

Dry Matter Accumulation and Water Use Relationships in Wheat Crops

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Abstract

In order to better understand crop growth (dry matter accumulation, DM), crop evapotranspiration (E_t), and their interrelationships, we studied dryland crops of wheat (*Triticum aestivum* L. cv. Timgalen) sown at various dates and seeding densities in each of three years at Tamworth, N.S.W. Soil water stress was minimal before anthesis in each year, but in two years substantial stress arose before maturity. DM was increased consistently by increased plant density, and decreased at anthesis and maturity by later sowing. Crop growth rates determined over 2-week intervals around anthesis ranged from 3 to 20 g m⁻² d⁻¹, representing a range in efficiency of utilization of intercepted total solar radiation of 0.48 to 2.35%, variation which was adequately explained ($R^2 = 0.80$) by ontogeny (days from anthesis) and E_t/E_p ratio (E_p = class A pan evaporation).

E_t at anthesis, but not at maturity, was increased slightly by higher seeding density; crop E_t was not consistently affected by sowing date. E_t/E_p over 2-week periods around anthesis was related to leaf area index, and to a lesser extent to available soil water and E_p ($R^2 = 0.58$). For the period from the first sowing date in June or July until the middle of October, the relationship of total E_t to DM production was linear and close each year, but the slope varied from 6.2 g m⁻² mm⁻¹ (cold dry year) to 14.0 g m⁻² mm⁻¹ (wet year). This variation could be attributed to annual variation in the soil evaporation component of E_t , and in the ratio of DM to crop transpiration (= transpiration efficiency, TE). For 2-week periods around anthesis, TE ranged from 2.9 to 5.4 g m⁻² mm⁻¹ and was inversely related to E_p ($R^2 = 0.56$). Provided soil evaporation can be allowed for, since it ranged from 18 to 41% of crop E_t from sowing to maturity, it is argued that the crop transpiration-transpiration efficiency approach is particularly useful for analysing the growth and water use of dryland wheat.

Introduction

The yield of dryland crops can be considered in terms of water use, dry matter production per unit of water use, and dry matter distribution to the grain or harvest index (Passioura 1977; Fischer and Turner 1978). De Wit (1958) originally pointed out the predictability for a given plant species of the ratio of dry matter accumulation to transpiration, which he found to be proportional to the reciprocal of daily potential evaporation. This ratio has been used as the basis of simple (Hanks 1974) and relatively complex (van Keulen 1975) models of dry matter production by water-limited crops and pastures. The ratio of dry matter accumulation to transpiration has been recently defined as transpiration efficiency (TE) by Fischer (1979).

Key questions in such modelling exercises are the distinction of the crop transpiration (T) and soil evaporation (E_s) components of crop evapotranspiration (E_t), and the degree of complexity required by functions for predicting TE. The work of de Wit (1958) and others, and unpublished data from outdoor pot experiments with wheat at Wagga Wagga conducted by J. F. Warren and W. J. Lill (personal

communication, see also Fischer 1979), suggest that simple empirical functions, based solely on mean daily class A pan evaporation (E_p), may be adequate to predict the influence of weather on TE. On the other hand, and contrary to earlier views (de Wit 1958; van Keulen 1975; Fischer and Turner 1978), some recent results suggest that TE may be influenced substantially by the level of plant water stress encountered (Rawson *et al.* 1977).

In the context of dryland wheat crops in south-eastern Australia, it is generally accepted that extra crop growth or dry matter accumulation incurs a cost in terms of extra water use. It follows that where water supply is limiting towards the end of the crop cycle, as is common in this region, there is an optimal amount of early (pre-anthesis) growth and water use for maximum yield (e.g. Fischer and Kohn 1966c; Passioura 1977; Fawcett and Carter 1973). An optimum date for flowering is also recognized (Doyle and Marcellos 1974; Nix 1975). The approach to these questions has invariably been through consideration of ratios of actual crop evapotranspiration to potential evapotranspiration or to pan evaporation. Despite useful efforts in wheat yield modelling based on these ratios (Nix and Fitzpatrick 1969; Fawcett and Carter 1973; Nix 1975; Berndt and White 1976; Greacen and Hignett 1976), our understanding of water use, growth and yield of the wheat crop is still very inadequate. The transpiration-transpiration efficiency approach to this problem may provide useful new insights into water use and dry matter accumulation as the bases of yield, and into crop management aimed to minimize the cost of dry matter production in terms of water use. This paper reports such an analysis of dry matter accumulation by wheat crops of a single variety grown at Tamworth, N.S.W. Quantitative relationships predicting rate of development, dry matter accumulation, evapotranspiration and transpiration efficiency are derived, and the relationship of evapotranspiration to dry matter accumulation is elucidated.

Materials and Methods

The experiments were conducted at the Tamworth Agricultural Research Centre of the New South Wales Department of Agriculture during 1973, 1974 and 1975, on a red-brown earth (Dr 2·12) (Northcote 1965).

Experiments each year comprised a single variety of wheat (*Triticum aestivum* cv. Timgalen) in a complete block split-plot factorial, with times of sowing as main plots and sowing densities as subplots, with four replications. There were three sowing dates (two in 1975) (Table 1) and six seeding densities (seven in 1975). The densities sampled for soil moisture status were (kg seed ha⁻¹) in 1973; D1 (17), D2 (34), D3 (68) and D4 (96). In 1974 and 1975 D3 was not sampled, and in 1975 D4 was raised to 136 kg ha⁻¹ in order to create a greater range of dry matter accumulation and water use.

