

Studies of Grain Production in *Sorghum bicolor* (L. Moench). V* Effect of Planting Density on Growth and Yield

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Abstract

Growth analysis was applied to grain sorghum (cv. RS610) grown at low, medium and high population densities, i.e. 14,352, 143,520 and 645,836 plants ha⁻¹ respectively. The medium densities had two arrangements of plants, square (S) and rectangular (R). Crop growth rates, inflorescence growth rates, leaf area indices, net assimilation rates and leaf growth rates were calculated from growth functions of plant dry matter and leaf area over time.

Differences in crop growth rate between populations in the early stages were attributed to leaf area development—specifically to the initial leaf area (dependent on seedling number) and not to differences in leaf growth rates. Peak crop growth rates were 15.0, 27.5, 26.0 and 45.8 g m⁻² day⁻¹ for the low, medium (S), medium (R) and high populations respectively.

The large difference between the growth rates of the medium (S) and the high populations was not explained by differences in the amount of radiation intercepted. Although leaf area indices were 4.6 and 10.2 respectively for the two populations, both canopies intercepted almost all of the noon radiation. Light extinction coefficients were 0.45 and 0.29 respectively. The relationship between net assimilation rate and leaf area index was such that for comparable leaf area indices above 2, plants at higher densities showed greater improvement in yield per unit increment in leaf area index.

A maximum grain yield of 14,250 kg ha⁻¹ was obtained at the high population density as a result of higher dry matter production, but a similar harvest index to that of the crops grown at the other densities. Inflorescence growth rate (g m⁻² day⁻¹) slightly exceeded crop growth rate in the latter part of grain filling, which indicated that there was some retranslocation to the grain of previously assimilated material. The maximum grain yield represents an efficiency of utilization of short-wave solar radiation during crop life of 2.5×10^{-6} g cal⁻¹.

Introduction

In cereals the grain comprises a high proportion of the crop above ground, and since most of the carbohydrate in the grain is produced after ear emergence, large yields depend upon a high rate or long duration of accumulation of dry matter after flowering (Thorne 1965; Allison and Watson 1966; Fischer and Wilson 1971). Furthermore, Goldsworthy and Tayler (1970) and Fischer and Wilson (1975) have produced evidence that the yield of improved grain sorghums is limited by the supply of assimilates during grain filling. Consequently, it is important to understand the factors controlling the accumulation of dry matter.

Density is influential during early stages of crop growth as it determines the amount of leaf area available for maximum interception of radiation (Watson 1952; Donald 1963; Iwaki 1968). Increasing density can also influence the distribution

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of the radiation independently of foliage cover (Pearce *et al.* 1967; Brown and Blaser 1968; Newton and Blackman 1970) by producing a more vertical orientation of the leaves (Pearce *et al.* 1967; Newton and Blackman 1970) and by changing leaf size and shape (Newton and Blackman 1970).

Total dry matter represents crop growth rate over the entire growth period and is related to grain yield by the harvest index. Harvest index tends to decrease as total dry matter increases because at higher population densities some plants are not reproductive (Kira *et al.* 1953), and constitute a loss in economic yield. Further loss in efficiency occurs when competition is so severe that some tillers and plants die (Bunting and Drennan 1965).

This paper reports an examination of the effects of plant population density on the growth and yield of grain sorghum. Density effects are described by growth analysis.

Materials and Methods

Grain sorghum (cv. RS610) was grown in low, medium and high density populations, namely 14,352, 143,520 and 645,836 plants ha⁻¹ respectively during the summer of 1968-69 at Redland Bay, Qld. There were two planting arrangements of the medium population, one approximately square (S) and the other rectangular (R). High and low density populations were planted on a square (approximately). The planting arrangements, experimental design and cultural conditions of this field trial (trial 1) were described by Fischer and Wilson (1975).

The above-ground parts of the plant were harvested at weekly intervals commencing 1 week after seedling emergence and continuing until grain maturity. At each harvest, with the exception of the last, plants from five consecutive planting positions in one row, randomly selected, were taken in each of the four replicate blocks. In order to determine grain yield at final harvest, the sample was increased to 15. Number of tillers, number of grains (as early as possible), leaf area per plant and the dry weights of leaf and stem, as well as inflorescence (when appropriate) and grain were determined for each harvest.

