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SECTION 1

PAPER No. 6

INTERRELATIONS OF LEAF AREA AND NON-STRUCTURAL CARBOHYDRATE STATUS AS DETERMINANTS OF THE GROWTH OF SUB-TROPICAL GRASSES

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Summary

Under the normal moisture and nutritional stresses of the sub-coastal southern Queensland pasture environment, leaf growth in green panic and buffel grass was not sufficient to intercept all light, and wide variations in the frequency and intensity of defoliation caused little difference in the annual yield of shoot growth. Heavy use promoted increased leaf growth and nitrogen content, and reduced root growth and carbohydrate accumulation.

When moisture and nutrients were in adequate supply, growth was more positively dependent upon LAI than on carbohydrate status.

The results of growth analyses are discussed and attention is directed to the equilibration of component growth factors which reduce defoliation-treatment effects.

Introduction

The maintenance of a high level of non-structural carbohydrate in the roots and basal stems of pasture plants has been the declared objective of much grazing and cutting practice (10, 6). A more recently developed concept is the need to maintain a leaf-area index (LAI) leading to maximum net photosynthesis (3). Some work assessing the interrelations of these 2 concepts has been reported (7, 4), but studies from sub-tropical areas are lacking.

Experimental

The salient features of 3 defoliation experiments are reported. They were conducted on a shallow basaltic chernozem soil at the Brian Pastures Research Station, Gayndah, Queensland (25°36' S., lat. 151°42' E. long.). In the first 2 experiments (E.1 and E.2) swards were grown under natural rainfall conditions (mean annual rainfall 70 cm) and under the moderate levels of nitrogen nutrition current in field practice in sub-coastal Queensland.

(1) In E.1 three defoliation intensities, referred to as lenient (L), medium (M) and heavy (H), were applied to a sward of green panic (*Panicum maximum* var. *trichoglume* (K. Schum.) Eyles). 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, consisting of 3 basic cycles, LHH, HMM and MLL, each phase of which was represented on each defoliation occasion. There were 3 replications, making a total of 27 plots. Twelve defoliations were imposed at intervals of 6 weeks during the growing seasons of 1959—60, 1960—61, and 1961—62. On each defoliation occasion, a variable number of steers was grazed on the whole experimental area overnight; the M treatments were then cut with a rotary chain slasher at 15 cm height and the H treatments at 10 cm height.

(2) In E.2 two defoliation frequencies were chosen to provide one in which maximum carbohydrate accumulation, root growth, and winter canopy might be expected (cut at 5 cm height each late winter only), and one in which the plants would be subject to stress (cut at 5 cm height every 8 weeks). These were imposed on green panic and on buffel grass *(Cenchrus ciliaris* L. cv. Gayndah), sown on 17 February, 1958. There were 4 absolute replications, and 12 destructive harvests, making a total of 192 plots. Plants were grown at a density of 18.9 plants m^{-2} in and surrounding 571 drums buried to ground level.

Drums were removed at intervals of 4 or 8 weeks during the 18-month period following the defoliation treatment on 1 May, 1958, and the dry-weight and non-structural carbohydrate content or "TAC" (8, 5) of the various plant organs was determined.

(3) The amount of residual leaf after defoliation and the non-structural carbohydrate status of the crown and roots were varied independently in E.3, to assess the relative importance of these 2 factors in the control of grass growth. Three levels of TAC status (and root-and crown-size) were induced by imposing different defoliation frequencies and nitrogen nutrition on green panic grown in 57l drums. All plants were then defoliated completely, given adequate nitrogen and moisture, and 3 levels of leaf area (LAI 0.0, 0.27, and 0.75), subsequently obtained by differentially plucking the new growth on 18 September, 1961. There were 6 absolute replications of the 9 treatment combinations. A subsidiary comparison evaluated "growth" produced under dark conditions as an index of sward vigour.

Results

(1) E.1. *Effect of residual LAI on growth in the field*

The residual LAI after defoliation varied according to seasonal conditions and management; the ranges of values were 0.14—1.45, 0.06—0.79, and 0.04—0.34 for the L, M, and H treatments, respectively. The data for the summation of the 12 6-weekly post-defoliation growth periods are summarized in Table 1.