In each year the field had been kept fallowed from December, following the harvest of a previous wheat crop, prior to which the field was sown to lucerne. In 1973 and 1974, phosphorus was applied as single superphosphate at 11 kg ha⁻¹, and in 1975 of phosphorus was applied as double superphosphate at 20 kg ha⁻¹, in contact with the seed at sowing. In 1975 only, nitrogen as urea at 29 kg ha⁻¹ was drilled at seeding between the seeding rows. In no case were weeds or diseases a significant factor.

Rainfall and temperatures were recorded at the meteorological enclosure, up to 600 m from the sites. Class A pan evaporation data were those recorded by the

Tamworth Meteorological Bureau, 15 km distant, but with a similar aspect to the experiment sites. The closest radiation data, however, were sunshine hours measured at Gunnedah, 60 km west of the site. These data are summarized in Table 2.

Each plot comprised 12 rows, 18 cm apart and 32 m long. They were sampled for dry weight at *c.* 2 weeks before anthesis, at anthesis, and 2 weeks, 4–5 weeks (about date of zero green leaf) and 6–7 weeks (maturity) later. Each sample consisted of two quadrat cuts (each eight rows by 35 cm = 0.5 m²), one from each half of the plot, cut at ground level. Quadrat centres were 2 m apart. Samples were dried at 80°C. Six quadrats were cut at maturity for yield and yield component determination. Green leaf lamina areas were determined from subsamples by using an air-flow planimeter.

Soil moisture was determined gravimetrically from a 4 cm diameter core obtained with a thin-walled tube driven into each quadrat immediately after every growth sample. In addition, soil moisture was measured for each sowing date treatment at or soon after sowing. Soil moisture was determined at 15-cm intervals to a depth of 135 cm; water movement below 135 cm was assumed to be negligible. The –15 bar values were determined on soil samples ground to pass a 2 mm sieve.

Plant numbers were counted *c.* 2 weeks after emergence. Plots were observed for anthesis (50% of primary tillers showing extruded anthers), date of zero green leaf, and maturity (when plants were considered dry enough to thresh).

Table 1. Dates of sowing, anthesis and maturity^A, and available soil water (ASW) on key occasions for all crops: mean of densities

Variable	1973			1974			1975	
	T1	T2	T3	T1	T2	T3	T1	T2
Sowing: Day	172	205	235	183	220	246	195	232
Date	20.vi	24.vii	23.viii	2.vii	8.viii	3.ix	14.vii	20.viii
Day of anthesis	279	291	310	298	310	321	287	306
Day of zero green leaf	316	323	334	329	336	344	321	331
Day of maturity	328	339	351	344	351	366	331	345
ASW sowing (mm)	129	120	141	98	118	124	123	122
Day when ASW < 30 mm	313	never	326	288	312	326	279	313

^A Average of densities sampled, in Julian days (days from 31 December).

Results and Discussion

Phenology, weather and soil water

Key phenological events for the crops are summarized in Table 1. Anthesis occurred from as early as 7 October (T1, 1973) to as late as 17 November (T3, 1974). D4 reached anthesis on the average 3 days before D1, but in all subsequent calculations this small effect of density is ignored, and the anthesis date for all densities is assumed to be that recorded for D2. Anthesis was later in 1974, the coldest year, than in other years, and was delayed by later sowing. It was 0.47 day later per day delay in sowing date ($r = 0.896^{**}$, Fig. 1), a figure close to that which can be calculated from other wheat sowings at Tamworth (Doyle and Marcellos 1974) and sowings at Wagga Wagga (Syme 1968).

Table 1 also shows available soil water (water 0–135 cm above –15 bars, ASW) on two occasions. At sowing ASW was substantial (>100 mm); maximum ASW

(field capacity) was about 140 mm. The growing season of 1973 was wetter than average (Table 2), and moderately low soil water (ASW < 30 mm, see later) did not

Table 2. Weather conditions during crop growth

Variable	July	Aug.	Sept.	Oct.	Nov.	Dec.
Julian days	182 212	213 243	244 273	274 304	305 334	335 365 ^A
Precipitation (mm)						
1973	34	62	51	93	96	20
1974	21	47	25	68	72	3
1975	25	41	36	86	41	9
long term	44	48	49	60	66	38
Mean temperature (°C)						
1973	11.6	10.8	14.2	18.4	20.9	23.6
1974	9.1	9.4	11.8	16.4	18.7	23.5
1975	10.6	11.5	15.1	16.1	21.1	26.4
long term	9.1	10.7	13.5	17.4	20.6	22.2
Pan evaporation (mm d ⁻¹)						
1973	2.5	2.6	4.2	5.0	7.4	9.0
1974	2.2	3.1	4.2	4.8	7.8	10.7
1975	2.4	3.2	4.0	5.7	7.7	10.0
Sunshine (h d ⁻¹)						
1973	6.4	5.9	7.6	7.1	8.8	8.5
1974	5.4	6.4	7.5	6.5	9.0	11.2
1975	6.7	5.9	5.2	7.0	8.8	8.8

^A All December data to day 350 only.

arise until close to maturity, if at all (Table 1). Conditions were drier and close to average in 1974 and 1975, with ASW falling below 30 mm at around anthesis, or a

