THE RELATIONSHIP OF GRAIN YIELD TO VEGETATIVE GROWTH AND POST-FLOWERING LEAF AREA IN THE WHEAT CROP UNDER CONDITIONS OF LIMITED SOIL MOISTURE

By R. A. FISCHER*† and G. D. KOHN*

[*Manuscript received November* 18, 1965]

Summary

Trials were conducted in 1961 and 1962 at Wagga Wagga in southern New South Wales to investigate the yield physiology of the wheat crop. Various cultural treatments were applied to a single variety (Heron). This paper covers aspects directly related to grain yield. In the rate of sowing and fertilizer trials relative differences in grain yield were invariably less than relative differences in total dry weight at or before flowering. In some cases increased vegetative growth depressed grain yield. These results appear to be mainly the consequence of increased post-flowering competition for limited soil moisture in denser crops. High soil nitrogen had an additional detrimental effect. When as a result of later sowing flowering was delayed, both vegetative growth and post-flowering plant water status decreased; as a consequence grain yield decreased with successively later sowings.

For the 1962 crops, grain yield was closely correlated ($r=0\cdot969^{**}$) with leaf area duration after flowering, which in turn was related to leaf area index at flowering and to the rate of senescence of photosynthetic tissue. Increased rates of senescence were usually associated with reduced post-flowering plant water status, as indicated by the relative turgidity of the leaves. These results are discussed in relation to the importance of numerical components of grain yield and to improvement of grain yield in the wheat crop.

I. INTRODUCTION

This is the last of three papers reporting a study of the physiology of grain yield in the wheat crop under field conditions at Wagga Wagga in southern New South Wales in 1961 and 1962. Emphasis was placed on understanding the relationship of yield to vegetative growth, a relationship which is complicated by an inadequate supply of water to the crop. This has particular relevance to the problem of "haying off", common in southern New South Wales, in which wheat yield is sometimes depressed by high soil nitrogen levels despite large responses in vegetative growth (Colwell 1963).

Variations in time of sowing, rate of sowing, and amount of fertilizer applied were used to alter the vegetative growth. Early sowing, heavy fertilizer rates, and to a lesser extent, heavy rates of sowing increased vegetative growth; this was associated with an increase in evapotranspiration and, as a direct consequence, an increase in plant moisture stress as measured by leaf relative turgidity (Fischer and Kohn 1966*a*, 1966*b*). This paper examines the nature of the subsequent effects on grain yield.

It is generally accepted that grain carbohydrate comes from photosynthesis after flowering. Recent physiological studies of cereal crops in the field have

---

* Agricultural Research Institute, New South Wales Department of Agriculture, Wagga Wagga.

† Present address: Department of Irrigation, University of California, Davis, Calif., U.S.A.

Aust. J. Agric. Res., 1966, **17**, 281–95

attempted, with some success, to relate grain yield to leaf area after flowering (Thorne and Watson 1955; Watson, Thorne, and French 1958, 1963; Denmead and Shaw 1960). Only Denmead and Shaw worked with conditions of moisture stress. In India, the grain yield of wheat under such conditions has been studied extensively (Asana *et al.* 1958; Asana, Saini, and Ray 1958); however, these studies have involved pot trials, or measurements have been restricted to the numerical components of yield. In the trials reported here, measurements were made not only of yield components, but also of the area of post-flowering photosynthetic tissue.

TABLE 1

SUMMARY OF TRIALS AND TREATMENTS

Trial	Treatment				
	Symbol	Date Sown	Rate of Sowing (lb/acre)	Super-phosphate (lb/acre)	Nitrogen (lb/acre)
Time of sowing, 1961 (T61)	T_1	April 28	60	224	Nil
	T_2	May 22	60	224	Nil
	T_3	June 8	60	224	Nil
	T_4	June 29	60	224	Nil
	T_5	July 18	60	224	Nil
Time of sowing, 1962 (T62)	T_1	May 4	60	224	Nil
	T_2	May 21	60	224	Nil
	T_3	June 7	60	224	Nil
	T_5	July 16	60	224	Nil
Rate of sowing, 1961 (R61)	R_1	June 9	30	224	Nil
	R_2	June 9	60	224	Nil
	R_3	June 9	120	224	Nil
Rate of sowing, 1962 (R62)	R_1	June 8	20	224	Nil
	R_2	June 8	60	224	Nil
	R_3	June 8	120	224	Nil
	R_4*	June 8	20	224	Nil
	R_5†	June 8	20	224	Nil
Fertilizer, 1961 (SN61)	S_0N_0	June 9	70	Nil	Nil
	S_2N_0	June 9	70	224	Nil
	S_2N_1	June 9	70	224	60
Fertilizer, 1962 (SN62)	S_0N_0	June 9	85	Nil	Nil
	S_0N_1	June 9	85	Nil	100
	$S_{\frac{1}{2}}N_0$	June 9	85	56	Nil
	$S_{\frac{1}{2}}N_1$	June 9	85	56	100
	S_2N_0	June 9	85	224	Nil
	S_2N_1	June 9	85	224	100

* Wide rows (21 in.).

† Wide rows (21 in.) plus inter-row straw.