Table 1. E.1. Growth data summed for 12 post-defoliation periods each of 6 weeks duration

Parameter	Defoliation treatment Lenient	Medium	Heavy	L.S.D. 5 %	1 %
Shoot growth $g\ m^{-2}$	1154	1161	1101	N.S.	
Leaf growth $g\ m^{-2}$	388	519	654	89	123
Leaf-area index LAI	9.85	14.23	17.69	1.94	2.83

No overall effect of defoliation intensity on shoot growth was recorded, although leaf growth was negatively related to residual LAI. Mean leaf area for a particular period is a function of the LAI present at the beginning of the period and the rate of LAI increase. In the first 3 weeks after each defoliation, the initial advantage of the L treatments was maintained in 10 of the 12 periods; from 3 to 6 weeks after defoliation this advantage was usually lost.

LAI did not exceed 3.4; light values near ground level rarely fell below 0.3 daylight, and never reached the critical 0.05 value. This is in contrast to green-panic swards receiving high levels of nitrogenous fertilizer, where shoot yields 10 weeks after defoliation reached 1320 g m^{-2} at LAI 7.3, and critical LAI values were 3.5—4.0 at shoot yields of 700—820 g m^{-2} (Humphreys, unpublished data). Leaf-area/leaf-weight ratio increased with advancing season, whilst leaf-weight/shoot-weight ratio declined. Both ratios were positively related to residual LAI immediately after defoliation, and negatively related as growth proceeded. Nitrogen content behaved similarly.

Net assimilation rates tended to be negatively related to residual LAI. The compensatory relationship between net assimilation rate and leaf-area duration militated against the appearance of treatment growth-differences. The higher rates of LAI increase in the M and H treatments did not overcome the disadvantage of low initial LAI sufficiently to promote higher leaf-area duration.

(2) E.2. *Effect of defoliation frequency and species on growth and carbohydrate accumulation*

(a) *Dry-weight changes.* The main effects are summarized in Table 2. Since long spelling intervals were involved, the convention has been adopted of summing positive growth changes only, measured at 4-or 8-week inter-

Table 2. E.2. Effect of defoliation frequency and species on the cumulative positive changes in dry weight (g plant^{-1})

Plant fraction	Buffel grass	Green panic grass	Defoliation treatment Infrequent	Defoliation treatment Frequent	L.S.D. 5 %	L.S.D. 1 %
Roots	53.60**	24.66	47.16**	31.09	9.93	14.26
Stem below 5 cm	22.65	21.83	22.58	21.89	N.S.	
Stem above 5 cm	19.31	26.40	29.63**	16.09	4.18	6.00
Green leaf	18.76	18.96	14.44**	23.27	1.76	2.53
Brown leaf	9.50**	5.71	11.89**	3.33	1.10	1.57
Total leaf	22.30	21.89	18.41**	25.78	2.00	2.87
Inflorescence	0.88	1.43	1.66**	0.66	0.62	0.89
Total shoots	60.64	63.87	64.77	59.74	N.S.	
Whole plant	105.82**	82.35	103.17**	85.01	12.11	17.40

vals, recognizing that this index has serious conceptual limitations.

Although very real treatment effects were recorded in the root, upper stem, leaf, and inflorescence fractions, total shoot-growth was insensitive to species or defoliation frequency. However, frequent defoliation reduced fluctuations in growth rates; these were substantially higher during the cooler months and lower during the rapid mid-summer growth period than under the infrequent defoliation regime. Rate of tillering was usually higher under frequent- than under infrequent-defoliation, and greater in buffel grass than in green panic, but significant short-term treatment differences in growth were occasioned more by shoot size than shoot number.

(b) *Carbohydrate changes.* Percentage TAC of roots reached its highest value in May and fell steadily until February. The range of values was 2.5 to 8.0, and these were significantly higher in buffel than in green panic. There was no effect of defoliation regime; however, these values were estimated immediately prior to and 8 weeks subsequent to defoliation. The time trends and treatment effects for stems below 5 cm were similar to those for roots, values ranging from 4.1 to 13.1.