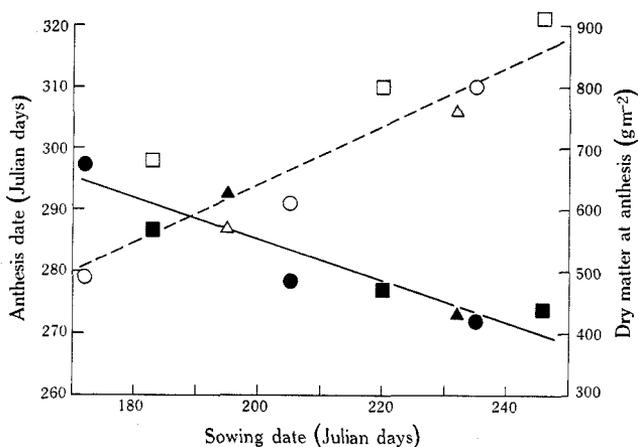


Fig. 1. Relationship of anthesis date (---) (open symbols) and dry matter accumulation at anthesis (—) (solid symbols) to sowing date: circles (1973), squares (1974) and triangles (1975): DM values refer to means of D1 and D2 (1973, 1975) and of D1, D2 and D4 (1974), i.e. a plant density of 61–71 m⁻².

few days sooner for T1, and substantial negative ASW values as maturity was approached, especially in 1974 (see also Table 4). In summary, soil water shortage,

and from other experience (Fischer and Kohn 1966b) plant water stress, were minimal before anthesis, and hence rates of dry matter accumulation were unlikely to have been limited before anthesis by water supply. On the other hand, as is believed to be typical in this environment, post-anthesis stress was evident in 1974 and 1975.

Table 3. Plant density, occurrence of 400 g m⁻² dry matter, and dry matter at anthesis and maturity as affected by density, season, and date of sowing

Density	1973			1974			1975		\bar{X}
	T1	T2	T3	T1	T2	T3	T1	T2	
	<i>Plant density (m⁻²)</i>								
D1	41	47	45	29	33	36	48	40	40
D2	77	74	83	46	55	57	80	88	70
D3	157	155	144	—	—	—	—	—	—
D4	208	216	209	142	133	106	260	334	201
\bar{X}	121	123	120	72	74	66	129	154	
	<i>Estimated days from sowing to DM = 400 g m⁻²</i>								
D1	95	82	76	111	91	79	85	76	87
D2	89	79	71	106	85	76	81	70	82
D3	84	75	66	—	—	—	—	—	—
D4	83	72	64	99	80	69	74	62	75
\bar{X}	88	77	69	105	85	75	80	69	
	<i>DM at anthesis^A (g m⁻²)</i>								
D1	580	460	380	476	388	375	620	380	457
D2	760	510	460	533	477	412	630	480	533
D3	910	580	580	—	—	—	—	—	—
D4	940	630	590	685	547	544	750	618	663
\bar{X}	798	545	503	565	471	444	667	493	
	<i>DM at maturity^B (g m⁻²)</i>								
D1	1150	860	635	924	800	675	875	780	838
D2	1185	995	760	947	915	730	1030	820	919
D3	1240	1015	855	—	—	—	—	—	—
D4	1245	1050	845	1006	947	784	1060	950	981
\bar{X}	1250	980	774	959	887	721	988	850	

^A Sampling within 2 days of anthesis; T1 1974 and T2 1975 adjusted to anthesis date because their anthesis sampling date fell 3 and 5 days respectively away from anthesis.

^B Mean of zero green leaf and maturity samplings.

Dry matter accumulation

Long Term

Seeding density treatments led to expected differences in plant density and in the time taken for crops to reach a level of 400 g m⁻² for above-ground dry matter (DM) (Table 3). This latter value is assumed to indicate the speed of approach to full ground cover (a lower value of DM, say 300 g m⁻², would have been a closer indicator of true full ground cover, but its estimation involved excessive extrapolation).

On the average, D4 reached 400 g DM m^{-2} 12 days sooner than D1 and had about 200 g m^{-2} and 150 g m^{-2} extra DM at anthesis and maturity respectively. Responses of DM at anthesis to sowing density in Table 3 were of the same order as those reported by Fischer and Kohn (1966a) and Fawcett and Carter (1973). It would seem reasonable to attribute these responses to differences in the time taken to reach full light interception (Puckridge and Donald 1967; Fischer *et al.* 1976). The difference in time for DM to reach 400 g m^{-2} of 12 days between D1 and D4 (Table 3) would, at an average rate of DM accumulation after full light interception of $17.5 \text{ g m}^{-2} \text{ d}^{-1}$, explain the DM difference between D1 and D4 observed at anthesis (Table 3).

Looking at averages of all densities, later sowing accelerated the attainment of full cover, while this interval was clearly greater in 1974 than in either 1973 or 1975 (Table 3). The seasonal effect is still evident after allowance for the low plant numbers in 1974 due apparently to poor seed, and probably reflects lower temperatures in 1974 (Table 2). Variation in days from sowing to 400 g DM m^{-2} over all crops in Table 3 was adequately explained by calculation of the day degree total above zero (ΣD) for the interval and the logarithm of the plant density ($\log_{10} P$):