II. EXPERIMENTAL DETAILS

Trials were conducted at Wagga Wagga in 1961 and 1962. Rainfall during the growing season was about average in each year, but September and October in 1961 were relatively warm and dry. All trial sites, except that for trial SN62, were on soils of high fertility, having previously grown pastures of subterranean clover (*Trifolium subterraneum*). The site of trial SN62 was of very low fertility. From three to six replicates were sown, plots being 30–36 ft long and 9 or 16 rows wide. The variety Heron was used throughout. More detailed climatic and experimental information was given in an earlier paper (Fischer and Kohn 1966*a*). Trials and treatments are summarized in Table 1.

There were additional fertilizer trials, not previously mentioned, in 1961 and 1962 at Boree Creek, 50 miles west of Wagga Wagga. Here soil fertility was moderate to low: without additional nitrogen, the soil nitrate nitrogen at 0–12 in. depth in mid August was about 8 p.p.m. in each year. This compares with 33 and 4 p.p.m. for trials SN61 and SN62 respectively. Rainfall during the growing season was somewhat less than at Wagga Wagga in 1961, and about equal in 1962. Soil type, treatments, and trial layout were similar to those in trial SN62, except for an additional superphosphate level (112 lb per acre, designated S_1) and a split–split plot design, the additional split being for 30 and 60 lb seed per acre. The Boree Creek trial was sown on June 4 in 1961 and on May 20 in 1962. These trials were sampled in September and at maturity.

In the Wagga Wagga trials in 1962, crop harvests were made at weekly intervals after flowering; subsamples from these harvests were taken for kernel weight and leaf area determinations. The area of leaf lamina was determined with a suction leaf-area planimeter, the area being recorded as that of one side of the lamina. Senescent yellow portions of leaves were excluded from the measurements. The photosynthetic tissues of the leaf sheath, the peduncle, and head are also important sources of grain carbohydrate (Porter, Pal, and Martin 1950). The area of green sheath and peduncle was calculated by considering this tissue as a cylinder; its equivalent "leaf area" was taken as half the surface area of the cylinder. Thorne (1959) reported that the rates of apparent photosynthesis in the leaf sheath and in the lamina of barley, compared on the above area basis, seemed about equal. The green head was considered as a rectangular prism and its equivalent leaf area was arbitrarily taken as half the surface area of the prism. The areas of all these photosynthetic tissues were added to give a total "leaf area" expressed as leaf area index, the area per unit ground area.

III. RESULTS AND DISCUSSION

(*a*) *Rate of Sowing and Fertilizer Trials*

In these trials, treatments did not alter the date of flowering more than a few days. The relative differences in grain yield (G) were less than the relative differences in vegetative growth as measured by total dry weight (W) of above-ground material at the beginning of October, just prior to head emergence (Fig. 1; Table 2). In fact at Wagga Wagga, heavy sowing rates reduced yields compared with lighter rates; with wide-row spacing, however, a reduction in vegetative growth was accompanied

TABLE 2

TOTAL DRY WEIGHT (W) AT ABOUT THE BEGINNING OF OCTOBER, FINAL GRAIN DRY WEIGHT (G), AND YIELD COMPONENTS: RATE OF SOWING AND FERTILIZER TRIALS AT WAGGA

Trial and Treatment	1961						1962					
	W (g/m²)	G (g/m²)	Heads per m²	Spikelets per Head	Kernels per Spikelet	Wt. of 1000 Kernels (g)	W (g/m²)	G (g/m²)	Heads per m²	Spikelets per Head	Kernels per Spikelet	Wt. of 1000 Kernels (g)
Rate of sowing:	*September 29*						*October 4*					
R_1	401	163	372	14·8	1·54	19·3	427	293	327	14·3	2·05	30·7
R_2	519	158	406	13·7	1·44	19·6	667	277	446	12·4	1·58	31·8
R_3	576	149	454	12·6	1·41	18·3	701	244	478	11·0	1·58	29·6
R_4							377	261	273	14·5	2·06	32·0
R_5							366	263	303	14·6	2·02	29·4
L.S.D. ($P = 0·05$)		25	73	0·5	0·11	2·9		29	42	0·7	0·20	2·3
Fertilizer:	*October 4*						*October 9*					
S_0N_0	384	164	356	13·7	1·64	20·8	191	159	205	11·6	1·92	35·1
S_0N_1							218	166	210	12·4	1·95	32·8
$S_{\frac{1}{2}}N_0$							329	188	255	10·8	1·93	35·6
$S_{\frac{1}{2}}N_1$							475	234	341	11·6	1·79	33·0
S_2N_0	626	163	474	13·5	1·39	18·5	359	199	262	10·8	1·87	37·5
S_2N_1	646	126	393	14·1	1·34	17·9	612	259	432	11·7	1·57	32·8
L.S.D. ($P = 0·05$): a*		15	52	0·5	0·16	1·3		41	40	0·7	0·14	1·8
b								38	42	0·6	0·18	1·5

* For testing S at given N level (a), and N at a given S level (b).

by a reduction in grain yield. At Boree Creek, if there had been no compensation of relative differences in vegetative growth, the regression line of grain yield upon *W* in Figure 1 would have passed through the origin. Also, in both years at Boree Creek, crops given nitrogen fertilizer had a significantly lower regression coefficient (sig. diff. ($P = 0 \cdot 05$), 0·14) than crops without nitrogen. In 1961 when conditions were very dry, grain yield actually decreased as vegetative growth increased under conditions of high nitrogen. The three treatments of trial SN61 at Wagga Wagga showed no response in grain yield to increased vegetative growth, and in fact the yield was depressed by nitrogen application (Table 2). If the data of trial SN62 are plotted on Figure 1, the regression equation would be $y = 112+0 \cdot 245x$ ($r = 0 \cdot 996$), with no separation of data due to nitrogen application.

