SOIL WATER RELATIONS AND RELATIVE TURGIDITY OF LEAVES IN THE WHEAT CROP

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[*Manuscript received November* 18, 1965]

Summary

Trials were conducted in 1961 and 1962 at 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). The increases in evapotranspiration and associated reductions in total soil moisture content caused by early sowing, by heavier fertilizer applications, and to a lesser extent by a heavier rate of sowing were reflected in an increased plant moisture stress (reduced leaf relative turgidity) at a given time in the spring. At a given stage of development, however, relative turgidity was not much affected by time of sowing, and in fact post-flowering plant moisture stress increased with later sowing.

There were only small treatment effects on the estimated depth and density of rooting. Relatively little water was extracted by crops from below 40 in.; dense crops reduced the soil moisture content throughout the root zone to less than the −15 bar value.

Leaf relative turgidity at sunrise showed a consistent inverse relationship to soil moisture content in the root zone. Leaf turgidity (sunrise) was maintained at 100% until root zone moisture levels approached the −15 bar value.

I. Introduction

This is the second in a series of three papers reporting a study of grain yield physiology in the wheat crop under field conditions at Wagga Wagga in southern New South Wales. Emphasis in this work was placed on understanding the relationship of grain yield to vegetative growth. This relationship is complicated in the Australian wheat belt by limited moisture supplies. Increased vegetative growth is sometimes accompanied by reduced grain yields (Colwell 1963), presumably — as suggested by many — because of excessive moisture usage before flowering. Few or no quantitative data are available, however, on plant and soil water relations in the wheat crop. This paper examines these aspects in appropriate field trials.

Treatments to alter vegetative growth involved variations in the time of sowing, the rate of sowing, and the amount of fertilizer applied. In an earlier paper (Fischer and Kohn 1966) it was shown that over the range of both time of sowing and fertilizer treatments used, two- and threefold differences occurred in crop growth (total dry weight) at about flowering time. These differences were associated with relatively smaller differences in total evapotranspiration; total soil moisture differences between extreme crops at a given time in the spring were never more than 2 to 2·5 in. This

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paper deals with the effects on root activity, available soil water in the root zone, and plant water stress as indicated by leaf relative turgidity.

II. Experimental Details

All work was done at the Agricultural Research Institute, Wagga Wagga. Table 1 summarizes trials and treatments. All trial sites, except that of trial SN62, have soils of high fertility, being areas which had previously grown subterranean clover pastures. From three to six replicates were sown, the plots being 30–36 ft long and 9 or 16 rows wide. The wheat variety Heron was used throughout. Climatic and other experimental details can be found in the earlier paper (Fischer and Kohn 1966).

Table 1

Summary of trials and treatments

Trial	Treatment				
	Symbol	Date Sown	Rate of Sowing (lb/acre)	Superphosphate (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, 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, 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.

For soil moisture studies, auger sampling to 48 in. was used in 1961. In 1962 the neutron moisture meter technique was used, records being taken to a depth of 52 or 61 in. Water contents at −15 bars water potential were determined with a pressure membrane apparatus for each depth interval at each trial site (Table 2 shows typical data). The information was used to obtain an integrated measure of available soil water, that is, the average amount over the whole root zone by which soil moisture content at each depth interval in this zone was greater than the −15 bar value. The root zone was assessed from the pattern of moisture extraction. Available soil moisture is expressed in milligrams per cubic centimetre.

The leaf relative turgidity technique of Weatherley (1950), as modified by Barrs and Weatherley (1962), was used to measure plant moisture stress. Leaf discs were collected and floated on distilled water for 3 hr under constant low illumination (approx. 25 f.c.) from fluorescent lights. Their water content when collected was

TABLE 2

BULK DENSITY AND MOISTURE CONTENT AT −15 BARS WATER POTENTIAL: TRIAL T62

Data are the means of 12 samples

Depth Interval (in.)	Bulk Density (g/c.c.)	—15 Bars Moisture Content	
		Moisture (%)	(mg/c.c.)
0 – 7½	1·42	6·5	92
7½–16½	1·60	10·4	166
16½–25½	1·53	14·3	219
25½–34½	1·60	14·7	235
34½–43½	1·63	16·1	262
43½–52½	1·72	15·4	265
52½–61½	1·72	14·8	255

expressed as a percentage of their water content after floating. There was no obvious infiltration of water through the edge of the discs. Samples were taken at about sunrise and again at 2 to 3 p.m. at approximately weekly intervals in the spring. The middle portion of the uppermost fully expanded leaf was sampled. Dew on the leaves at sunrise was removed with a cloth before sampling. A total of 15 to 25 leaf discs were collected from each treatment at each sampling. In 1962 when samples were taken separately on each half of the trial for each treatment, the calculated standard error of the treatment mean at a given date averaged 2%.