$$\Sigma D = 1645 - 297 \log_{10} P \quad (r = -0.918^{**}; n = 27).$$

Season had little effect on dry matter production at anthesis or maturity (Table 3, also Fig. 1), but later sowing clearly depressed DM at anthesis and at maturity (Table 3). Allowing for seasonal changes in density by calculating DM at a given density ($61\text{--}71 \text{ plants m}^{-2}$), showed DM at anthesis to fall 3.3 g m^{-2} per day delay in sowing date ($r = -0.917^{**}$, Fig. 1). Thus development (days to anthesis) was accelerated more than crop growth rate by the higher temperatures, longer days and higher solar radiation encountered with later sowing dates. This is probably a general phenomenon in such environments (Fischer and Kohn 1966a; Fawcett and Carter 1973): in the absence of pre-anthesis moisture stress the data of Fischer and Kohn (1966a) from Wagga Wagga show a decline in DM at anthesis of 5.2 g m^{-2} per day delay in sowing (1962 data, $r = -0.977^{*}$). Thus reduced yield potential, in terms of less DM at anthesis, may be another reason for reduced yields with delayed sowing, a reason quite independent of the often-invoked deterioration of post-anthesis plant water status with later sowing (Fischer and Kohn 1966c; Kohn and Storrier 1970; Doyle and Marcellos 1974).

It is often argued that for maximum yield in water-limited situations there is an optimal amount of pre-anthesis growth or DM at anthesis and an optimal date for the occurrence of anthesis. Considering frost risk, Doyle and Marcellos (1974) indicate that this date is 10 October (day 283) at Tamworth. As pointed out elsewhere (Fischer 1979), a figure such as Fig. 1 provides one way of examining the closeness with which a cultivar, in this case Timgalen, meets both the above-mentioned criteria. If, for purposes of illustration, we assume that the optimum DM at anthesis is 640 g m^{-2} , then Timgalen fits perfectly: sown on day 175 (24 June) at $60\text{--}70 \text{ plants m}^{-2}$ it would reach anthesis on the optimum date (day 283) and have the optimum amount of DM.

Density and time of sowing effects on the leaf area index at anthesis were proportional to their effects on dry matter at anthesis seen in Table 3 ($L = 0.07 + 0.0046M$; $r = 0.852^{**}$, where L is LAI and M is DM). After anthesis LAI declined fairly rapidly, so that at 2 weeks after anthesis it was only about one-half of the value at anthesis, and 2 weeks later it was close to zero (Table 1).

Short Term

The crop samplings around anthesis permitted calculation of rates of DM accumulation over approximate 2-week intervals from about 2 weeks before anthesis until 4–5 weeks after. Averaging density treatments to increase precision gave a total of 22 sowing date–sampling interval combinations over the three years, crop growth rate ranging from 3.2 to 20.3 g m⁻² d⁻¹. Growth in terms of efficiency of utilization of solar radiation intercepted by green tissue was estimated for each interval. Total green tissue area index (GAI) was estimated from LAI, assuming LAI/GAI = 1.0 at 20 days before anthesis, but that LAI/GAI decreased by 0.01 per day after this date (R. A. Fischer, unpubl. data). The proportion of incident radiation intercepted by this tissue (I/I_0) was estimated by $1.0 - \exp(-0.45 \text{GAI})$. I/I_0 ranged from 0.34 to 0.86. Total solar radiation (MJ m⁻² d⁻¹) was estimated by using sunshine hours and a relationship given by Van Wijk and Scholte Ubing (1966, p. 85), assuming latitude to be 30° S. and the relationship constants to be those quoted by those authors for Deniliquin, N.S.W. Solar radiation ranged from 18.8 to 31.3 MJ m⁻² d⁻¹; multiplication by I/I_0 gave intercepted total solar radiation. Crop growth rate in energy terms (assuming 1.68 KJ g⁻¹ dry matter) as a percentage of intercepted radiation gave the efficiency of radiation utilization in crop growth; it ranged from 0.48 to 2.35%.

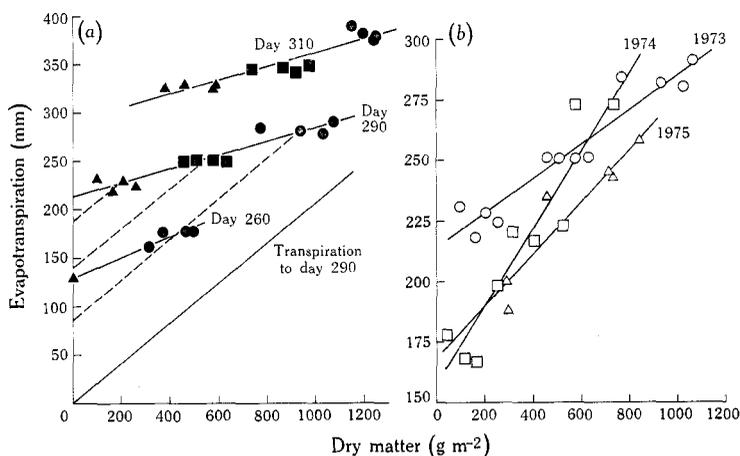


Fig. 2. Relationship of crop evapotranspiration (E_t) to dry matter production (DM) over periods commencing with the first sowing date each year; all densities shown. (a) 1973 data showing the relationship at day 260, 290 and 310; first sowing date (circles), second sowing date (squares) and third sowing date (triangles); see text for full explanation. (b) Data for 1973 (circles, period 172–290 days), 1974 (squares, period 183–301 days) and 1975 (triangles, period 195–295 days); see text and Table 6 for details.

