dried in open plastic bags. Moisture determinations on bulked samples were then made after drying in a forced-draught oven at 105°C to constant weight.

On both sampling occasions, 15 determinations of light interception per plot were made, using the method outlined subsequently for experiment 2.

(b) Experiment 2: Growth of Green Panic Swards Under Varying Defoliation Intensity

(i) *Objective.*—The aim of the experiment was to determine the effect of variations in residual LAI, induced by defoliation on different occasions, on the subsequent growth of shoots and leaves of green panic swards when grown under natural rainfall conditions and moderate fertility.

(ii) *Treatments and design.*—There were three defoliation intensities, referred to as lenient (L), medium (M) and heavy (H). In order to avoid the confounding of previous defoliation history with the main effect of treatment variation in LAI imposed on any defoliation occasion, a cyclic arrangement of treatments was adopted. This consisted of three basic cycles, LHH, HMM, MLL, each phase of which was represented on each defoliation occasion, making nine treatments. These were arranged in three fully randomized blocks, each comprising nine plots. Table 1 shows the treatment sequence.

TABLE 1

SEQUENCE OF TREATMENTS IN EXPERIMENT 2*

Treatment No.	Defoliation No.					
	I	II	III	IV	V	VI
1	L	H	H	L	H	H
2	H	L	H	H	L	H
3	H	H	L	H	H	L
4	H	M	M	H	M	M
5	M	H	M	M	H	M
6	M	M	H	M	M	H
7	M	L	L	M	L	L
8	L	M	L	L	M	L
9	L	L	M	L	L	M

* The sequence given here was continued for subsequent defoliations

It will be noted that, for example, of the three heavy treatments of a particular defoliation occasion, one receives lenient, one medium and one heavy defoliation intensity on the previous defoliation occasion, and that balance is also maintained for the defoliation occasion previous to that.

(iii) *Method.*—The experimental area, which was located in the "Brian Pastures" nursery block, received 6 months' ground preparation, was drill-sown on February 20, 1959, at the rate of 6 lb green panic and 1 lb Hunter River lucerne per acre, and rolled with a tyre-roller. Moisture conditions at sowing were good, but no follow-up rain occurred until mid March. Green panic emerged initially in the strips rolled by the tractor tyres, and further emergence occurred at the end of March. The area was carefully hand-weeded in May 1959 and again at the end of October 1959, when green panic seed was surface broadcast in an attempt to improve plant density. Owing to the unsatisfactory lucerne distribution, the area was sprayed with 2,4-D ester to eradicate this component, Plot size was 40 m x 2·5 m, within which a datum area of 31·8 m x 1·7 m was defined for sampling. Defoliation treatments were imposed at intervals of 6 weeks during the growing season. On each occasion a number of steers, varying from 50 to 5 according to the amount of pasture present, were allowed to graze overnight on the whole experimental area of 0·65 ac. The M treatments were then cut with a rotary chain slasher at 15-cm height, and the H treatments at 10-cm height. The cut material was raked and removed from the plots. Twelve defoliations were applied over three seasons as shown in Table 2.

TABLE 2

Treatment Characteristics in Experiment 2

Defoliation No.	Date	Residual LAI After Defoliation			L.S.D.	
		Lenient	Medium	Heavy	5%	1%
I	13.x.59	0·26	0·19	0·08	0·15	0·22
II	24.xi.59	0·88	0·23	0·12	0·32	0·46
III	5.i.60	0·94	0·24	0·10	0·42	0·61
IV	17.ii.60	0·56	0·35	0·07	0·39	0·57
V	29.iii.60	0·61	0·42	0·10	0·22	0·31
VI	8.xii.60	1·03	0·79	0·22	0·41	0·59
VII	18.i.61	0·82	0·31	0·34	0·35	0·51
VIII	2.iii.61	0·33	0·30	0·10	0·20	0·29
IX	14.iv.61	0·14	0·06	0·04	0·07	0·10
X	29.xi.61	1·45	0·72	0·22	0·25	0·36
XI	10.i.62	0·90	0·23	0·07	0·27	0·39
XII	21.ii.62	0·46	0·19	0·07	0·06	0·08

Within-treatment variability was increased by the selective grazing of plots receiving H or M defoliation intensity 6 weeks previously.

Pasture measurements were made immediately after each defoliation, 3 weeks after defoliation, and 6 weeks after defoliation (immediately prior to the next grazing). During the winter and spring months, measurements were also made at intervals of 3 weeks. Five 1·01 m x 0·40 m quadrats were cut in each plot on each sampling occasion. The sampling plan, which was based on a grid system, incorporated several elements of randomness, prevented the occurrence of contiguous sampling positions along the longer side of the quadrat for at least 12 weeks, and provided for resampling of the same position only after an interval of 18 months. Leaf weight ratio was determined on a subsample from each plot, but leaf area/leaf weight ratio was estimated only in the plots of two of the three blocks. Thus shoot and leaf weight determinations were based on 27 plots, and LAI and dependent data on 18 plots only. For harvests 1-12 (to 28.iii.60) leaf area was determined as described for experiment 1; thereafter the method outlined in the previous paper (Humphreys and Robinson 1966) was employed.

A light meter was constructed for these studies by P. B. Hogg Scientific Supplies Ltd., Brisbane. It was necessary to use an instrument which would cause as little displacement of the pasture as possible. A small EEL selenium cell with an exposure aperture of 5 x 0·8 cm was mounted on the extremity of a telescopic probe 1 m long and 1·9 cm in diameter, and connected to an ammeter with three resistances built in. These gave reading scales of 0–20, 0–200 and 0–2,000 f.c. A detachable filter of transmission 0·112 further increased the range. A circular spirit bubble was mounted on the probe on the opposite end to the cell to enable the operator to hold the cell level.

The procedure adopted was to take random points in a plot, which were fixed by measurement and which were greater than 1 m from a recent harvest site. The spirit bubble was placed over the point, the probe was then inserted into the pasture at ground level, and five measurements were taken on the approximate compass points, N., NE., E., SE. and S. Sky illumination above the pasture was also determined. The light value at ground level was then calculated as the ratio of illumination at ground level to illumination above the pasture.

On the first four occasions, when the treatment mean light values at ground level varied from 0·86 to 0·60, the S.E. of a treatment mean was 11·7% of the general mean, using 2 points (= 10 determinations) per plot. The sampling intensity was thereafter increased to 3 points (= 15 determinations) per plot.

A statistical examination of early data also revealed that light values at ground level (as defined above) were independent of variations in illumination intensity due to changing cloudiness. However, to minimize the effects of variations in sun elevation on each harvest day, observations were always recorded as close to noon as possible.