III. Results

(a) Soil Moisture Content

Figure 1 shows soil moisture contents relative to the −15 bar values throughout the profile for treatments causing the largest differences in evapotranspiration in the time of sowing trial and in the fertilizer trial in 1962. Error values shown are typical of those involved in the other trials.

Soil moisture contents increased during the winter when rainfall exceeded evapotranspiration. Only in the latest sowing (treatment T_5) in both 1961 and 1962, however, were there significant increases in soil moisture down to 50 in. In all other treatments and trials the winter wetting front reached depths between 30 and 40 in., and increases in soil moisture were small even at these depths.

After the soils had reached their maximum moisture content, which was in late winter, the moisture content progressively declined until crop maturity was reached. The greatest depth at which significant reductions in soil moisture occurred during this period was assumed to indicate the deepest penetration of the effective root zone, i.e. effective in moisture extraction.

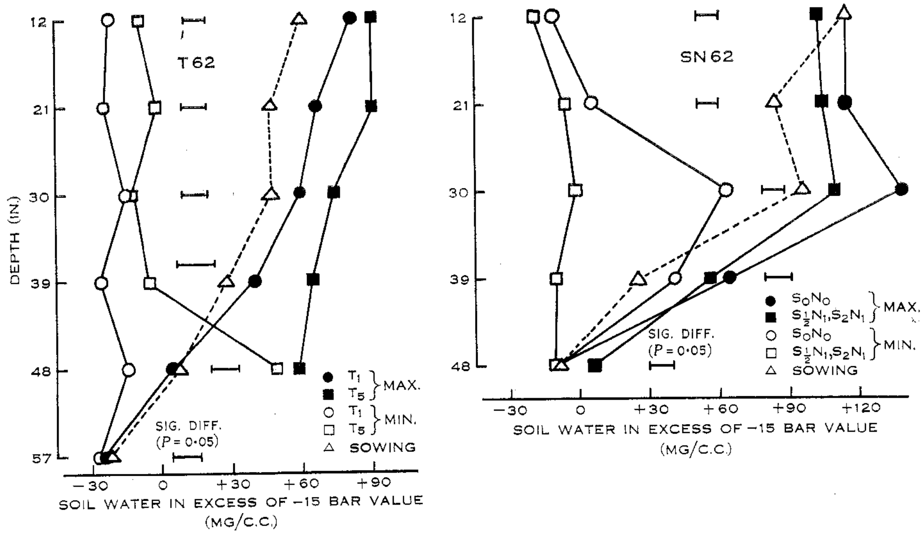

Fig. 1.—Maximal and minimal amounts by which the soil water content exceeded the −15 bar value throughout the profile for extreme treatments: trials T62 and SN62. Significant differences shown are for changes within a given treatment.

The depth of the root zone varied little with treatment. Although in the time of sowing trials significant decreases in soil moisture were recorded at the lowest depth of measurement (about 50 in.) for all treatments except T_1 in 1962, changes below 40 in. were relatively small. With treatment T_1 in 1962, measurements were made to 61 in., but there was no change below 52 in. (see Fig. 1). In the rate of sowing and fertilizer trials, only in 1962 were observations detailed enough to permit conclusions. In the former trial there were no treatment differences at the lowest depth at which soil moisture was removed in the spring (43 in.). In the fertilizer trial this was also the case except with the denser crops, treatments $S_{\frac{1}{2}}N_1$, S_2N_0, and S_2N_1, for which significant water losses occurred to a depth of 52 in. Both in this trial and in trial T62, the overall decreases in soil moisture content in the $43\frac{1}{2}$–$52\frac{1}{2}$ in. depth interval amounted to less than 0·2 in., that is, less than 3% of evapotranspiration over the spring period. The greatest value for changes in the interval $34\frac{1}{2}$–$43\frac{1}{2}$ in. was 0·7 in. (10% of the evapotranspiration).