Multiple stepwise regression analysis using all crop and weather variables measured during the 22 intervals for which growth efficiency was calculated gave the following relationship:

$$\text{Efficiency} = 0.98 - 0.02N_a + 1.11 E_t/E_p \quad (R^2 = 0.80),$$

where N_a refers to the number of days from the centre of the interval to anthesis (positive if interval post-anthesis). This model predicted efficiency with a standard

deviation of 0.22%. All terms were highly significant ($P < 0.01$), but the ontogenetic N_a term was dominant in the model, alone explaining 69% of the variation, and meant that the average efficiency declined from 1.96% (-9 to -4 days before anthesis, $n = 7$, $\sigma = 0.29\%$) to 1.68% (+3 to +10 days after anthesis, $n = 8$, $\sigma = 0.24\%$) to 1.08% (+18 to +27 days after anthesis, $n = 7$, $\sigma = 0.33\%$). Absolute efficiencies of pre-anthesis crop growth agree well with results for irrigated spring wheat in Mexico (R. A. Fischer, unpubl. data) and winter wheat in Kansas (Hodges and Kanemasu 1977), the latter authors also observing a decline in efficiency after heading. Mean available soil water (see Table 5), which varied from 104 to -45 mm across the 22 periods, did not enter the regression model for efficiency of dry matter accumulation, but it was correlated with E_t/E_p (range 0.34-1.03, $r = 0.75^{**}$), through which it may have been having a small effect on efficiency. Also soil water stress may have affected crop growth rate, rather than efficiency, through long-term effects on GAI and hence I/I_0 .

Table 4. Effect of year, sowing date and sowing density on available soil water (ASW) at anthesis and maturity

Variable	Density	1973			1974			1975		\bar{X}
		T1	T2	T3	T1	T2	T3	T1	T2	
ASW at anthesis ^A (mm)	D1	64	115	86	26	59	64	15	44	59
	D2	66	115	80	0	51	40	5	41	50
	D3	58	115	81	—	—	—	—	—	—
	D4	58	115	79	-28	19	11	-21	16	31
	\bar{X}	62	115	82	-1	43	38	0	34	
ASW at maturity ^B (mm)	D1	23	37	21	-47	-50	-67	-1	-24	-14
	D2	30	41	13	-61	-53	-74	-7	-40	-19
	D3	30	40	4	—	—	—	—	—	—
	D4	46	33	9	-65	-52	-82	-12	-35	-20
	\bar{X}	32	38	12	-58	-52	-74	-7	-33	

^A As for footnote in Table 3.

^B Actually zero green leaf sampling. Only six sowing dates were sampled at maturity, and the mean change in ASW relative to the zero green leaf sampling was an increase of 5 mm.

Soil moisture and evapotranspiration

In 1974 and 1975 increased sowing density increased early crop evapotranspiration (E_t), as reflected in soil moisture at anthesis (Table 4), but effects were minimal in 1973. On average at anthesis, soil moisture under D4 was 28 mm less (E_t 28 mm greater) than for D1. By maturity the difference between these densities had been reduced to only 6 mm. Later sowing tended to increase soil moisture at anthesis and reduce moisture at maturity (Table 4). The effect of the wet year, 1973, is evident in soil moisture levels both at flowering and maturity (Table 4).

The ratio (E_t/E_p) was calculated for each sampling interval. For the first interval of each crop, namely from sowing to the sampling about 2 weeks before anthesis, a period of 62-104 days depending on the particular crop, the ratio E_t/E_p ranged from 0.47 to 0.92 with an average value of 0.62. The ratios for all subsequent shorter intervals are summarized in Table 5. For the first two intervals it is possible to examine the effect of available soil water (ASW) on E_t/E_p without complications

due to differences in the other variable shown. Thus a mean ASW of 20–26 mm, i.e. c. 16% of maximum ASW (142 mm), only reduced E_t/E_p slightly (no more than 10%) relative to crops for which the mean ASW was 86–90 mm. E_t/E_p was less sensitive to soil water deficit than is assumed in the model upon which the analysis of Nix and Fitzpatrick (1969) is based; Berndt and White (1976) reached a similar conclusion. Lower ASW was encountered in the third period shown in Table 5 and larger effects on E_t/E_p were apparent, but differences in E_p and rain may also have been involved in this case.

Table 5. Ratio of evapotranspiration to pan evaporation (E_t/E_p) for 2-week intervals around anthesis, as affected by mean available soil water (ASW), pan evaporation, leaf area index (LAI) and rainfall: all years, sowing dates and densities

Interval midpoint days with respect to anthesis	ASW class (mm)	n	E_t/E_p		Mean ASW (mm) ^A	Mean E_p (mm d ⁻¹)	Mean LAI	Mean rainfall (mm d ⁻¹)
			Mean	σ				
-8 to -4	>45	13	0.80	0.19	90	5.6	2.5	2.2
	<45	6	0.80	0.13	26	5.8	2.8	1.5
	all	19	0.80					
+3 to +10	>45	15	0.76	0.15	86	6.3	2.2	2.6
	<45	12	0.68	0.11	20	7.5	2.2	2.6
	all	27	0.72					
+18 to +28	>45	10	0.68	0.11	68	6.6	0.9	2.0
	0-45	8	0.51	0.09	24	7.8	0.8	1.9
	<0	9	0.37	0.09	-40	9.1	0.7	0.9
	all	27	0.53				0.8	
+33 to +44	all	21	0.18	0.08	10	10.1	0	1.4

^A Mean available soil water for each period was calculated to allow for rainfall during the period.