Soil moisture was determined by successive sampling with a 5-cm soil auger, taking one site per plot in 18 of the 27 plots, and separating the horizons 0–15 cm, 15–30 cm, 30–60 cm, and 60–90 cm. The whole sample was placed in a tin with a close-fitting lid, weighed, and dried at 105°C to constant weight.

The experiment was also sampled in the 1963 summer to determine whether the three defoliation cycles exerted differential residual effects on growth.

Fertilizer dressings of sulphate of ammonia equivalent to 3·4 g N/m^2 (=30 lb/ac) were applied at defoliations III, V, VI, IX and X.

III. RESULTS

(a) Experiment 1: Inter-relations of Yield, Leaf Area and Light Interception in Green Panic Swards

In this experiment, positive growth responses to the application of both nitrogen and sulphur were obtained; yield variation and its associated parameters were therefore confounded with nutritional effects.

The data for the harvest on January 8, 1960, are presented in Figure 1.

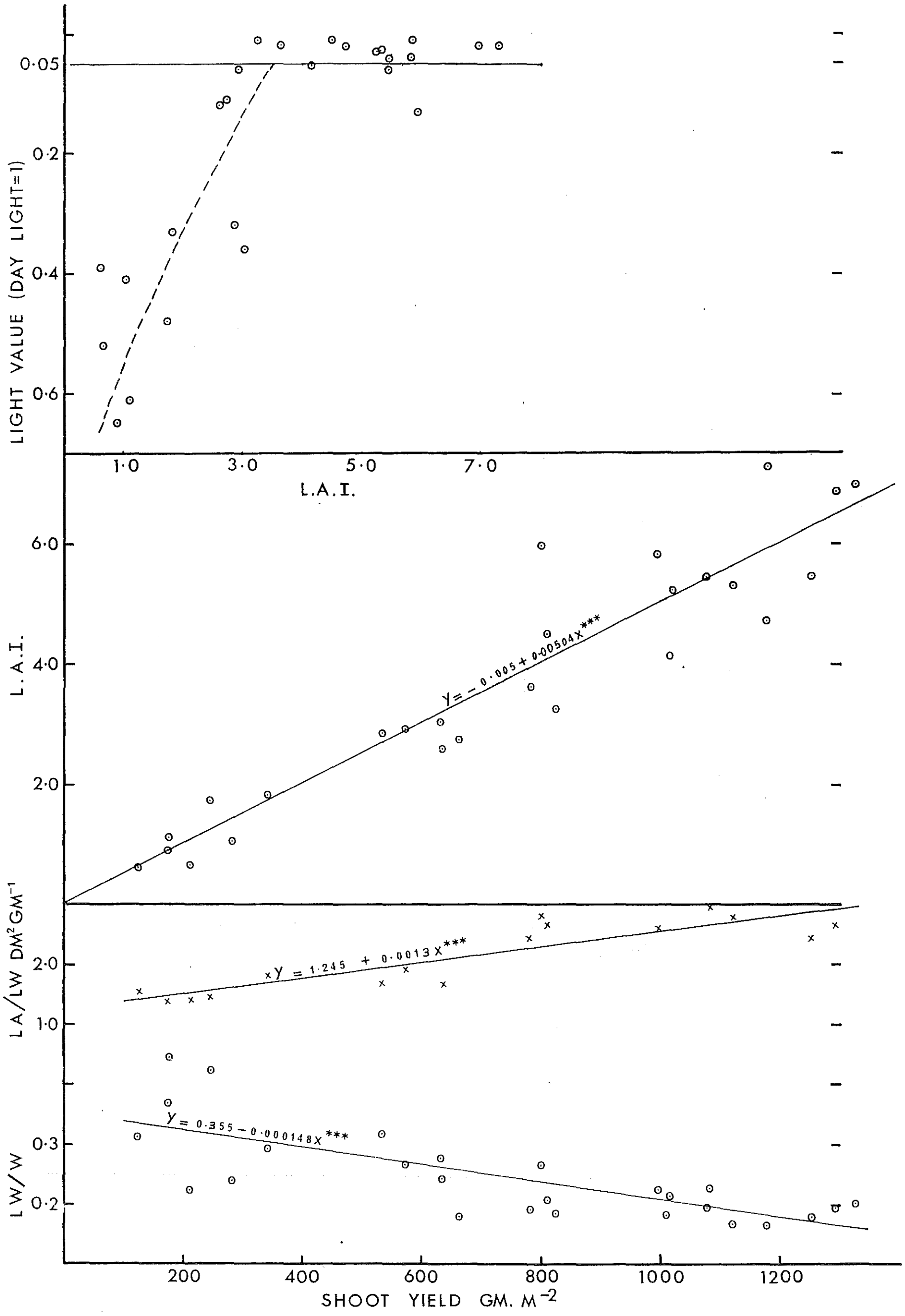

Fig. 1—Experiment 1: Relationships for green panic swards on January 8, 1960, between yield and light values at ground level, LAI, leaf area/leaf weight ratio, and leaf weight ratio.

Critical LAI (light value 0·05 daylight) had a value of approximately 3·5, an unexpectedly low value, when shoot yield was 700 g/m^2 (= 6,300 lb/ac), and values of LAI ranged up to a maximum of 7·3. Maximum recorded shoot yield was 1,320 g/m^2 (= 11,800 lb/ac). Leaf area/leaf weight ratio increased with rising yield, whereas leaf weight ratio was negatively related to yield. The compensating effect of these two parameters gave a positive relationship between LAI and yield which showed little departure from linearity over the range of values recorded. On the other hand, leaf weight, which is not shown in Figure 1, showed a curvilinear relationship with yield ($Lw = 0{\cdot}3553\ W - 0{\cdot}0001479\ W^2$, where Lw and W are the leaf and shoot weights expressed as g/m^2).

The values obtained from the harvest on January 8, 1960, provided a more representative series than those recorded on March 23, 1960, since on the latter occasion only two values reached critical LAI. The form of the relationships was similar. Leaf weight ratio declined more sharply with increasing yield, and critical LAI, though still in the range of 3·5–4·0, occurred at the higher yield of about 820 g/m^2 (= 7,300 lb/ac). The relationship between LAI and light values was more variable; stem surface area was not measured but it appeared that this factor was influential. On this second occasion development was more advanced and moisture stress reduced yields.

(b) Experiment 2: Growth of Green Panic Swards Under Varying Defoliation Intensity

(i) *Dry-weight changes.*—Defoliation intensity had no overall effect on the summation of shoot growth over the 12 periods after each defoliation. The results are summarized in Table 3; it will be noted that the range in total increments for treatments did not exceed 5%. Variability in this experiment was high, owing to the inherent variation in plant density occasioned by unfavourable post-sowing conditions. Nevertheless, significant differences in residual LAI (Table 2) and in leaf growth were demonstrated, suggesting that the absence of overall treatment effects on shoot dry-weight increase was real.