Total soil water in the 6–50 in. depth interval (the uppermost 6 in. being excluded to avoid the complication of direct soil evaporation) was calculated for a given date when the crops had ripened and soil water contents were minimal (Fig. 1). This revealed no significant differences between treatments in the time of sowing trials except in the case of treatment T_5, the latest sowing: in 1962 this treatment had 0·7 in. more water than did the other treatments (sig. diff. ($P = 0{\cdot}05$), 0·4 in.). In the rate of sowing trial in 1962, treatment differences were again non-significant, but there was a tendency for more water under the wide row crop at maturity. In the fertilizer trial there was 1·2 in. (sig. diff. ($P = 0{\cdot}05$), 0·8 in.) more water under the

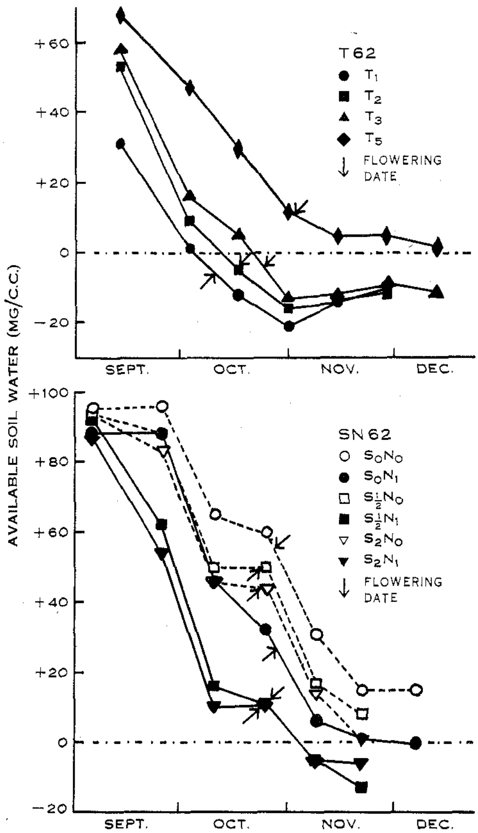

Fig. 2.—Available soil water changes with time: trials T62 and SN62. Available soil water is the amount, averaged over the whole root zone, by which the soil moisture content at each depth interval is greater than the −15 bar value.

sparsest crop (S_0N_0) than under the thickest crops ($S_{\frac{1}{2}}N_1$ and S_2N_1), receiving high superphosphate and nitrogen dressings (Fig. 1); other treatments were intermediate. The moisture content over the entire root zone at maturity was less than the −15 bar value by 10–25 mg/c.c., i.e. about 0·7–1·5% gravimetric, for all crops except the sparser ones in the fertilizer trial (Fig. 1).

(*b*) *Available Soil Water in the Root Zone*

Since differences in the depth of the root zone among treatments in any trial were small, differences in the calculated available soil water in the root zone corresponded fairly closely to differences in evapotranspiration found earlier (Fischer and Kohn 1966). Thus the greater was evapotranspiration for a treatment, the less was both total soil water and available soil water in its root zone. Changes in available soil water with time are shown for two trials in Figure 2. These data further illustrate the fact that the root zone was often dried to less than the −15 bar value, and that for dense crops the post-flowering period was commonly one of quite low available water over most of the root zone.