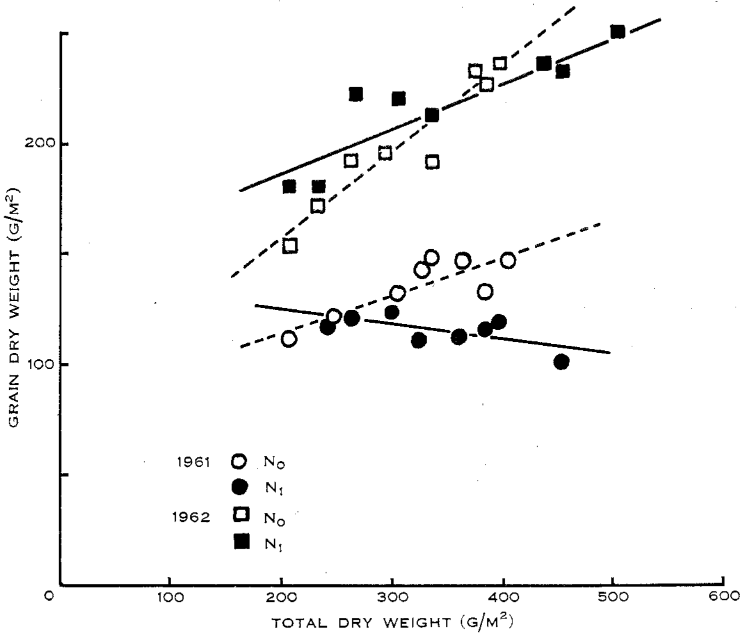

Fig. 1.—Relationship of final dry grain weight and total dry weight at about ear emergence. Linear regressions were calculated for each nitrogen level in each trial, as follows:

1961, N₀: $y = 81+0 \cdot 17x$ ($r = 0 \cdot 80$) 1962, N₀: $y = 80+0 \cdot 39x$ ($r = 0 \cdot 96$)

1961, N₁: $y = 138-0 \cdot 07x$ ($r = 0 \cdot 67$) 1962, N₁: $y = 146+0 \cdot 21x$ ($r = 0 \cdot 89$)

Sowing rate subtreatments were not bulked; hence there were eight points for each nitrogen level. Trials at Boree Creek.

The reduction of the effect on grain yield of differences in vegetative growth may be largely the consequence of increased competition for limiting resources in the denser crops. The components connecting grain yield to vegetative growth are heads produced per unit of vegetative growth, spikelets per head, grains per spikelet, and individual kernel weight. To determine the causes of grain yield variation from these numerical yield components is difficult in view of their interdependence. Several points, however, can be made.

(1) Some compensation occurred before the onset of water stress, that is, before mid September. In the thicker crops, a larger percentage of the shoots produced in the winter failed to give rise to heads, and a portion of this loss of shoots occurred before mid September (Fischer, unpublished data). There was also a significant reduction in spikelets per head in thicker crops, except where nitrogen applications were involved; the nitrogen increased spikelets per head despite increases in vegetative growth (Table 2). Since spikelets per head appears to be determined very early in the development of the plant (Single 1964), the results probably reflect increased light or nutrient competition in thicker crops; the positive response to nitrogen indicates that nitrogen competition may be important.

TABLE 3

LEAF RELATIVE TURGIDITY (SUNRISE) AT FLOWERING AND THE NUMBER OF DAYS AFTER FLOWERING FOR WHICH LEAF RELATIVE TURGIDITY REMAINED ABOVE 75% FOR COMPARABLE CROPS IN EACH TRIAL:* SOWING RATE AND FERTILIZER TRIALS

Trial		Treatment	Leaf Relative Turgidity (%) at Flowering†	Days of Relative Turgidity >75% after Flowering
Wagga	R61	R_2	95	9
	R62	R_2	95	14
	SN61	S_2N_0	95	9
	SN62	S_2N_1	100	16
Boree Creek	1961	S_2N_1	80	10
	1962	S_2N_1	95	30

* That is, crops of approximately equal total dry weight at a given stage in the spring.

† Approximate values estimated by interpolation of data.

(2) Differential competition for water was probably the most important factor causing the compensation of differences in vegetative growth. Leaf relative turgidity at and after flowering decreased as vegetative growth increased in each trial (Fischer and Kohn 1966*b*). The levels of relative turgidity for comparable crops from the various trials also indicate approximately the severity of water shortage and therefore the severity of competition for water under the conditions of each trial (Table 3). Post-flowering water shortage was very severe in 1961, particularly at Boree Creek, but only moderately severe in 1962. The degree of compensation of differences in vegetative growth in each trial (Fig. 1; Table 2) increased with increased severity of moisture stress.

The actual grain yield components affected by this water stress depend on when the stress arises and on the degree of interdependence between yield components. For example, in trial SN62 with no pre-flowering moisture stress and moderate post-flowering stress, the thicker crops (treatments $S_{\frac{1}{2}}N_1$ and S_2N_1) showed a significant reduction in kernel weight. In contrast, the trial at Boree Creek in 1962, with moderate pre-flowering stress but relatively adequate post-flowering water, showed no such differences in kernel weight. In the 1961 trial at Boree Creek where there was considerable pre-flowering stress, the main component reduced in denser crops was the number of heads emerging per unit of vegetative dry weight (Fischer, unpublished data).