Shoot growth rates varied markedly within and between seasons; midsummer growth rates could be lower than those of early or late summer if moisture stress occurred. In each of the twelve 6-week periods some wilting was observed, at least in the lenient defoliation treatments. These wilted before the heavily defoliated swards; the medium defoliation swards were distinguished in an intermediate position, or wilted at the same time as heavy defoliation. The onset of wilting varied by up to 10 days between heavy and lenient; the degree of wilting was also affected.

Maximum growth rate (9·0 g/m^2 day) was recorded in the first 3 weeks after defoliation X (November 29, 1961) in the lenient swards. Although some suggestive treatment differences were recorded for individual growth periods significant effects appeared only in the three defoliation periods at the end of each season, and these do not form a consistent pattern. In each case flowering

TABLE 3

EXPERIMENT 2: EFFECT OF DEFOLIATION INTENSITY ON GROWTH OF SHOOTS AND LEAF, AND ON LEAF EXPANSION IN THE 6 WEEKS AFTER DEFOLIATION

Defoliation No.	Defoliation Date	Rainfall during Growth Period (in.)	Growth of Shoots ($g/m^2/day$)					Growth of Leaf ($g/m^2/day$)					Leaf Area Growth Rate ($m^2/m^2/day$)				
			Lenient	Medium	Heavy	L.S.D.		Lenient	Medium	Heavy	L.S.D.		Lenient	Medium	Heavy	L.S.D.	
						5%	1%				5%	1%				5%	1%
I	13.x.59	6·45	3·86	2·70	3·82	..	..	2·72	2·29	2·29	..	..	0·435	0·0456	0·0394	..	..
II	24.xi.59	7·53	4·00	4·15	4·37	..	..	1·46	1·53	2·31	0·83	1·14	0·0418	0·0358	0·0362	..	..
III	5.i.60	5·51	2·04	3·38	4·04	..	..	−0·39	0·81	1·64	0·73	1·00	0·0013	0·0277	0·0485	0·0161	0·0234
IV	17.ii.60	5·72	4·68	2·89	2·05	..	..	1·55	1·60	1·21	..	..	0·0457	0·0417	0·0333	..	..
V	29.iii.60	1·44	1·73	−0·14	−0·27	1·89	2·60	0·40	0·34	0·45	..	..	0·0036	0·0070	0·0112	0·0073	0·0106
VI	8.xii.60	5·03	1·60	2·31	1·68	..	..	0·72	1·05	1·20	..	..	0·0147	0·0304	0·0346	0·0175	0·0255
VII	18.i.61	5·94	1·55	0·76	2·23	..	..	1·16	0·68	1·28	0·53	0·73	0·0430	0·0277	0·0472	..	..
VIII	2.iii.61	1·39	0·41	0·56	0·88	..	..	0·23	0·39	0·71	0·31	0·43	0·0081	0·0137	0·0208	0·0114	0·0166
IX	14.iv.61	0·58	−1·06	0·00	−0·25	0·88	1·21	−0·21	−0·05	−0·06	0·09	0·13	−0·0031	−0·0010	−0·0007	0·0016	0·0023
X	29.xi.61	5·45*	5·77	7·12	5·66	..	..	0·32	1·36	2·38	0·76	1·05	0·0103	0·0477	0·0779	0·0191	0·0277
XI	10.i.63	5·25	1·23	1·26	1·03	..	..	0·69	1·43	1·44	..	..	0·0169	0·0399	0·0355	..	..
XII	21.ii.62	4·73	2·47	3·47	1·73	1·61	2·22	0·88	1·30	1·15	0·34	0·47	0·0259	0·0364	0·0372	0·0109	0·0158
Total increment		..	1,154	1,161	1,101	..	..	388	519	654	89	123	9·85	14·23	17·69	1·94	2·83

* 6·31 in. in preceding 3 weeks

was well advanced in the lenient swards and moisture limitations were apparent, albeit less influential after XII. First frosts occurred in the 6 weeks following defoliations V and IX. After defoliation V, growth rate for lenient exceeded that for heavily defoliated swards, and after defoliations IX and XII, medium treatment swards grew faster than lenient and heavily defoliated swards respectively. In all three periods, treatment effects were due to variation in net assimilation rate rather than to leaf area. In the dry 3 weeks after defoliation VII, heavy treatment swards grew significantly faster than lenient, but this advantage was largely lost in the subsequent very wet 3 weeks, when lenient exceeded heavy. In both the 1960 and the 1961 winters, the rate of pasture deterioration was, naturally enough, inversely proportional to the intensity of defoliation.

Compensating effects between leaf and stem growth were evident. The weight of lamina produced (Table 3) was increased by a factor of 1·3 by medium defoliation, and by a factor of 1·7 by heavy defoliation. After seven of the 12 defoliations, significant effects were recorded which were indicative of a positive relationship between leaf growth and defoliation intensity. After defoliation I (October 13, 1959), when growth was vegetative, the highest leaf growth rate was registered from the lenient swards, but this effect was non-significant. On the other hand, stem growth was usually reduced by medium or heavy defoliation.

The effects of previous defoliations were usually non-persistent. Occasionally these reinforced the main effects of current defoliation; for instance, in the 1961-62 growing season heavy defoliation following heavy defoliation stimulated increased leaf weight compared with heavy following lenient, and lenient after heavy was superior to lenient after lenient. Residual effects of defoliation cycle on shoot growth were measured in the 1962-63 summer. These effects were non-significant; the cycles HMM, MLL and LHH produced growth in the ratio of 100 : 104 : 112 respectively.

(ii) *Growth analysis.*—Absolute growth rate is the product of net assimilation rate (E) and mean leaf area (LAI). Values of E, which are derived from difference measurements of both yield and leaf area, are inherently subject to great variability. In this experiment, treatment differences in E reached significance on only three occasions, and in these, values of E for the M and/or H treatments exceeded those of the L treatments. This trend was not consistent, (see Figure 2), but the distribution of E values tended to be lower under lenient defoliation than under either heavy or medium defoliation. The range of values over all treatments was from negative to 0·14 g/dm^2/day.