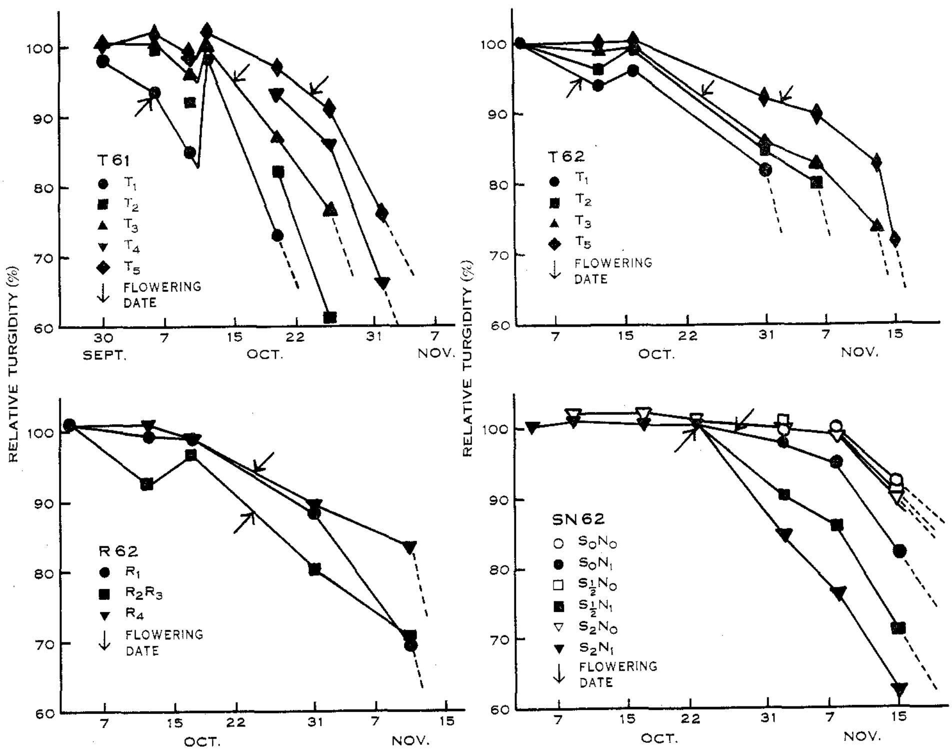

Fig. 3.—Changes in leaf relative turgidity at sunrise with time: trials T61, T62, R62, and SN62.

(c) *Plant Moisture Stress*

Values of leaf relative turgidity ranged from maxima of 103% at sunrise and 99% in the afternoon to minima of 65 and 50% respectively. The diurnal range in relative turgidity varied from 2 or 3% to about 20%.

Relative turgidity at a given time in the late spring was decreased by early sowing, by fertilizers (particularly nitrogen, and nitrogen plus superphosphate), and to a lesser extent by increased sowing rates (Fig. 3). In two other fertilizer trials not previously mentioned, high superphosphate and nitrogen dressings produced marked responses in vegetative growth, similar to those in the SN62 trial. These growth responses were also accompanied by reductions in relative turgidity. Relative turgidity at about flowering time was reduced 10–15% for high fertilizer compared with nil fertilizer.

A better estimation of the rather small differences in plant moisture stress in the rate of sowing trial (R62) is provided by measurements in the afternoon when relative turgidity appeared more sensitive to soil moisture differences (Table 3). A sowing rate of 20 lb seed per acre (R_1, R_4, and R_5) was accompanied by significantly higher relative turgidities than the heavier sowing rates, R_2 and R_3, the results of which were bulked because they appeared to be similar. At the lowest sowing rate, wide rows

TABLE 3

LEAF RELATIVE TURGIDITY IN THE AFTERNOON (3 P.M.): TRIAL R62

Treatment	Leaf Relative Turgidity (%)				
	Oct. 3	Oct. 12	Oct. 31	Nov. 6	Mean
R_1	94·4	83·3	75·6	62·9	79·1
R_2	91·7	77·2	65·8	55·1	72·9
R_3	93·7	77·6			
R_4	95·4	85·9	76·4	66·0	80·9
R_5	98·0	88·8	83·0	71·7	85·4
L.S.D. ($P = 0{\cdot}05$)					3·0

(R_4) did not alter relative turgidity compared with narrow rows (R_1); however, straw mulch between the wide rows (R_5) was accompanied by a small increase in relative turgidity. In a rate of sowing trial in 1961, the limited sampling did show that at about flowering time, the mean relative turgidity was 7% greater at 30 lb seed per acre than at 120 lb, while 60 lb had an intermediate value (sig. diff. ($P = 0{\cdot}05$), 3%).

TABLE 4

DAYS AFTER FLOWERING FOR WHICH LEAF RELATIVE TURGIDITY AT SUNRISE WAS GREATER THAN 75%: TRIALS T61 AND T62

Treatment	Days after Flowering for which Relative Turgidity at Sunrise >75%	
	1961	1962
T_1	12	22
T_2	10	21
T_3	10	19
T_4	9	—
T_5	7	13

At a given stage of development in the spring, relative turgidity was not greatly affected by sowing time (see Fig. 3) since later sowing delayed development. However, a further comparison is provided by noting the number of days after flowering before the leaf relative turgidity at sunrise fell below 75% (Table 4). It was observed that once the relative turgidity (in this instance that of the flag leaf) had reached about 75% at sunrise, leaf senescence and desiccation soon followed. Table 4 shows that post-flowering plant moisture stress increased with later sowings in both 1961 and 1962, and incidentally shows the comparative severity of the 1961 season.