(3) The results also indicate that high soil nitrogen may have modified the nature or consequences of the competition just described (Fig. 1). At the initially low soil nitrogen levels of trial SN62, added nitrogen caused a 30% increase in the ratio of leaf area to total dry weight during the early spring. Since evapotranspiration was directly related to photosynthetic area in these trials (Fischer and Kohn 1966*a*), one might expect evapotranspiration and the consequences of moisture shortage to be somewhat greater for a given amount of growth achieved under high nitrogen conditions, as for example in the 1961 trial at Boree Creek. This effect of nitrogen on the leaf area ratio also explains why the relatively small effects of nitrogen on crop dry matter production, as for example in the Boree Creek trials, appear in the field as quite marked effects on crop "leafiness".

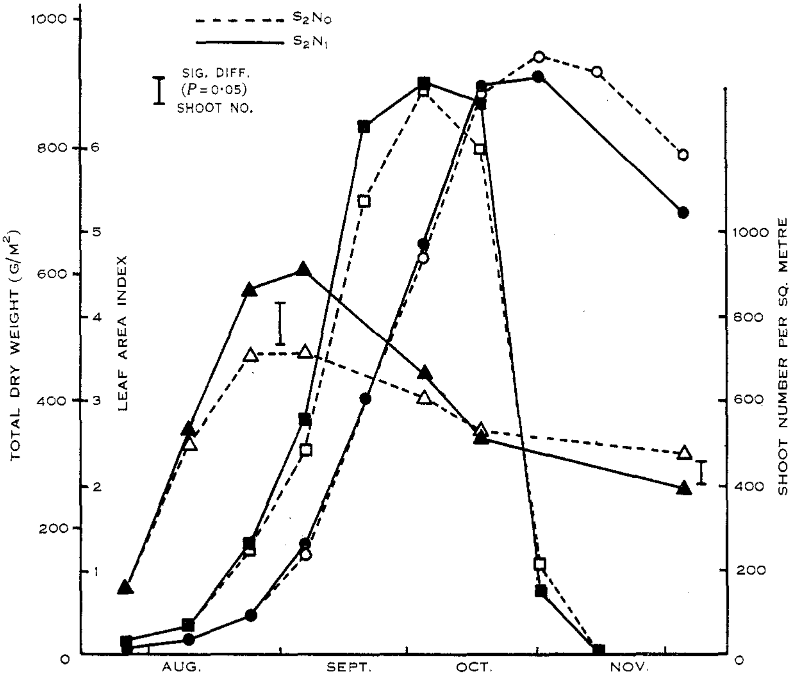

Fig. 2.—Changes with time in total dry weight (● ○), leaf area index (■ □), and shoot number (▲ △) with and without nitrogen fertilizer. Trial SN61.

At the very high soil nitrogen levels of trial SN61, added nitrogen failed to stimulate any extra dry weight or even to increase leaf area index to any extent, but it did cause a significant increase in shoot production, followed by significant decreases in the percentage of shoots surviving, in head number, and in grain yield (Fig. 2). Similar results with added nitrogen under high soil nitrogen conditions were obtained in the following year by Storrier (1965). Although comparative soil moisture and leaf relative turgidity measurements were not taken for either of these trials, it does not appear likely, in view of the small leaf area response to nitrogen, that the poor shoot survival resulted from any increase in evapotranspiration which may have decreased the soil water supply available to the high nitrogen crops. It is possible that the effect is more directly related to the increased shoot numbers and reduced mean shoot size with high nitrogen in the face of subsequent severe competition. Barley and Naidu (1964) reported a similar stimulation of tillering and a reduction of shoot survival in wheat with added nitrogen.

TABLE 4

DATE OF FLOWERING, TOTAL DRY WEIGHT (W) AT SEPTEMBER 30, FINAL GRAIN DRY WEIGHT (G), AND RELEVANT INTERMEDIATE CROP PARAMETERS: TRIALS T61 AND T62

Trial and Treatment	Date of Flowering	W (g/m^2)	G (g/m^2)	W at Flowering (g/m^2)	Spikelets per m^2	Kernels per Spikelet	Wt. of 1000 Kernels (g)	Days of Turgidity >75%*	Mean Temp.† (°F)
T61: T_1	Oct. 6	960	286	1020	6190	1·75	26·2	12	61·4
T_2	Oct. 11	750	189	875	6180	1·49	20·9	10	62·2
T_3	Oct. 15	575	172	785	6090	1·38	20·6	10	64·2
T_4	Oct. 19	350	118	540	4800	1·34	18·3	9	64·0
T_5	Oct. 24	200	110	465	4670	1·18	19·9	7	65·1
L.S.D. ($P = 0·05$)		50				0·16	2·9		
T62: T_1	Oct. 10	930	333	1025	5960	1·69	33·1	22	55·5
T_2	Oct. 17	725	320	990	5960	1·61	33·4	21	56·4
T_3	Oct. 24	575	303	925	5390	1·72	32·6	19	58·7
T_5	Nov. 2	200	242	660	4830	1·83	27·3	13	63·7
L.S.D. ($P = 0·05$)			23			0·15	1·1		

* Number of days after flowering for which leaf relative turgidity (sunrise) remained greater than 75%.

† Over period of 22 days after flowering.

(*b*) *Time of Sowing Trials*

Grain yield results in these trials were related largely to the effect of time of sowing on date of flowering (Table 4). Results were consistent between years, and on the average there was a delay of about 2 days in date of flowering for each week's delay in sowing time. This represents a considerable hastening of development with later sowing, a fact no doubt related to seasonal changes.