Mean leaf area for a particular period is a function of the LAI present at the commencement of the period and the rate of LAI increase. For the first 3 weeks after each defoliation, the initial advantage of the L treatments was maintained in 10 of the 12 periods (see Figure 2). In the second period from 3 to 6 weeks after defoliation, mean LAI was significantly greater in the lenient

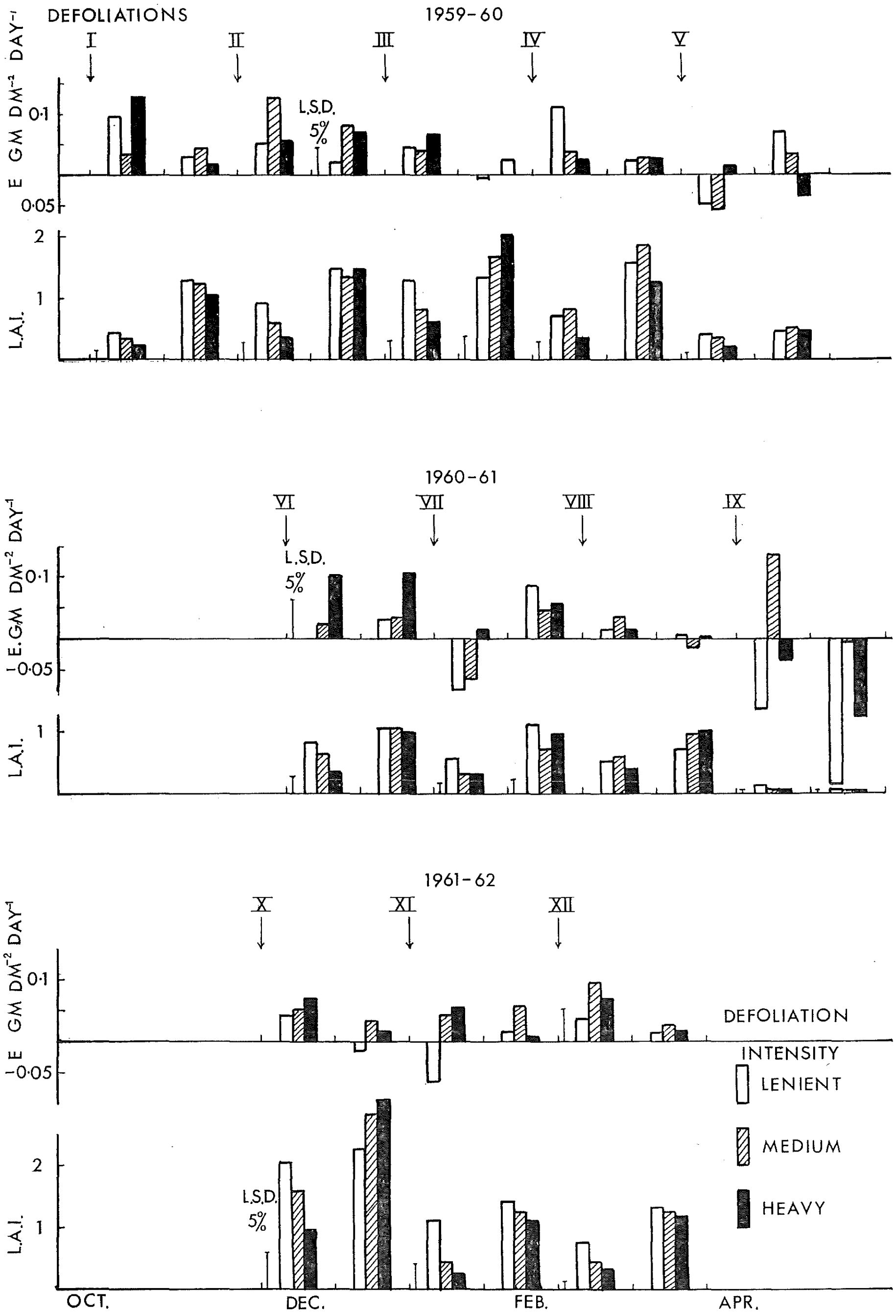

Fig. 2.—Experiment 2: Values of net assimilation rate (E) and mean leaf area (LAI) for periods of 0–3 and 3–6 weeks after each of 12 defoliations of varying intensity.

treatment after defoliations VII (satisfactory growing conditions) and IX (declining LAI in all treatments); it was significantly greater under heavy defoliation after defoliation III. LAI did not exceed 3·4. Light values near ground level throughout the experiment rarely fell below 0·3 daylight and never reached the critical 0·05 value. Maximum illumination recorded above the pasture was 11,100 f.c.

The rates of leaf area increase are summarized in Table 3. Significant treatment effects were recorded on seven of the 12 occasions; each of these indicated a positive relationship between leaf area increase and intensity of defoliation. The summation for the 12 periods showed that leaf area increase was enhanced by medium defoliation by a factor of 1·5, and by 1·8 by heavy defoliation.

Leaf area at any moment may be considered as the product of leaf area/leaf weight ratio, leaf weight ratio and shoot yield. Leaf area/leaf weight ratio is proportional to the thinness of the lamina, and inversely proportional to the specific gravity of the lamina. This parameter is plotted in Figure 3. A tendency of values to rise with advancing season, at least until the cessation of growth in the autumn, was evident in 1959-60 and 1960-61. Immediately after defoliation, La/Lw was negatively related to defoliation intensity; this effect was significant for defoliations II, III, X and XI, but was reversed at XII, where a high value after heavy defoliation was recorded. The residual leaf area after slashing comprised a higher proportion of basal leaves, and of severed leaves consisting only of the younger, proximal portion of the lamina. Three weeks after defoliation, treatment order was changed radically. On seven of 12 occasions, a significant positive association with defoliation intensity was recorded; 6 weeks after defoliation this positive association was still evident, and reached significance on five occasions.

Similar relationships were shown for leaf weight ratio. The negative relationship of Lw/W to defoliation intensity immediately after defoliation was significant on nine of 12 occasions; the positive relationship was significant on four occasions 3 weeks after defoliation, and on seven occasions 6 weeks after defoliation (Figure 4). Values tended to fall with advancing season; this was related to development stage. The amount of flowering was negatively related to defoliation intensity, but flowering was not prevented by heavy defoliation on any occasion.

In general, it may be stated that the negative relationship between E and LAI militated against the appearance of treatment growth differences. This relationship was not entirely consistent, but frequently the lower values of E in the lenient treatments were compensated by the higher initial LAI of the lenient treatments. The higher rates of LAI increase in the medium and heavy treatments did not overcome the disadvantage of low initial LAI sufficiently to promote higher leaf area duration.