Relative turgidity patterns obviously are closely related to changes in the available soil water, some of which are shown in Figure 2. Figure 4 summarizes these relationships. All time of sowing treatments in both years, and the rate of sowing treatment in 1962, appear to fit approximately the same relationship, with the exception of treatment T_5 in 1962 and treatment R_4. These treatments, the latest sowing and wide-row spacing respectively, reduced the relative turgidity at a given available soil water value as compared with other treatments. In the fertilizer trial, all treatments,

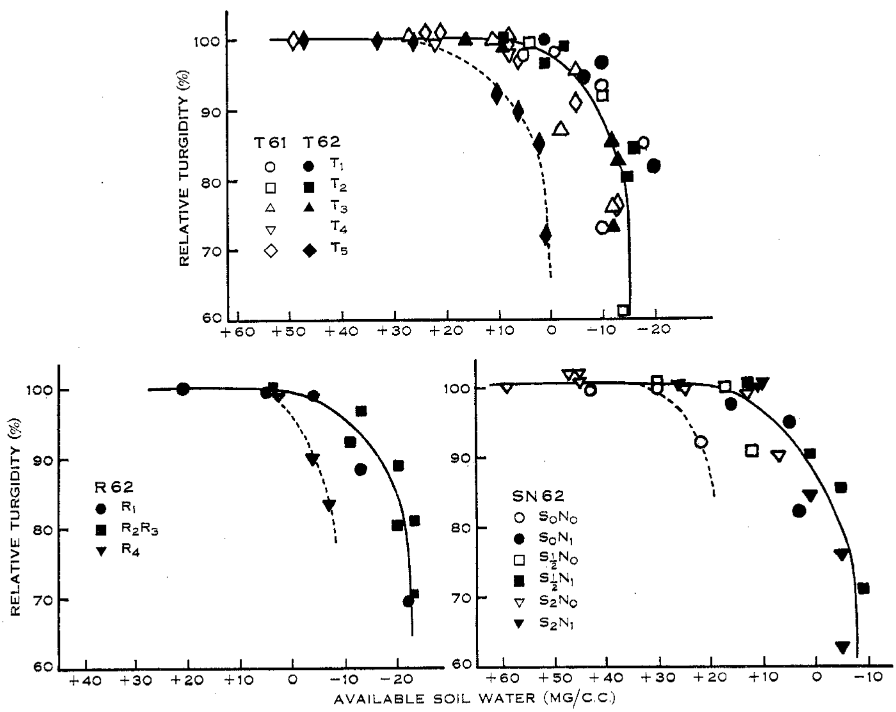

Fig. 4.—Relationship between leaf relative turgidity at sunrise and available soil moisture: trials T61 and T62, R62, and SN62.

except possibly S_0N_0, also show a common relationship between relative turgidity (sunrise) and available soil water; however, this relationship appears to differ slightly from that in the other trials.

Relative turgidity at sunrise appeared insensitive to moderate soil moisture stress. It was only after the available soil water fell below *c.* +10 mg/c.c. in the fertilizer trial and below +5 mg/c.c. in the time and rate of sowing trials that relative turgidity at sunrise for dense crops fell below 100%. These soil values correspond respectively to *c.* −10 and −13 bars soil water potential.

IV. Discussion

(a) *Moisture Stress in the Crop*

The earlier paper (Fischer and Kohn 1966) demonstrated that during the spring there were significant differences in crop growth and in the total evapotranspiration as a result of the various treatments used. Since cumulative evapotranspiration was calculated assuming no run-off and no deep percolation, both reasonable assumptions under the conditions, the differences in evapotranspiration corresponded to the same differences, in an opposite direction, in total soil water. This paper shows that the effects of treatment on plant moisture stress, as measured by leaf relative turgidity, were closely related to these total soil water differences.

In examining this relationship, the first step is to calculate available soil water in the root zone. This step depends on the extent of the root zone as well as on the total soil water in the profile. However, no treatment altered the final depth of the crop root zone more than about 9 in., a small amount relative to its overall depth (*c.* 40–50 in.). Thus differences in available soil water corresponded closely to differences in total soil water.

The second step concerns water potential at the plant root surface and involves the thoroughness of exploration of the crop root zone, i.e. the density of roots or the effective length of roots per unit volume of soil (Gardner 1964). Under conditions of non-equilibrium there exists a water potential gradient towards each root, and the closer together the roots are the closer the water potential at the root surface will approach the overall average soil water potential. For a given level of available soil water, therefore, increased root density increases the water potential at the root surface. Conditions of non-equilibrium in the soil, even at sunrise, are not unlikely. Weatherley (1951) has shown with cotton that the effect of day-time transpiration losses on plant water content may not be completely eliminated by sunrise next day.