Grain yield, vegetative growth, and other relevant parameters are also shown in Table 4. Grain yield decreased with each successive delay in sowing in each year, as did also vegetative growth at a given time in the spring. Evapotranspiration and leaf relative turgidity results indicate that, except for treatment T_1 in 1961, plant moisture stress did not arise before the end of September; thus treatment differences in total dry weight at this date are not greatly confounded by the effects of differential plant moisture stress. The similarity in the 1961 and 1962 results indicate that these differences in growth may reflect solely the interaction between sowing time and seasonal changes in temperature and, in particular, radiation.

The later flowering dates and greater relative growth rates for later-sown crops meant that differences in total dry weight at flowering were less than the differences measured at the end of September (Table 4). In 1961, however, significant plant moisture stress arose before flowering, and was relatively greater for later-sown crops (Fischer and Kohn 1966*b*). This limited the compensation of growth differences in 1961; relative differences in growth at flowering in 1962, when moisture was more nearly adequate, were smaller than in 1961. Thus it is suggested that when pre-flowering soil moisture conditions are favourable, there would be only relatively small differences in total dry weight at flowering among crops sown over the period from late April to mid June. The very late sowing in 1962 produced considerably less dry matter at flowering despite reasonably favourable conditions.

TABLE 5

FINAL GRAIN YIELD, PROTEIN CONTENT, AND BUSHEL WEIGHT OF GRAIN: TRIALS T61 AND T62

Trial and Treatment	Time of Sowing	Grain Yield* (bushels/acre)	Grain Protein* (%)	Grain Weight (lb/bushel)
T61: T_1	April 28	49·1	13·4	57
T_2	May 22	32·5	15·8	52½
T_3	June 8	29·6	15·5	54
T_4	June 29	20·2	16·1	52
T_5	July 18	18·8	16·1	53
L.S.D. ($P = 0·05$)		8·7		
T62: T_1	May 4	57·2	12·5	63
T_2	May 21	54·8	13·4	63
T_3	June 7	52·0	14·1	61½
T_5	July 18	41·7	14·4	59
L.S.D. ($P = 0·05$)		3·9		

* Values on 13·5% moisture basis.

Relative differences in the number of spikelets per unit area (spikelet number) were less in both years than the relative differences in total dry weight at flowering. This was because the increases in total dry weight of earlier sowings were reflected in greater weights of stem and leaf material rather than in head material. Head numbers increased to a small extent with earlier sowing, but spikelets per head did not change significantly.

Final grain yield involves two more components, grains per spikelet and individual kernel weight (Table 4). The increased severity of plant moisture stress probably resulted in the significant reduction, with later sowing, of both these components in 1961, and of the latter component in 1962. Increased kernel weight was associated with earlier flowering and with an increase in the number of days after flowering for which leaf relative turgidity at sunrise was greater than 75% (Table 4). The warmer post-flowering conditions which accompanied later sowing may also have had a direct effect in reducing kernel weight (Asana and Williams 1965).

Some practical aspects of these results are shown in Table 5. In view of the changes in kernel weight (Table 4), it is not surprising that the grain protein percentage increased with later sowing, and that the bushel weight decreased. More interesting are the grain yield results which, from regressional analysis, showed a linear decrease in grain yield of 2·6 and 1·5 bushels per acre in 1961 and 1962 respectively, for each week's delay in time of sowing during the period from the end of April to the middle of July.

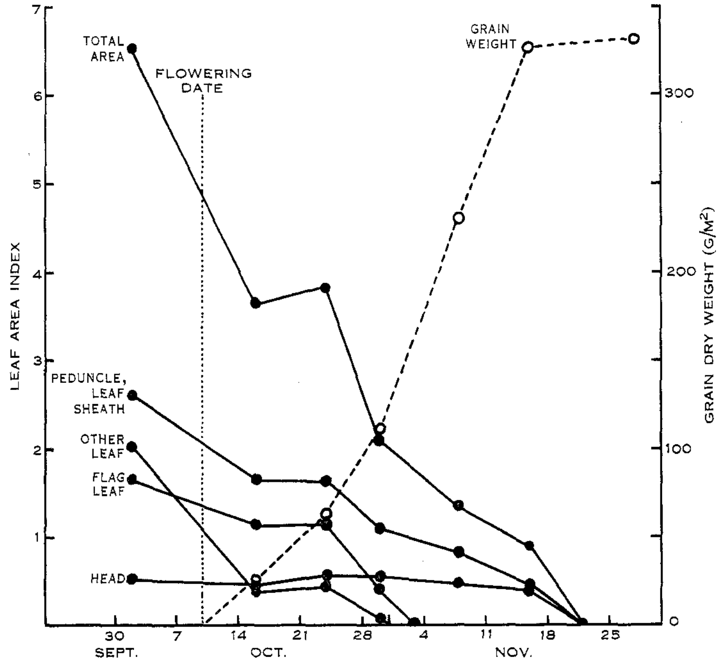

Fig. 3.—Changes with time in leaf area index and its components after flowering, and the increase in grain dry weight. Treatment T_1, trial T62.