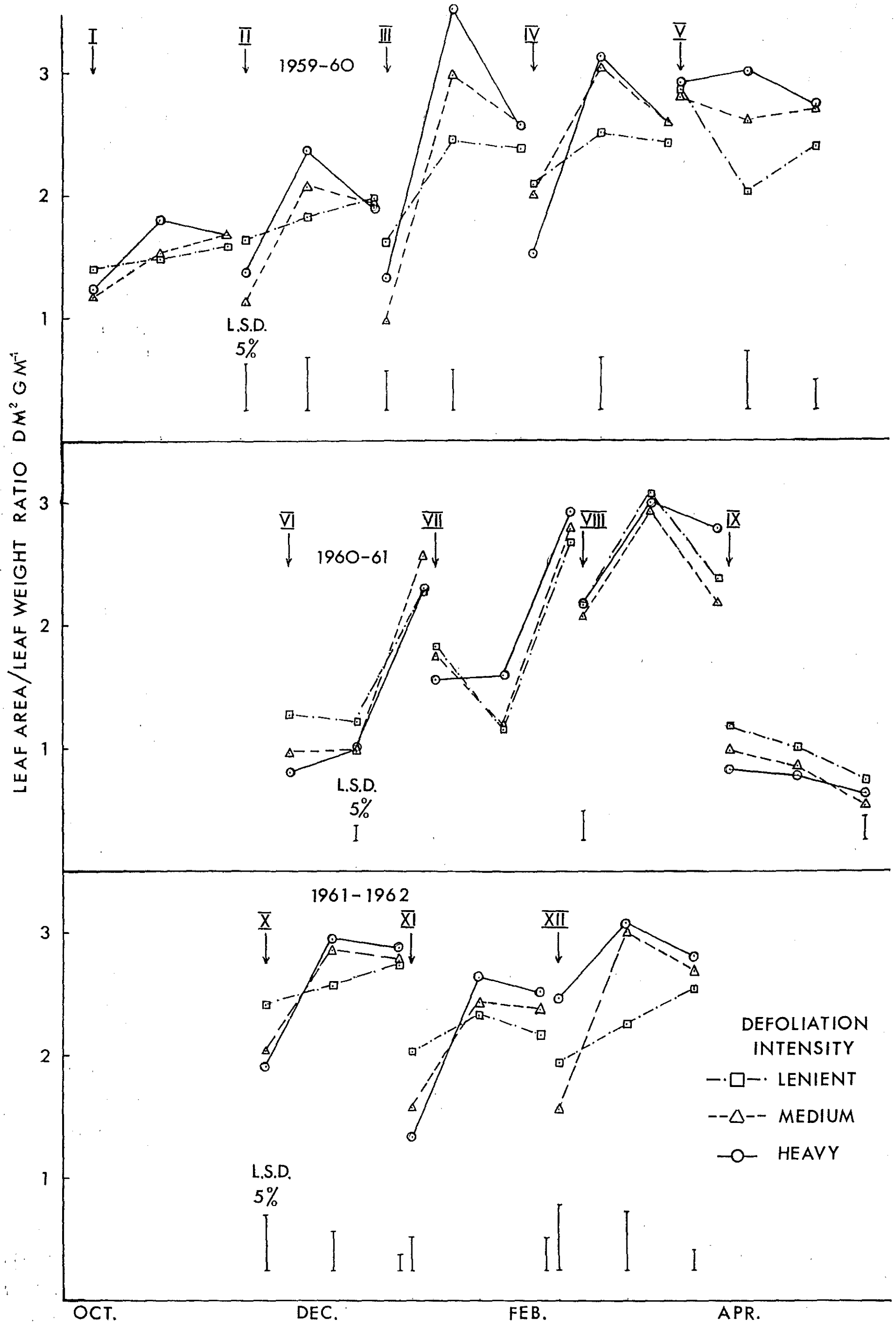

Fig. 3.—Experiment 2: Values of leaf area/leaf weight ratio (dm²/g) subsequent to each of 12 defoliations of varying intensity.

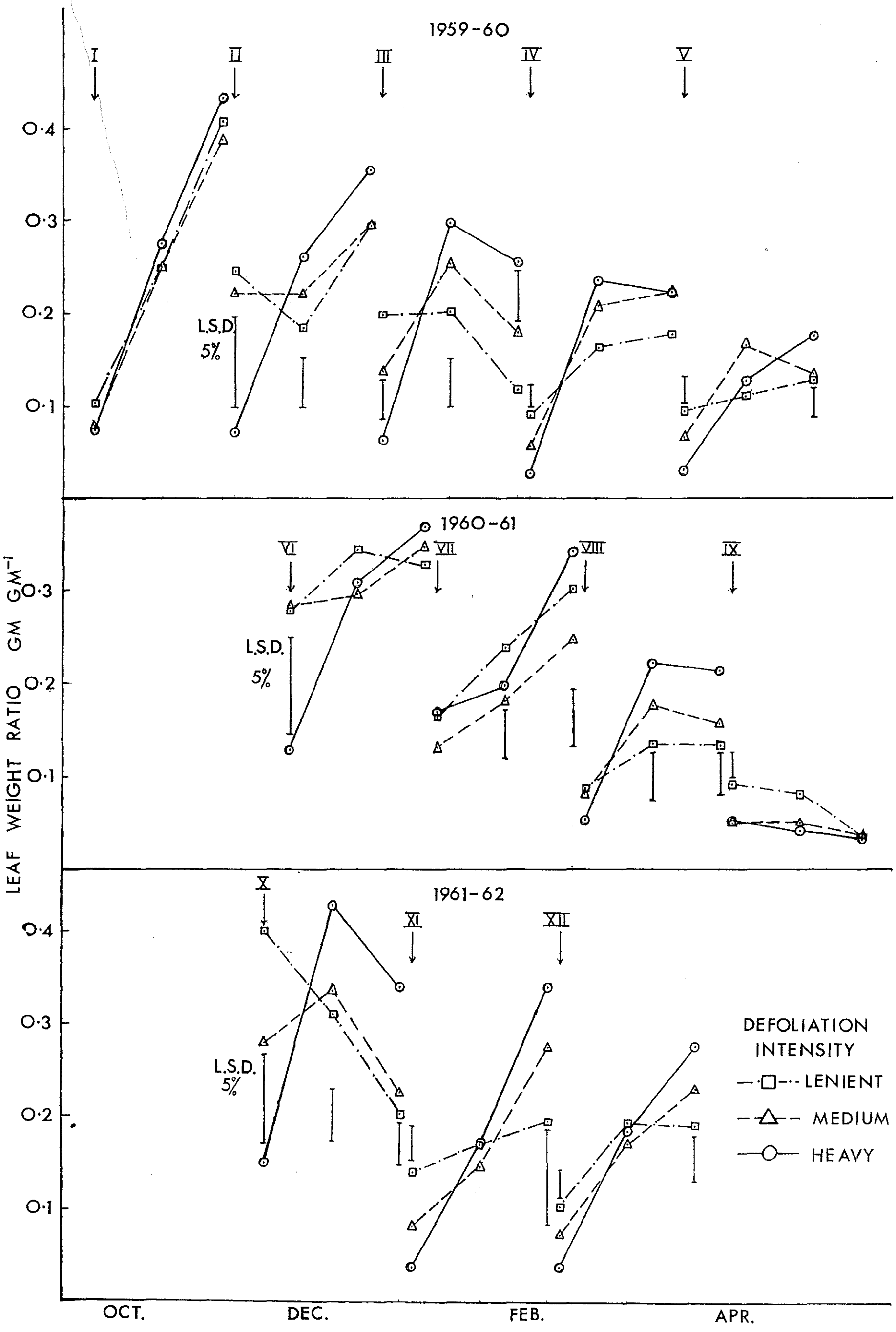

Fig. 4.—Experiment 2: Values of leaf weight ratio (g/g) subsequent to each of 12 defoliations of varying intensity.