Table 3. E.3. Effect of previous carbohydrate status and leaf area on whole-plant growth (g drum^{-1} day^{-1})

Initial LAI	Initial carbohydrate status (g drum^{-1})			Mean
	C$_1$ 0.55	C$_2$ 1.06	C$_3$ 1.49	
L$_0$ 0.0	1.21	1.02	1.65	1.30
L$_1$ 0.27	1.95	1.77	2.15	1.96
L$_2$ 0.75	2.72	1.87	2.89	2.49
Mean	1.96	1.55	2.23	
L.S.D.	5 %	1 %		
C**, L**	0.28	0.38		
C × L	0.49	0.65		

The amount of TAC in the roots and stem bases accumulated in the autumn, winter, and early summer, and was depleted in the spring. At the end of the second winter, the amounts of TAC in roots and stem bases were 5.1 and 3.7, 2.0 and 1.2 g plant^{-1} for the infrequently and frequently defoliated buffel grass, and the infrequently and frequently defoliated green panic treatments, respectively.

(3) *E.3. Interrelations of residual LAI and carbohydrate status*

(a) *Dry-weight changes.* The growth rates recorded over the 20 days subsequent to differential plucking are shown in Table 3.

Initial LAI was a greater determinant of growth rate than the TAC status of the roots and crowns. Plants at the lowest TAC status which had been close to the point of death but had then been allowed to develop some leaf canopy, grew faster than plants leniently treated in the past but which entered the growth period with little leaf canopy.

The proportion of whole-plant growth distributed to the roots was positively related to residual LAI. Net assimilation rate showed a substantial treatment variation of from 0.10 to 0.17 g dm^{-2} day^{-1}, was negatively related to residual LAI, and higher in C$_3$ than C$_1$ or C$_2$.

Mean LAI was, however, a more potent influence on growth rate than net assimilation rate. Both mean LAI and rate of LAI increase were closely related to growth rate. Leaf-area/leaf-weight ratio and rates of leaf and shoot appearance were negatively related to residual LAI; the more rapid increase of LAI in the high residual LAI treatments was due to an increased rate of expansion of leaves already in existence at the beginning of the growth period. On the other hand, increased leaf growth-rate in the highest carbohydrate treatment was due mainly to the increased rate of shoot appearance.

(b) *Carbohydrate changes.* The decline in amount of TAC in roots was negatively related to residual LAI and positively related to initial TAC status. The accumulation of TAC in the crown was positively related to residual LAI and highest at C_3.

The amount of "shoot growth" produced in light-proof boxes was 0.65, 2.22 and 3.88 g drum^1 for the C_1, C_2 and C_3 treatments respectively. This could not be accounted for in terms of loss of TAC, and it is concluded that substances other than non-structural carbohydrates were involved in shoot synthesis in the absence of light (2). Loss of weight and of TAC was greater from roots than from crown. Under dark conditions, the time to reach 80 % mortality did not distinguish the C_2 and C_3 treatments.

Discussion and conclusions

A consistent pattern in these experiments was the manner in which components of growth operated in a compensatory, self regulatory fashion, reducing the effects of defoliation on plant growth. This equilibration was well illustrated in E.2, where 2 species of differing habit were grown under 2 extreme defoliation frequencies. Between treatments, root mass varied by a factor of 3.8, TAC 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 only 8 % between the 4 treatments.

In E.1 and E.2 shoot growth was not limited by management factors. The failure of low residual LAI to reduce yield is attributed to:

(a) the intermittent checks to growth imposed by moisture or N shortages, which set a low ceiling to leaf expansion (the onset of wilting was positively related to residual LAI);

(b) the compensating effect of high net assimilation rate in the more severely defoliated treatments (1);

(c) the effect of flowering in inhibiting axillary-bud expansion and growth.

Flowering was positively related to residual LAI. However, it is of some significance that heavy use promoted increased leaf growth, increased the N content of pasture and whilst extending the duration of leaf growth, reduced the standing forage reserves.

When moisture and nutrients were in adequate supply, as in E.3, reductions in the leaf surface diminished the rate of growth. The need for a supra-minimal canopy was of greater importance than plant carbohydrate status. No explanation can be offered for the aberrant behaviour of the intermediate TAC treatment in E.3; a similar instance has been reported elsewhere (9). It will be appreciated that in these experiments TAC status was confounded with other plant factors. The view is accepted that much TAC is lost in respiration or decay.

It is suggested that advances in defoliation practice depend upon:

(a) creating conditions for growth where compensatory 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 animals;

(d) reducing short-term fluctuations in the forage supply;

(e) synchronizing more nearly grazing pressure and pasture growth.

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