(*c*) *Photosynthetic Area, Yield Components, and Grain Yield*

Data for changes in leaf area index after flowering were obtained for three trials at Wagga Wagga in 1962. Figure 3 illustrates typical changes in the components of leaf area and in kernel weight. The area beneath the leaf area index curve for the post-flowering period was calculated, and is called the leaf area duration after flowering (*D*). Figure 4 shows the relationship between final grain dry weight and *D* for all treatments in the three trials. Grain yield was highly correlated with *D* over the wide range of *D* values recorded (21–99 days). These data and other relevant information are listed in Table 6.

Thorne and Watson (1955) showed that for one variety of wheat grown at three nitrogen levels the ratio of grain yield to leaf area duration after ear emergence was constant. Hence they suggested that the variation in grain yield which they observed was due to variation in the area of photosynthetic tissue during the period of grain growth. Such a conclusion cannot be immediately inferred from the Wagga Wagga data, since the ratio of final grain dry weight to *D*, called the grain/leaf ratio, varied considerably among treatments. In fact, the grain/leaf ratio was related inversely to *D* (Table 6). Table 6 also reveals that the proportion of *D* derived from head tissue was inversely related to *D*, and thus the parallel variation in grain/leaf ratio may be explained by an underweighting of the head area component in assessing its relative contribution to grain growth. This is not unlikely, considering the rather arbitrarily selected scheme for measuring and weighting green head area.

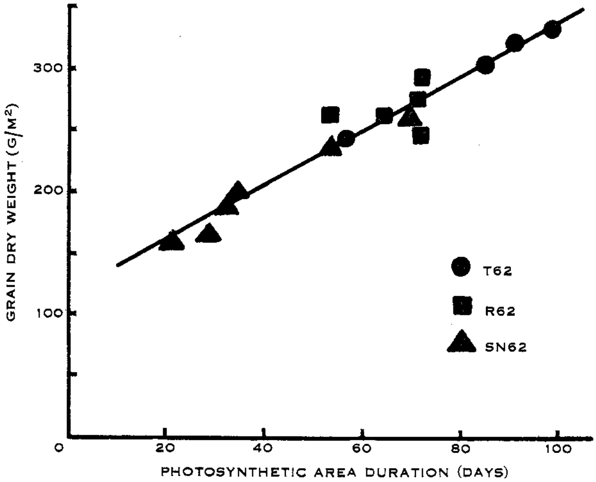

Fig. 4.—Relationship of final grain dry weight to leaf area duration after flowering (*D*). Trials T62, R62, and SN62. Equation of regression line:

$$y = 117+2\cdot21x \ (r = 0\cdot969).$$

Thus although there was considerable variation in the grain/leaf ratio between treatments, it bore no positive relation to grain yield or even to variation in relative turgidity. It is interesting therefore to examine the variation in *D* more closely upon the hypothesis that it largely determines the amount of post-flowering photosynthesis, and the grain yield, as has been suggested by Thorne and Watson (1955) and Watson, Thorne, and French (1958, 1963). This hypothesis of causality cannot be tested unequivocally; it rests upon an understanding of physiology and a good correlation coefficient. Even the correlation coefficient is not unique since, over the same trials at Wagga in 1962, grain yield was also well correlated with total dry weight at flowering (0·875), head number per unit area (0·826), and spikelet number per unit area (0·934).

For a given crop, D can be characterized by the leaf area index at flowering and the mean duration of the photosynthetic tissue, which is simply the ratio of D to leaf area index at flowering (Table 6). Leaf area index at flowering was largely dependent on the level of vegetative growth, although in some instances this relationship was complicated by pre-flowering moisture stress, and in the fertilizer trial by the effects of nitrogen on leaf area ratio. The mean duration of photosynthetic tissue appears to be related to leaf relative turgidity levels: within each trial a reduction in relative turgidity in the post-flowering period was accompanied by a decrease in this parameter. In the time of sowing trial, the period after flowering during which leaf relative turgidity at sunrise remained above 75% decreased from 22 to 13 days, from the first to the last sowing. The mean duration of photosynthetic tissue showed a corresponding decrease (Table 6). Leaf senescence was rapid once the 75% level was reached. Plant water stress has been observed by others (Milthorpe 1945; Morton and Watson 1948) to hasten senescence. Asana, Saini, and Ray (1958) attributed the reduction in grain yield of wheat under drought to a hastening of head senescence. The fact that plant moisture stress could not be measured after flag leaf senescence

TABLE 6

FINAL GRAIN DRY WEIGHT (G), LEAF AREA DURATION AFTER FLOWERING (D), GRAIN/LEAF AREA RATIO, AND RELATED PARAMETERS: TRIALS T62, R62, AND SN62

Trial and Treatment	G (g/m²)	D (days)	Grain/Leaf Ratio (G/D)	Head Area (% of D)	Leaf Area Index at Flowering	Ratio D to Leaf Area Index at Flowering	Days of Turgidity >75%*
T62: T_1	333	98·6	3·4	19·9	5·0	20	22
T_2	320	90·9	3·5	19·7	5·2	18	21
T_3	303	85·1	3·5	19·4	5·1	17	19
T_5	242	56·4	4·3	24·7	4·0	14	13
L.S.D. ($P = 0·05$)	23	13% of mean					
R62: R_1	293	71·9	4·1	21·3	3·8	19	15
R_2	277	70·9	3·9	20·4	5·0	14	13
R_3	244	71·5	3·4	20·3	5·3	14	
R_4	261	64·0	4·1	23·0	3·4	19	20
R_5	263	53·2	4·9	24·5	3·2	16	
L.S.D. ($P = 0·05$)	29	16% of mean					
SN62: S_0N_0	159	21·3	7·5	30·2	1·3	17	22
S_0N_1	166	28·5	5·9	30·0	1·7	17	22
$S_{\frac{1}{2}}N_0$	188	31·7	5·9	25·2	1·7	19	25
$S_{\frac{1}{2}}N_1$	234	53·0	4·4	20·6	3·9	13	21
S_2N_0	199	34·4	5·8	22·7	2·0	17	25
S_2N_1	259	69·0	3·8	18·9	5·0	14	17
L.S.D. ($P = 0·05$)	40	25% of mean					