In an attempt to encompass all crop-period combinations for the first three intervals shown in Table 5 ($n = 73$) multiple regression analysis was used. As in the aforementioned examination of crop growth rates LAI was converted to a radiation interception term (I/I_0), again assuming an extinction coefficient of 0.45. The following function was derived:

$$E_t/E_p = 0.56 + 0.31I/I_0 + 0.0018W - 0.023E_p,$$

where W is ASW, with R^2 of 0.58. The final term was not significant ($P < 0.1$), while the other terms were highly significant ($P < 0.01$); the residuals were not correlated with any other variables measured or derived. The function predicted the measured E_t/E_p values with a standard deviation of 0.12. The range of ASW was from -58 to 115 mm and that of E_p from 4.9 to 10.9 mm d⁻¹. For obvious reasons this function may be limited to these and other particular edaphic and atmospheric conditions of the situation studied.

Relationship of water use to dry matter accumulation

Sowing to Full Cover

Although it is argued that DM accumulation to anthesis was not in these experiments limited by water shortage, water use until anthesis and the effect of DM accumulation

on this are vital considerations, because soil water at anthesis is one component of water available after anthesis. It is appropriate, therefore, to examine water use as a function of DM accumulation, as illustrated for the 1973 crops in Fig. 2*a*. It is seen that at each date there was a close linear relationship between E_t and accumulated DM, E_t increasing as DM increased with a slope the reciprocal of which is defined here as the marginal water use efficiency ($\text{g m}^{-2} \text{mm}^{-1}$). Extrapolation of the relationships to zero DM indicates bare soil evaporation (E_{sb}) to that date, provided the extrapolated distance is not excessive.

The line through the origin in Fig. 2*a* (slope $1/4 \cdot 85$) represents transpiration versus dry matter production for a fixed value of TE, namely $4 \cdot 85 \text{ g m}^{-2} \text{mm}^{-1}$. This value of TE is used because it is equivalent to the slope of the dotted line joining the mean of data for the first sowing date on days 260 and 290. These early-sown crops were dense enough for soil evaporation to have been minimal after day 260, so the slope should be a good estimate of TE for the period, and with less certainty for the period up to day 260. Since the crops of the other sowing dates made most or all of their growth in the period day 260 to day 290, a TE value of $4 \cdot 85 \text{ g m}^{-2} \text{mm}^{-1}$ can also be applied to them. Thus soil evaporation (E_s) for each crop up until day 290 is given by the vertical distance between the E_t v. DM relationship for day 290, and the transpiration line in Fig. 2*a*, or alternatively the intercept of the dashed lines of slope $(1/4 \cdot 85)$ extrapolated from the day 290 data to the zero DM axis. Soil evaporation until the sowing of the second and third sowing dates (i.e. bare soil evaporation, E_{sb}) was determined by soil sampling. Subtracting E_{sb} from E_s above gives soil evaporation under each crop (E_{sc}), which will be presented later (see Table 7).

From the above considerations, it is obvious from Fig. 2*a* that the marginal water use efficiency will depend on the magnitude of soil evaporation and its diminution by crop cover, and on the prevailing mean TE. The usefulness of the approach depends on the extent to which these components can be explained.

Other workers have undertaken detailed quantitative modelling of soil evaporation under crops (van Keulen 1975; Tanner and Jury 1976) and of TE (van Keulen 1975) with reasonable success. However, soil and crop information in our case is only adequate for a relatively crude examination of the question. This is based on a comparison of data for growth and water use from comparable periods in the three years, beginning with the first sowing date each year and lasting until just after anthesis of this sowing (Fig. 2*b*, Table 6). It is clear in Fig. 2*b* that each year studied differed considerably in marginal water use efficiency and that the soil evaporation (E_{sb}) alone, or as a fraction of cumulative E_p , was greater in 1973 (Table 6). Since soil evaporation proceeds at its maximal rate following rain for a given amount of cumulative evaporation (van Keulen 1975), after which the rate drops substantially, the differences in frequency and amount of rainfall in each year (Table 6) probably explain the differences in soil evaporation. Thus high rainfall is one reason why marginal water use efficiency of 1973 was high.

The examination of possible differences in TE between the three years relies on the relationship between TE and E_p derived for wheat at Wagga Wagga by J. F. Warren and W. J. Lill (see Fischer 1979). This predicts that TE falls as E_p rises, but, since the average E_p was not very different between years in our study, predicted TE also varied little (Table 6). For comparison, mean TE for each of the three years was estimated in two ways, neither of them entirely satisfactory. One was based on the

growth and E_t of the first-sown crops. As already outlined, E_{sc} for this crop in 1973 was estimated to be 88 mm (see Fig. 2a); a similar procedure gave a value of 69 mm in 1974, but there were insufficient data to apply this extrapolation procedure in 1975, and a value of 70 mm was assumed; T and hence TE could then be calculated for the first-sown crops (Table 6, TE method 1). The second method simply extrapolated the E_t v. DM relationship until E_t was equal to $0.85E_p$ for the whole period: this point was assumed to represent the growth and transpiration of a hypothetical crop with full cover and hence zero soil evaporation throughout the period; thus its TE could be calculated (Table 6, TE method 2).