There is evidence that late sowing, wide-row spacing, and nil or reduced fertilizer application reduced the root density, contributing to the somewhat different relationship of leaf relative turgidity to available soil water found for those treatments (Fig. 4). Total soil moisture at maturity was greater for these treatments. Under conditions of limiting soil moisture as maturity is approached, one might expect the soil moisture content at maturity to be related inversely to root density.

Notwithstanding these small effects of some treatments on root density, differences in leaf relative turgidity closely reflected differences in available soil water (Fig. 4), which in turn reflected the total soil water situation. Apparently treatments did not greatly alter the relationship between water potential at the root surface, water potential in the plant, and leaf relative turgidity.

Thus there is quantitative evidence that late sowing, high sowing rates, and high fertilizer rates do increase plant moisture stress, and in a manner directly related to the increase in evapotranspiration caused by these treatments. In the case of time of sowing treatments, this conclusion refers to the post-flowering period rather than to a given time in the spring, and emphasizes the moisture stress problem of delayed flowering in this environment (Table 4).

The rate of sowing and fertilizer trials provide evidence of the increased plant water stress associated with increased crop growth. Various workers have shown added nitrogen and superphosphate to increase the depth and amount of wheat roots (Lees 1924; Kmoch *et al.* 1957) and the degree of moisture extraction (Ramig and Rhoades 1963; Warder *et al.* 1963). There is evidence that this occurred to a small extent in the fertilizer trial, but apparently it was insufficient to improve markedly the water relations of the heavily fertilized crops. Finally, although some of the differences in leaf turgidity are small, there is nothing to indicate that grain yield may not be sensitive to such changes, or to indicate the degree to which the increase in crop growth can compensate for the concomitant reduction in leaf relative turgidity when soil moisture is limiting. It is interesting that over the range of values encountered, a 1% decrease in leaf relative turgidity corresponded to a decrease in leaf water potential of about 1 bar (Fischer, unpublished data), a figure comparable with that found for privet by Weatherley and Slatyer (1957).

(*b*) *Root Depth and Moisture Extraction*

It should be pointed out that moisture extraction patterns do not necessarily correspond to the presence of actual roots in the soil profile (Doss, Ashley, and Bennett 1960). The lowest depth of significant moisture extraction in the trials reported here was *c.* 48 in. for dense crops. Lees (1924) reached a similar conclusion at Wagga.

Other workers have reported deeper penetration of wheat roots (Butler and Prescott 1955; Kmoch *et al.* 1957). Butler and Prescott found soil moisture losses down to 5 ft on a red-brown earth in South Australia. Probable factors limiting the depth of water extraction by roots at Wagga are the absence of available water at lower depths (Fig. 1) and the increase in bulk density to above 1·70 at about 40 in. in Gombalin clay loam (Table 2). Reduction of soil moisture to below −15 bars, which commonly occurred, is not unusual for wheat crops (Richardson and Fricke 1931; Kmoch *et al.* 1957; Lehane and Staple 1960).

(*c*) *Leaf Relative Turgidity*

Leaf relative turgidity was useful for comparing plant moisture stress levels. In some well-watered microplots located within the trials, there were significant effects of treatment and leaf age on relative turgidity at sunrise, even though soil moisture was always high. For example, values of relative turgidity at sunrise were maintained at around 100% until flowering, after which the turgidity fell progressively until, as the flag leaf began to senesce, values of 90–95% were measured. Such effects, however, were relatively small, and were insufficient to prevent the overall demonstration of a relationship between leaf relative turgidity at sunrise and average available water in the root zone (Fig. 4). The few departures from the relationship may have arisen from root density differences referred to earlier. Apparently the carry-over of diurnal plant water deficits such that relative turgidity at sunrise the next day is affected (Weatherley 1951; Werner 1954) was not a very important confounding factor in this situation.