* Days after flowering before leaf relative turgidity at sunrise fell below 75%.

somewhat limits our conclusions, particularly as up to 50% of grain growth (and 10–20% of *D*) occurred after that time (Fig. 3). There were also complications due to the effect of nitrogen supply. At nil nitrogen in the SN62 trial, where soil nitrogen levels were low, leaf senescence proceeded at comparatively high relative turgidity levels (85%), and involved gradual yellowing rather than the rapid necrosis observed in most other treatments.

The measurements of *D*, its breakdown into components, and the calculation of the grain/leaf ratio provides an understanding of grain yield responses in the Wagga trials, upon the assumption that photosynthate production limits grain yield. A complication is the possibility that yield is limited by the number of grains set by the crops. Indeed the correlation of grain yield with grain number (0·966) was as good as its correlation with *D*. In addition, kernel weight was relatively constant among treatments, since the linear regression line of *G* on grain number passed almost through the origin. Many other workers have reported kernel weight to be the yield component showing least variation (Forster and Vasey 1930; Asana and Mani 1955). Since there was a large range in grain number in the trials reported here (from 445 to 1007 grains per m^2), the constancy of kernel weight shows an interesting absence of competition among the developing grains. This in turn indicates that the supply of photosynthate for grain growth was always adequate for the rates of grain growth permitted by other external or inherent factors. If yield is limited by the number of grains set in the wheat crop — a possibility deserving further attention — it is to be expected that *D* would be a less useful indicator of grain yield and that yield components, particularly grain number, by virtue of their being direct measures of sink size would show higher correlations. In the present results yield was closely related both to *D* and to grain number.

IV. Conclusion and Application

In the time of sowing trials at Wagga in 1961 and 1962, each week's delay in the time of sowing, and in turn each corresponding 2-day delay in the time of flowering, resulted in an average reduction in grain yield of 2 bushels per acre. Measurements of leaf relative turgidity levels suggest that this effect on yield was due largely to increased plant moisture stress after flowering. Inspection of average rainfall and potential evapotranspiration data indicates that these 1961 and 1962 results may be fairly typical of the average season at Wagga (Fischer and Kohn 1966*a*).

Our results provide quantitative evidence for the long-held theory concerning the desirability of early flowering in the Australian environment. Probably the delayed flowering of a later-developing variety would result in even greater increases in post-flowering plant moisture stress than were associated in these trials with delayed flowering caused by later sowing dates. Early flowering is necessary to permit a long post-flowering period during which photosynthetic components remain green. Chinoy (1947) found that for a wide range of varieties sown together in India and maturing under conditions of rising temperature, reduction of the vegetative period over the range from 170 to 90 days was associated with an increased ripening period, from less than 20 days to more than 60 days, and with increased grain yields. Consideration of optimal flowering dates must also involve the increased likelihood of frost damage associated with earlier flowering; this factor, however, did not appear to be important in the present trials.

In the rate of sowing and fertilizer trials an attempt was made to relate grain yield to vegetative growth. It has been shown that as the amount of growth at flowering increased, the amount of water available to the crop after flowering decreased. An increase of 100 g/m² in growth was associated with a reduction in soil water of about 0·5 in. (Fischer and Kohn 1966*a*). Thus, under dry-land conditions there is an optimal level of vegetative growth, depending on the water supply, for maximal grain yield; this has been implied in the discussion of the results of many fertilizer trials with cereals. At Boree Creek in 1961 when the water supply was very low, results showed that this optimal level of growth was surpassed in some treatments. The point is also illustrated by the results of the rate of sowing trial in 1962 (Fig. 5).

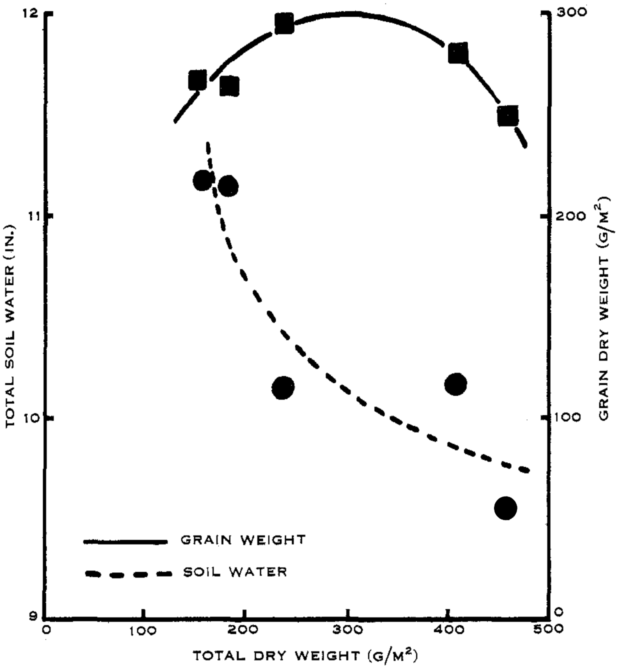

Fig. 5.—Relationships of total soil water (0–48 in.) at about flowering time (Oct. 18), and final grain dry weight, to the total dry weight at Sept. 19. Trial R62.