Table 6. Aspects of the relationship of evapotranspiration (E_t) to crop growth (see Fig. 2 and text) for a given period each year commencing with the first sowing date and terminating soon after anthesis of the first sown crop

	1973	1974	1975
Period, Julian days	172–290	183–301	195–295
E_p (mm)	382	415	387
Mean E_p^A (mm d ⁻¹)	3.6	4.0	4.8
Rain (mm)	238	145	142
Wet days (> 1 mm)	29	19	18
E_{sb} (mm) ^B	214	157	168
E_{sb}/E_p	0.56	0.38	0.43
Marginal water use efficiency ^B (g m ⁻² mm ⁻¹)	14.0	6.2	9.2
r value for E_t v. dry matter ^B	0.956**	0.936**	0.936**
TE method 1 ^C (g m ⁻² mm)	4.9	3.3	4.3
TE method 2 ^C (g m ⁻² mm)	4.8	3.5	4.5
TE predicted ^D (g m ⁻² mm)	6.3	6.0	5.7
Mean max. temperature ^A (°C)	19.9	18.6	20.0
Mean min. temperature ^A (°C)	7.1	5.9	7.6
Heavy frosts ^A (min. <0°C)	2	12	3

^A Mean for period but excluding first 30 days.

^B Calculated from data of Fig. 2b.

^C TE estimated from crop growth and water use data (see text).

^D Based on mean E_p above and function of Warren and Lill (see text).

Estimated TE values for 1973 and 1975 were close to the values predicted from E_p when allowance is made for the fact that TE estimations ignored dry matter accumulating in roots, while the predicted TE included root dry matter; 15% of total dry matter in roots would be a typical figure for pre-anthesis growth and would explain most of the discrepancy. On the other hand, the estimated values of TE for 1974 are lower than expected. Another way of presenting this difference is to estimate DM production for a given value of E_t (Fig. 2b), this being lower in 1974 than in 1975, despite similar values of E_{sb} and E_p . In Table 3 it was seen that early crop growth rates were lower in 1974 and examining all possible causes (soil moisture stress, plant density, sunshine, temperature, and soil fertility), lower temperatures and frosts in 1974 seem most likely (Table 6). Several workers have demonstrated adverse effects of frost on leaf photosynthesis (e.g. Marcellos 1977); our results suggest that TE may also be depressed by frost. Reduced TE is the main reason why the marginal water use efficiency in 1974 was less than in 1975.

Until now it has been assumed that changes in growth via altered sowing density are comparable with changes via altered sowing date, in so far as their influence on E_t is concerned. There was some evidence, particularly in 1973, that this was not exactly true (Fig. 2) and that extra growth through higher sowing density cost less in terms of E_t than extra growth through earlier sowing. It seems unlikely that TE differences explain this for in fact TE should have been slightly higher with earlier sowing because of lower mean E_p values encountered. Soil evaporation on the other hand was a major component of E_t in 1973, and the effect could be explained if overall soil evaporation was greater for the early crop sown at a low density than the later crop sown at a higher density. How this could arise is, however, unclear.

Full Cover to Maturity

The frequent samplings around anthesis, when averaged across sowing densities, provide reasonably precise information on growth- E_t relationships then. For some of these intervals LAI was high enough (>2.0) for soil evaporation to have been minimal; thus E_t was assumed equal to T , and TE calculated. There were 11 such sowing date-sampling intervals spread across the three years and involving the sampling intervals either immediately before or immediately after anthesis; LAI fell below 2.0 for later sampling intervals. Measured TE ranged from 2.9 to 5.4 g m⁻² mm⁻¹ and mean E_p from 4.9 to 8.4 mm d⁻¹. The two were significantly and inversely correlated ($r = -0.750^{**}$). Measured TE was close to TE predicted by the aforementioned E_p -based function of Warren and Lill; the mean difference measured less predicted was -0.35 g m⁻² mm⁻¹ ($\sigma = 0.52$ g m² mm⁻¹, $r = 0.758^{**}$). Since assimilate allocation to roots is likely to have been small at this stage of development, the agreement is considered satisfactory. E_t/E_p was low (0.55–0.75) for several of the intervals considered, yet there was at the most only a slight tendency for TE to increase. Thus it seems that DM accumulation during this period, even in the presence of soil water deficit and transpiration rates below potential, is adequately explained in terms of total transpiration and TE. This is also likely to apply after 2 weeks after anthesis, when there was a further 100–200 g m⁻² DM accumulation, but is more difficult to verify then because of the likely rise of the soil evaporation component and the loss of precision with dry matter measurements.

Whole Crop Cycle

We can now look at overall growth and water use and attempt some generalization regarding the effect of sowing date. Sowing densities are averaged to give eight crops over the 3 years for which key information is summarized in Table 7. We consider firstly the period from sowing of the earliest crop (T1) until anthesis of each particular crop. The decline of dry matter at anthesis (line 3) is expected to be general for this environment. Evapotranspiration from sowing of T1 to anthesis of each crop (line 10) is made up of two components, transpiration (line 6) and evaporation under the crop (line 7) and, for T2 and T3 bare soil evaporation (line 9). Evapotranspiration to anthesis increased with later sowing, largely associated with a substantial E_{sb} component between sowing dates. Soil evaporation under the crop was reckoned to be largely unaffected by sowing date, ranging over 70–100 mm. TE declined with later sowing, at least in 1973 and 1975. These relationships are considered general, since they depend largely on the seasonal march of E_p . Sub-

tracting period rainfall (line 11) from E_t gives the decrease in ASW from the date of sowing of T1 (line 12), and taking this off starting ASW (line 1) gives ASW at anthesis. The small increase in ASW at anthesis with later sowing is not expected to be general, since in all three years there was above-average rainfall between anthesis of T1 and that of later-sown crops. Considering the expected rainfall in October–November (2 mm d^{-1} , Table 2), expected ASW at anthesis is not likely to be affected by sowing