Leaf relative turgidity at sunrise was maintained close to 100% for dense thick crops until the average available soil water in the root zone had fallen below +10 to +5 mg/c.c. (*c.* −10 to −13 bars soil water potential). Slatyer (1957) demonstrated a progressive decline in relative turgidity for tomatoes and cotton growing in pots, as the soil moisture content decreased below field capacity. Rutter and Sands (1958) showed similar results for water deficit in needles of Scots pine. Vaadia, Hagan, and Raney (1960), however, found relative turgidity at sunrise in ryegrass in the field to be fairly insensitive until soil water potential fell below −10 bars. It is possible that the continued gradual extension of the wheat roots into moister regions of the soil enabled leaf turgor to be completely restored overnight until the average soil moisture content approached the −15 bar value. Such a possibility may indicate a shortcoming in the use of a figure for available soil water averaged over the root zone. The large portion of the root zone which is dry may not be so important as the small portion, probably at the bottom of the root zone, which is still relatively wet.

It is interesting that on some mornings when considerable dew had formed on the leaves, leaf relative turgidity values as low as 70% were recorded. This indicates that little dew had moved into the leaf overnight. Weatherley (1950) found that dew did not directly affect leaf relative turgidity at sunrise.

V. Acknowledgments

We are grateful for the assistance of Mr. N. Wooden in this work, and to the New South Wales Wheat Research Committee, which supplied funds for purchasing equipment.

VI. References

Barrs, H. D., and Weatherley, P. E. (1962).—A re-examination of the relative turgidity technique for estimating water deficit in leaves. *Aust. J. Biol. Sci.* **15**: 413–28.

Butler, P. F., and Prescott, J. A. (1955).—Evapotranspiration from wheat and pasture in relation to available moisture. *Aust. J. Agric. Res.* **6**: 52–61.

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.

Doss, B. D., Ashley, D. A., and Bennett, O. L. (1960).—Effect of soil moisture regime on the root distribution of warm season forage species. *Agron. J.* **52**: 569–72.

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

Gardner, W. R. (1964).—Relation of root distribution to water uptake and availability. *Agron. J.* **56**: 41–5.

Kmoch, H. G., Ramig, R. E., Fox, R. L., and Koehler, F. E. (1957).—Root development of winter wheat as influenced by soil moisture and nitrogen fertilization. *Agron. J.* **49**: 20–5.

Lees, R. D. (1924).—Root development in wheat. *Agric. Gaz. N.S.W.* **35**: 609–12.

Lehane, J. J., and Staple, W. J. (1960).—Relationship of the permanent wilting percentage and the soil moisture content at harvest to the 15-atmosphere percentage. *Canad. J. Soil Sci.* **40**: 264–9.

Ramig, E. R., and Rhoades, H. F. (1963).—Interrelationships of soil moisture level at planting time and nitrogenous fertilization on winter wheat production. *Agron. J.* **55**: 123–7.

Richardson, A. E. V., and Fricke, E. F. (1931).—Effect of nitrogenous fertilizers on the growth and yield of wheat and barley. *J. Dep. Agric. S. Aust.* **35**: 57–86.

Rutter, A. J., and Sands, K. (1958).—The relation of leaf water deficit to soil moisture tension in *Pinus sylvestris L.* I. The effect of soil moisture on diurnal changes in water balance. *New Phytol.* **57**: 50–65.

Slatyer, R. O. (1957).—The influence of progressive increases in total soil moisture stress on transpiration, growth, and the internal water relationships of plants. *Aust. J. Biol. Sci.* **10**: 320–36.

Vaadia, Y., Hagan, R. M., and Raney, F. C. (1960).—Relative turgidity, transpiration, growth and soil moisture during a depletion cycle. Rep. Univ. Calif. Dep. Irrig. No. W67: 23–33.

Warder, F. G., Lehane, J. J., Hinman, W. C., and Staple, W. J. (1963).—The effect of fertilizer, nutrient uptake and moisture use of wheat on two soils in south western Saskatchewan. *Canad. J. Soil Sci.* **43**: 107–16.

Weatherley, P. E. (1950).—Studies in the water relations of the cotton plant. I. The field measurement of water deficits in leaves. *New Phytol.* **49**: 81–97.

Weatherley, P. E. (1951).—Studies in the water relations of the cotton plant. II. Diurnal and seasonal variations in relative turgidity and environmental factors. *New Phytol.* **50**: 36–51.

Weatherley, P. E., and Slatyer, R. O. (1957).—Relationship between relative turgidity and diffusion pressure deficit in leaves. *Nature* **177**: 1085–6.

Werner, H. O. (1954).—Influence of atmospheric and soil moisture conditions on diurnal variations in relative turgidity of potato leaves. Res. Bull. Neb. Agric. Exp. Sta. No. 176.