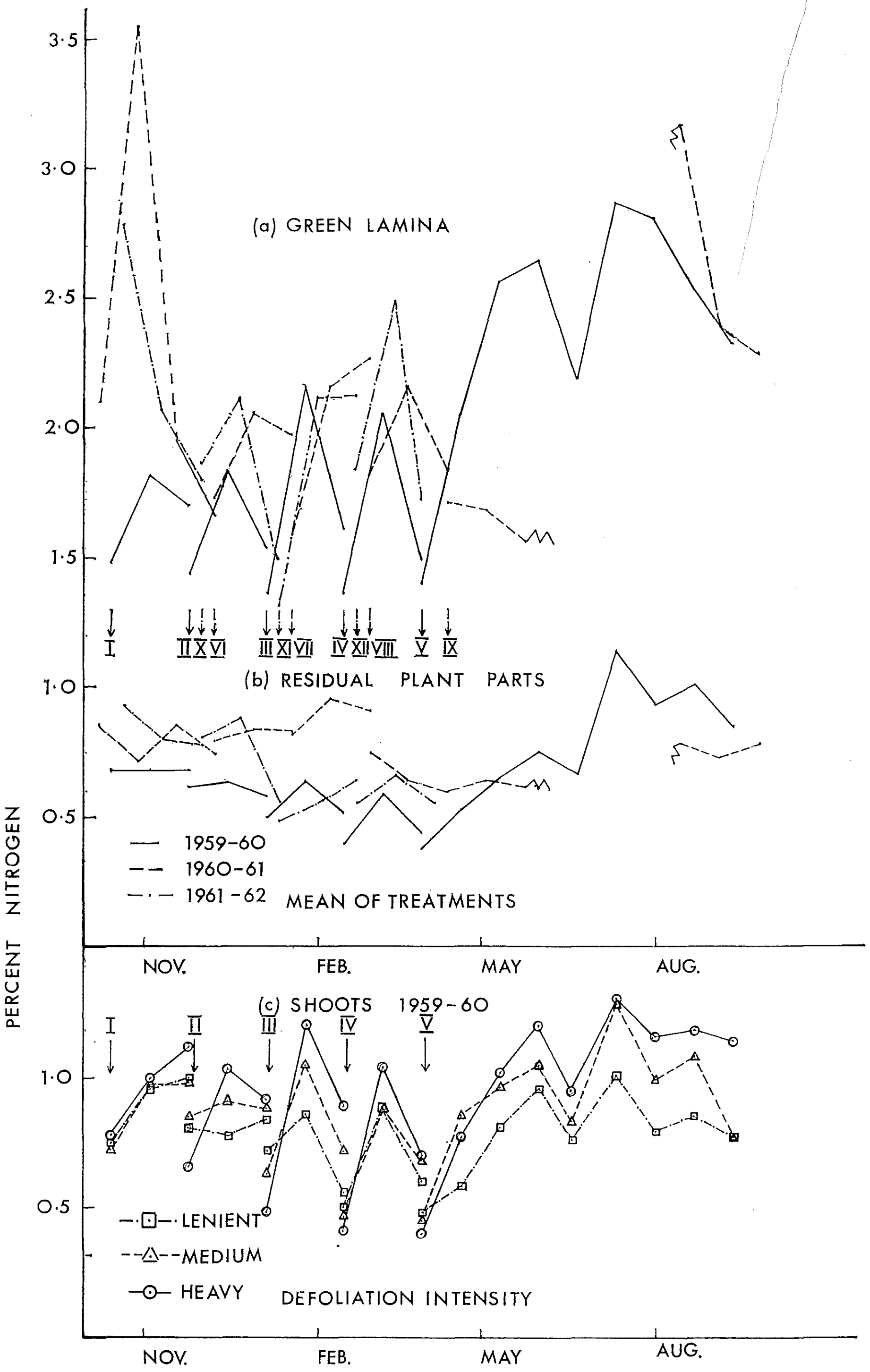

Fig. 5.—Experiment 2: Nitrogen percentage in (*a*) green lamina and (*b*) residual plant parts, for the mean of defoliation treatments over three seasons, and in (*c*) shoots after defoliations of varying intensity in 1959-60.

(iii) *Nitrogen content.*—Since the effect of treatments on pasture quality is of interest, some data for nitrogen percentage are shown in Figure 5. Defoliation reduced the nitrogen content of shoots, and immediately after defoliation nitrogen content was negatively related to defoliation intensity. As growth proceeded, nitrogen content became positively related to defoliation intensity. This effect was due both to the altered proportions of lamina to residual plant parts and to a higher nitrogen content of the respective plant parts in the more heavily defoliated treatments.

The nitrogen percentage of green lamina over the whole course of the experiment averaged 2·9 times the nitrogen percentage of residual plant parts (leaf sheath, attached brown lamina, stem and inflorescence).

In general, values were lowest in midsummer, late summer and autumn, and rose very sharply in the spring and early summer. Percentage nitrogen was maintained at better levels into the summer in the drier 1960-61 season. The very high values of nitrogen content in green lamina recorded in winter, which were of the order of 2·5–3%, were noteworthy.

IV. DISCUSSION

(a) Inter-relations of Yield, Leaf Area, and Light Interception

The values of critical LAI of 3·5–4 recorded for green panic are equivalent to the lower values reported by workers for temperate grasses and clovers (Brougham 1956, 1958; Davidson and Donald 1958; Black 1963; Anslow 1965); they might be contrasted with the value of 14 reported for pearl millet (McCloud 1965). However, the values for leaf area ratio (leaf area/shoot weight, LAR) are very much lower than other reports; the yields of 700–820 g/m^2 (6,300–7,300 lb/ac) which were necessary before 95% light interception occurred are not commonly encountered in field grazing practice. With adequate nitrogen nutrition it is possible to achieve this condition in summer, but it would be very difficult indeed to maintain this quantity of pasturage present under grazing in the Gayndah environment. In experiment 2, where fertilizer additions amounted to 6·8 g/N/m^2 per annum (60 lb N/ac), light values near ground level rarely fell below 0·3 daylight and did not reach the critical level. It is obvious that under current pastoral practice, light is not a limiting factor in the growth of green panic swards in the Gayndah environment; attention must be directed to improving soil nutrient conditions and ameliorating moisture stress before an attempt may be made to apply the conventional concepts of optimum LAI and efficient light use.