Table 7. Summary of pre- and post-anthesis evapotranspiration (E_t), its components, and dry matter (DM) accumulation as affected by year and sowing date: mean of sowing densities

	1973			1974			1975	
	T1	T2	T3	T1	T2	T3	T1	T2
<i>Period from sowing date of T1 to anthesis of each crop^A</i>								
1. Starting ASW (mm)	129	129	129	98	98	98	123	123
2. Duration (days)	107	119	138	115	127	138	92	111
3. DM at anthesis (g m^{-2})	798	545	503	565	471	444	667	493
4. Mean E_p^B (mm d^{-1})	3.4	4.0	5.0	3.8	4.7	5.6	4.1	5.3
5. TE ($\text{g m}^{-2} \text{mm}^{-1}$)	5.0	4.9	3.6	3.2	3.4	3.1	4.2	3.4
6. Transpiration (mm)	159	112	141	175	139	143	159	144
7. E_{sc}	88	98	108	69	93	91	70	70
8. Crop E_t^C (mm)	247	210	249	244	232	234	229	214
9. E_{sb} (mm)	0	42	80	0	20	44	0	46
10. E_t from sowing of T1 (mm)	247	252	329	244	252	278	229	291
11. Rainfall (mm)	180	238	282	145	197	218	106	171
12. Decrease in ASW (mm)	67	14	47	99	55	60	123	89
13. ASW at anthesis (mm)	63	115	82	-1	43	38	0	34
<i>Period from anthesis to maturity^D</i>								
14. Duration (days)	34	32	30	34	27	29	37	25
15. Decrease in ASW (mm)	30	77	70	57	95	112	7	67
16. Rainfall (mm)	106	76	74	88	36	18	106	41
17. Crop E_t (mm)	136	153	144	145	131	130	113	108
18. E_{sc} (mm) ^E	33	37	54	17	3	24	34	3
19. Transpiration (mm)	103	116	90	128	128	106	79	105
20. Mean E_p (mm d^{-1})	5.3	6.3	7.9	7.5	8.4	9.2	5.9	7.4
21. TE^E ($\text{g m}^{-2} \text{mm}^{-1}$)	4.3	3.9	3.1	3.3	2.9	2.5	4.1	3.4
22. DM accumulation (g m^{-2})	442	452	280	423	371	264	321	357

^A All items were measured except E_{sc} , which was estimated as discussed earlier, transpiration, which was calculated by subtraction, and TE which was calculated by division of (3) by (6).

^B Period from 30 days after sowing of the particular crop to its anthesis date.

^C E_t from sowing of the particular crop being considered.

^D Maturity in this case taken as date of the second last crop sampling for dry matter and moisture (zero green leaf sampling). Between this sampling and the final sampling, dry matter declined, on the average 14 g m^{-2} .

^E E_{sc} was calculated by difference, transpiration being estimated as DM accumulation divided by predicted TE. TE was predicted from mean E_p for the period.

date variation in the range studied. Fischer and Kohn (1966a) similarly calculated that expected ASW at anthesis would increase only slightly (10 mm), as sowing of Heron wheat was delayed over the period 1 May to 18 July.

Later sowing, therefore, is expected to give later anthesis and lower dry matter at anthesis, but no extra conserved soil moisture at anthesis. What happens after anthesis? If water limits transpiration, as is likely, it is suggested that DM accumulation

will depend on total transpiration and TE. Because E_p rises rapidly with later anthesis, TE must deteriorate. At that time of the year for a 25 day delay in anthesis a 30% rise in E_p and 24% fall in TE could be expected. From the point of view of expected transpiration after anthesis, ASW at the start of the period will not vary on average and rainfall probability changes little with time (Table 2), but the duration of the ontogenetic period after anthesis when the crop can respond to water will shorten as temperatures increase with later flowering. Estimated soil evaporation (line 18) seems small and not consistently affected by sowing date, while soil water extraction under the dry conditions of 1974 and 1975 was no less with later sowings than earlier ones (Table 4). The whole profile was dried to well below -15 bars, a result agreeing with work at Wagga Wagga (Fischer and Kohn 1966a; Kohn and Storrier 1970), but in marked contrast to that observed in South Australia (Schultz 1971; Greacen and Hignett 1976). In summary, later anthesis through later sowing may not be disadvantaged so much in terms of expected transpiration after anthesis as in expected TE. We suggest that it is more appropriate to consider the disadvantages of later flowering in these terms than in terms of soil- and atmosphere-induced plant water stress.

Combining pre- and post-anthesis data, we find that crop E_t ranged over 342–399 mm (mean 375 mm), and E_{sc} over 73–162 mm (mean 112 mm or 30% of E_t). Because of above-average spring rains, water supply to all crops studied here, regardless of sowing date, was somewhat better than average. Long-term average weather conditions could be expected to produce crops for which, like T1 in 1974 and 1975, soil moisture throughout the profile approaches -15 bars at anthesis, but which receive 70 mm (2 mm d^{-1}) rather than 90–100 mm of rain after anthesis. The high proportion of dry matter produced after anthesis for our crops (average of 39% of total) is a reflection of the good spring rains. It should have favoured high harvest indices (Passioura 1977). This and other aspects of grain yield will, however, be dealt with elsewhere.

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