In applying these results to the local problem of "haying off" under conditions of high soil nitrogen, there are not yet enough data to indicate the optimal levels of vegetative growth. In fact, there is some evidence that high nitrogen has special effects on the crop, independent of the effect on dry matter production. These include the effect on leaf area ratio and mean shoot size already mentioned. To these should be added the possibility that high nitrogen may delay flowering and may increase lodging. The sensitivity of grain yield to delays in flowering has already been indicated; however, there are conflicting reports on the effect of nitrogen on time of flowering. In the present trials, added nitrogen never caused more than a 2-day delay in flowering. There is much evidence to show that crop lodging after flowering causes a considerable depression in grain yield (Weibel and Pendleton 1964).

V. ACKNOWLEDGMENTS

We wish to acknowledge the assistance of Mr. N. Wooden in this work and the New South Wales Wheat Research Committee, with whose funds equipment was purchased. Some of the trials reported here were conducted on the property of Mr. J. R. Fischer, Boree Creek.

VI. REFERENCES

ASANA, R. D., and MANI, V. S. (1955).—Studies in the physiological analysis of yield. II. Further observations in varietal differences in photosynthesis in the leaf stem ear of wheat. *Physiol. Plant.* **8**: 8–19.

ASANA, R. D., MANI, V. S., PILLAY, K. P., and GAHLOT, K. N. S. (1958).—Analysis of drought resistance in crop plants. II. The influence of soil-drought on the relation between yield and ear characteristics in wheat (field experiments). *Indian J. Genet.* **18**: 187–98.

ASANA, R. D., SAINI, A. D., and RAY, D. (1958).—Studies in physiological analysis of yield. III. The rate of grain development in wheat in relation to photosynthetic surface and soil moisture. *Physiol. Plant.* **11**: 655–65.

ASANA, R. D., and WILLIAMS, R. F. (1965).—The effect of temperature stress on grain development in wheat. *Aust. J. Agric. Res.* **16**: 1–13.

BARLEY, K. P., and NAIDU, N. A. (1964).—The performance of three Australian wheat varieties at high levels of nitrogen supply. *Aust. J. Exp. Agric. Anim. Husb.* **4**: 39–48.

COLWELL, J. D. (1963).—The effect of fertilizers and season on the yield and composition of wheat in southern New South Wales. *Aust. J. Exp. Agric. Anim. Husb.* **3**: 51–61.

CHINOY, J. J. (1947).—Correlation between yield of wheat and temperature during ripening of grain. *Nature* **159**: 442–4.

DENMEAD, O. T., and SHAW, R. H. (1960).—The effect of soil moisture stress at different stages of growth on the development and yield of corn. *Agron. J.* **52**: 272–4.

FISCHER, R. A., and KOHN, G. D. (1966*a*).—The relationship between evapotranspiration and growth in the wheat crop. *Aust. J. Agric. Res.* **17**: 255–67.

FISCHER, R. A., and KOHN, G. D. (1966*b*).—Soil water relations and relative turgidity of leaves in the wheat crop. *Aust. J. Agric. Res.* **17**: 269–80.

FORSTER, H. C., and VASEY, A. J. (1930).—Some census studies on the wheat crop in Victoria. *J. Dep. Agric. Vict.* **28**: 449–59.

MILTHORPE, F. L. (1945).—Fibre development of flax in relation to water supply and light intensity. *Ann. Bot., Lond.* **9**: 31–53.

MORTON, A. G., and WATSON, D. J. (1948).—A physiologic study of leaf growth. *Ann. Bot., Lond.* **12**: 281–310.

PORTER, H. K., PAL, N., and MARTIN, R. V. (1950).—Physiologic studies in plant nutrition. XV. Assimilation of carbon by the ear of barley and its relation to the accumulation of dry matter in the grain. *Ann. Bot., Lond.* **14**: 55–68.

SINGLE, W. V. (1964).—The influence of nitrogen supply on the fertility of the wheat ear. *Aust. J. Exp. Agric. Anim. Husb.* **4**: 165–8.

STORRIER, R. R. (1965).—Excess soil nitrogen and the yield and uptake of nitrogen by wheat in southern New South Wales. *Aust. J. Exp. Agric. Anim. Husb.* **5**: 317–22.

THORNE, G. N. (1959).—Photosynthesis of lamina and sheath of barley leaves. *Ann. Bot., Lond.* **23**: 365–70.

THORNE, G. N., and WATSON, D. J. (1955).—The effect on yield and leaf area of wheat of applying nitrogen as a top dressing in April or in sprays at ear emergence. *J. Agric. Sci.* **46**: 449–56.

WATSON, D. J., THORNE, G. N., and FRENCH, S. A. W. (1958).—Physiological causes of differences in grain yield between varieties of barley. *Ann. Bot., Lond.* **22**: 321–52.

WATSON, D. J., THORNE, G. N., and FRENCH, S. A. W. (1963).—Analysis of growth and yield of winter and spring wheats. *Ann. Bot., Lond.* **27**: 1–22.

WEIBEL, R. O., and PENDLETON, J. W. (1964).—Effect of artificial lodging on winter wheat grain yield and quality. *Agron. J.* **56**: 487–8.