It is interesting to note the near constancy of LAR in swards whose yield was varied by nitrogen and sulphur nutrition in experiment 1. The constancy of LAR above critical LAI indicates adaptation to provide more efficient light use at higher LAI's, perhaps through the better spatial distribution of leaves on flowering stems. The increasing values of La/Lw with rising yield may be ascribed to the increase in mutual shading; the effect of shade in enhancing La/Lw is well known (e.g. Blackman and Wilson 1954). This was compensated by declining Lw/W with rising yield, which was related to advancing development stage. Values for Lw/W were similar to those reported for *Panicum antidotale* (Holt 1963). In experiment 2, yield 3 and 6 weeks after defoliation was also negatively related to Lw/W, but was not necessarily positively related to La/Lw; mutual shading was less apparent in this experiment. In view of the low values of LAR and of the rise in the variability of the relation between LAI and light interception at the second harvest of experiment 1 when flowering was well advanced, it is obvious that stem tissue and inflorescence tissue need to be taken into account as modifying influences on the light environment of green panic swards (cf. Archbold 1942; Watson, Thorne, and French 1963). An over-estimation of E must have resulted from neglecting the contribution of other green surfaces and basing this parameter on lamina area only.

(b) Effect of Residual LAI on Growth in the Field

No consistent relationship was discovered in the field between residual LAI after defoliation and subsequent growth. This finding from experiment 2 was supported by the results of a concurrent experiment in which green panic swards in the late summer of 1960, 1961 and 1962 were cut for hay at heights of 5, 12·5 and 20 cm, or were not cut at all (Humphreys, unpublished data). Regrowth of leaf was proportional to defoliation intensity, but shoot growth was independent of treatment. As indicated previously, while many investigators have found low cutting height detrimental to yield (e.g. Stapledon 1924; Killinger and Bledsloe 1954; Brougham 1956; Davis 1960; Hirose *et al.* 1960; Hovelard and Andrews 1962; Langille and Warren 1962; Kretschmer and Hayslip 1963), a substantial section of the literature indicates beneficial effects on yield (e.g. Robinson and Sprague 1947; Sprague and Garber 1950; Duell and Gausman 1957; Gervais 1960; Bryant and Blaser 1961; Caro-Costas and Vicente-Chandler 1961; Chestnutt 1961; Langille and Warren 1961; Wilson and McGuire 1961; Burger, Jackobs, and Hittle 1962; Holt and McDaniel 1963; Jones 1963), or little effect of defoliation intensity (e.g. Barnes 1960*a*, 1960*b*; Bryan and Sharpe 1965). Almost all studies reported utilized yield figures rather than growth, and the techniques of growth analysis have only occasionally been used to provide a more detailed description of effects.

The finding of experiment 2 reported by Humphreys and Robinson (1966), that growth was positively related to residual LAI, was obtained with vegetative plants unchecked by moisture or nutritional stresses. The failure of low residual LAI in this experiment to reduce yield is ascribed to a number of factors:

(1) The intermittent checks to growth imposed by moisture or nitrogen shortages, which set a low ceiling to leaf expansion; growth variations positively related to the amount of leaf surface exposed to the light were of short duration only, since leaf area differences between treatments tended to disappear with time.

It was noted consistently that the onset of wilting was negatively related to the residual LAI after defoliation. It was also recorded that in the autumn, winter and spring, evapotranspiration was reduced according to the intensity of defoliation. During the summer months no consistent relationship was noted. These data, which do not include allowance for run-off water, are illustrated in Figure 6.

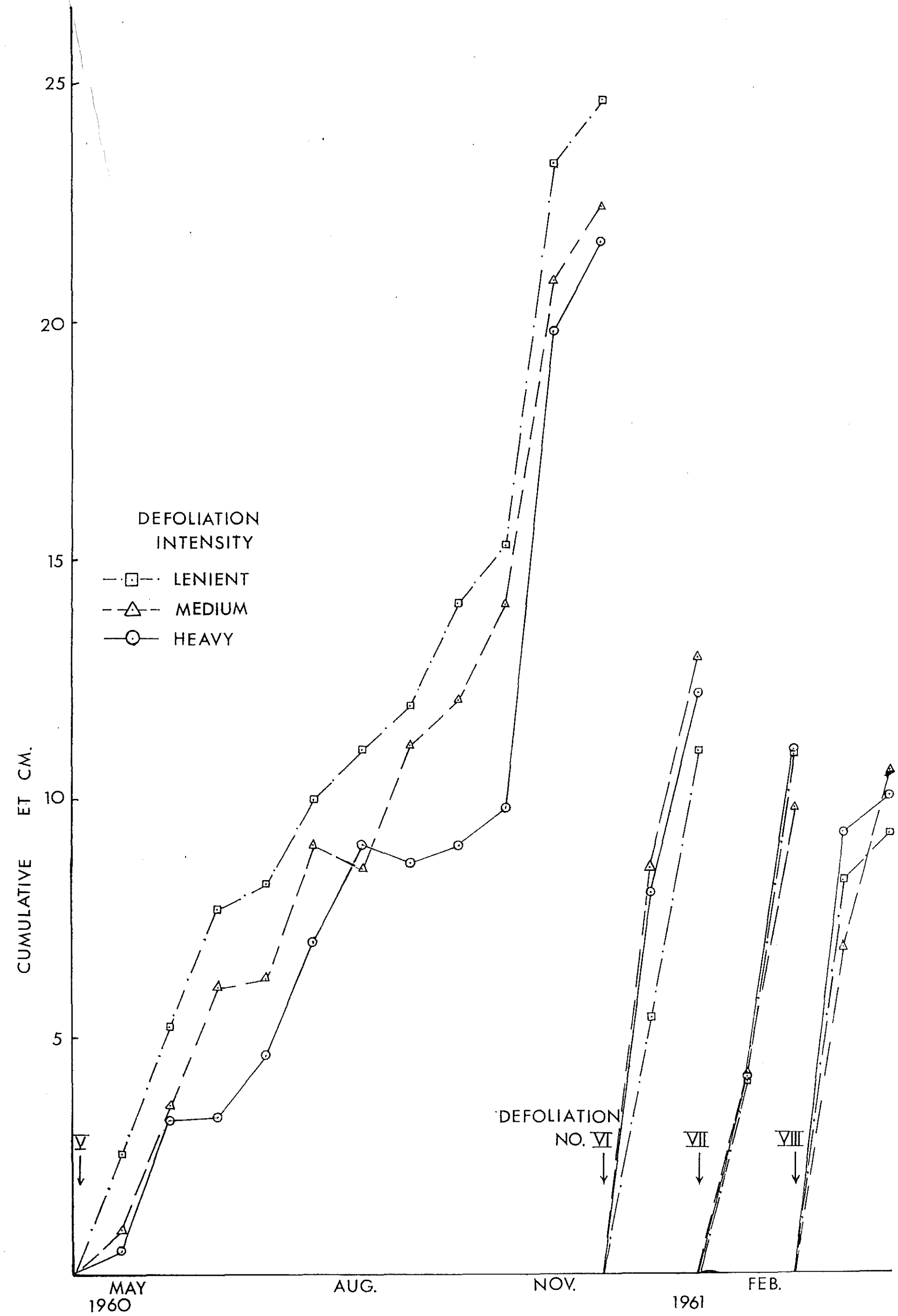

Fig. 6.—Experiment 2: Cumulative evapotranspiration (ET) of green panic swards defoliated with varying intensity in 1960-61.

Jantti and Heinonen (1957) in their Figures 1–5 show a similar effect of ET moving in sympathy with residual stubble height. However, in support of their theory that heavily defoliated plants cannot absorb water as well as plants with intact shoots, they claim a significant interaction between the effects of variations in defoliation intensity and soil moisture level on pasture growth—i.e. whereas drastic defoliation is detrimental to growth at all moisture levels, it is peculiarly so if moisture is in short supply. This claim is considered illegitimate on the basis of their data. For growth (the important parameter) the interaction is non-significant (their Table 3). They do obtain a statistically significant interaction for the ratio of yield of pasture present at the end of the experimental period for particular cutting treatments divided by the yield of pasture present under that cutting treatment on very moist soil (their Figure 6). However, these ratios are stabilized for the leniently cut treatments by the presence of more residual stubble in the first harvest yields. If there were no interaction at all between defoliation intensity and moisture level for growth, one could still expect a significant interaction to appear for the ratio described. Their theory is not in line with modern concepts of water uptake in plants.

Mitchell and Closs (1958) reported that at Palmerston North moisture loss from short pasture was less than from long pasture in spring. On the other hand, the reverse situation applied during summer. They suggest tentatively that differences in leaf temperature between long and short pasture and the compensating effect of canopy size may explain these effects. Van Riper and Owen (1964) recorded less moisture loss from grasses cut at 2-in. height than from grasses cut at 5-in. height.

It has been claimed that heavy defoliation can restrict moisture uptake through reduction in root surface. This effect is considered unlikely in the range of normal grazing practice with species such as buffel grass and green panic.

(2) The compensating effect of high E in the more severely defoliated treatments. This finding had numerous exceptions in experiment 2, but was influential in many of the growth periods. It is in sympathy with the studies of Brougham (1956) and Davidson and Donald (1958), and may be ascribed to the better illumination of individual leaves, the higher leaf nitrogen status and the lower respiratory load from stem and inflorescence material in the slashed swards.

(3) The effect of flowering in inhibiting axillary bud expansion and growth. The degree of flowering was consistently and negatively related to defoliation intensity. It might be mentioned that of the 12 post-defoliation periods studied, only following defoliation I (October 13, 1959) was flowering absent in the ensuing 6 weeks; in this period there was no suggestion that higher residual LAI inhibited leaf expansion or reduced leaf weight ratio. The effects of flowering will be considered in more detail in a subsequent paper (Humphreys 1966*a*).

Since growth was independent of defoliation intensity, utilized yield was substantially enhanced in the severely defoliated swards. However, the design of the experiment precluded consideration of the effects of persistent heavy defoliation. It should also be recognized that any policy of heavy pasture utilization creates conditions where, with an extended drought, stock are more dependent upon non-paddock feed reserves.

(c) Defoliation Effects on Pasture Quality

No direct measurements of nutritive value were made, but the following indirect indices are of interest:

(*a*) In experiment 2, animals selectively grazed the previously slashed swards in preference to the leniently defoliated pasture.

(*b*) Both Lw/W and the yield of leaf were positively related to defoliation intensity, and treatment effects were large. The question of the relationship of leafiness to nutritive value has been discussed elsewhere (Humphreys 1966*b*), and the reservations of Milford (1965) noted. More work is required to elucidate this question; it should be emphasized that the percentage nitrogen of the lamina fraction was three times that of the residual plant parts (cf. Henzell and Oxenham 1964). The opportunity for improvement in animal diet by selective grazing is obvious when percentage nitrogen is, for example, 0·8 in shoots and 2·2 in lamina.

(*c*) Percentage nitrogen of shoot growth 3 and 6 weeks after defoliation was a function of intensity of defoliation. This effect was due to an increase in Lw/W and to an increase in percentage nitrogen of constituent plant parts. Severe defoliation increased nitrogen uptake; this may be related to the superior nutrient uptake of non-flowering tillers (Williams 1957; Koontz and Vose 1961; Henzell and Oxenham 1964).

Percentage nitrogen was low in midsummer, when growth was rapid, and was fairly well maintained in the winter; no doubt the pattern described by Christian and Shaw (1949) would be modified by sequential defoliation and autumn fertilizer application. The high values recorded in spring and early summer were probably associated with the increased release of nitrogen upon wetting a long-dried soil (Birch 1960).

Percentage nitrogen is a meaningful index of quality in tropical grasses (Milford 1960), and the evidence from experiment 2 is suggestive that lenient defoliation not only occasioned inefficient pasture use but also caused a serious decline in pasture quality.

V. ACKNOWLEDGEMENTS

I am much indebted to Dr. G. L. Wilson (University of Queensland) and Dr. J. P. Ebersohn (Department of Primary Industries) for advice and criticism; to the Australian Meat Board for provision of facilities; to the late P. B. McGovern for statistical analyses; to Mr. W. J. Cartmill (Department of Primary Industries) for nitrogen analyses; and to Messrs. N. D. Young and W. J. Scateni, Miss D. E. Davidson, Mr. J. G. Schoneveld (Queensland Department of Primary Industries) and field staff of the "Brian Pastures" Pasture Research Station, Gayndah, for assistance in the collection of data.

Experiment 1 was laid down by Mr. N. D. Young, and the opportunity to collect subordinate data from it for the purpose of this study is appreciated.

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(Received for publication February 16, 1966)

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