Leaf areas were determined from leaf length and maximum leaf breadth as described by Stickler and Pauli (1961). The general use of one relationship for all leaves of the plant would require similarity of shape. By measuring leaf area with an airflow planimeter, the relationships between area and the product of length (l) and maximum breadth (b) of the various leaves (flag, leaf 2, 3, etc.) were established (not shown here). A sample of five plants from each of the four plots at each density was used. The relationship for the flag leaf was significantly different from that for the other leaves, but there was no significant effect of density. Leaf areas of the flag leaves and other leaves were determined by the relationships:

$$\text{flag (cm}^2\text{)} = 0.54 (l \times b) + 8.5 \quad (r = 0.98),$$

$$\text{other leaves (cm}^2\text{)} = 0.63 (l \times b) + 17.6 \quad (r = 0.95).$$

Growth equations were fitted to the data on harvests and differentiated to provide estimates of growth rates as described by Hughes and Freeman (1967). The standard error of the treatment means of a derived variate was obtained from an ordinary analysis of variance of the estimates for the individual plots. Data on a land area basis were calculated from the data for single plants and the population number.

Standard errors increase from the mean towards extreme values of the growth index for any one population and vary between populations. They are not generally shown on the figures.

The total short-wave radiation during the experimental period was recorded with a silicon cell radiometer. Transmission by the canopies was measured at noon.

Results

Final Dry Weight of Plant and Parts

Total above-ground dry matter at grain maturity, grain dry weight and its components (per unit land area) and harvest index are shown in Table 1. Dry matter

Table 1. Yield data for plants grown at low (14,352 plants ha⁻¹), medium square and medium rectangular (143,520 plants ha⁻¹) and high (645,836 plants ha⁻¹) populations in the field

Yield parameter	Density			
	Low	Medium (Square)	Medium (Rectangular)	High
Grain dry matter (g m ⁻²)	341c*	697b'	745b'	1257a'
1000 grain weight (g)	27.1a	22.3b	27.7a	26.5a
10 ⁻³ × Grain number (m ⁻²)	12.6c'	31.2b'	27.5b'	47.4a'
Number of inflorescences per planting site	3.18a	1.14b	1.18b	0.91c
Total above-ground (shoot) dry weight (g m ⁻²)	704c'	1472b'	1538b'	2800a'
Harvest index	0.48a	0.47a	0.49a	0.45a

* Values indicated by the same letter do not differ significantly; a, b, c, indicate significant differences at $P = 0.05$; a', b', c' at $P = 0.01$.

yields and grain number (m⁻²) increased significantly with plant density, and there was no difference between the two planting arrangements of the medium population. Grain size was similar at all densities except for the medium (S) population which had smaller grains. The number of inflorescences per plant decreased with increasing population. There were no significant differences in harvest index between densities, although for the high population it tended to be lower (6% less than the mean value for the other three densities).

Values of mean daily radiation (short-wave) for the developmental stages—emergence to floral initiation, floral initiation to three-quarter anthesis and three-quarter anthesis to grain maturity—were 30.2, 26.0 and 25.5 MJ m⁻² day⁻¹ respectively.

Pattern of Growth and Development

To describe the changes in total dry weight of shoot and inflorescence, leaf area of single plants and average grain size (1000 grain weight) with time, cubic polynomials were fitted to the observed data. The regression components accounted for more than 90% of the variation in weights or leaf area. At each harvest, total above-ground (shoot) dry matter yield per unit land surface was greatest for the high population and least for the low (Fig. 1). The two medium densities did not differ one from another and were above the low but below the high populations.

At the low and medium (S) densities rapid tillering (data not shown) occurred within 2 weeks after emergence, maximum numbers of 2.0 and 0.6 tillers per plant being reached by the fifth and fourth weeks in the low and medium (S) populations respectively. Subsequently, the medium (S) population lost tillers until anthesis when it and the medium (R) population had similar numbers (0.2 tiller per plant) which did not change thereafter. No tillers were produced at the high density.

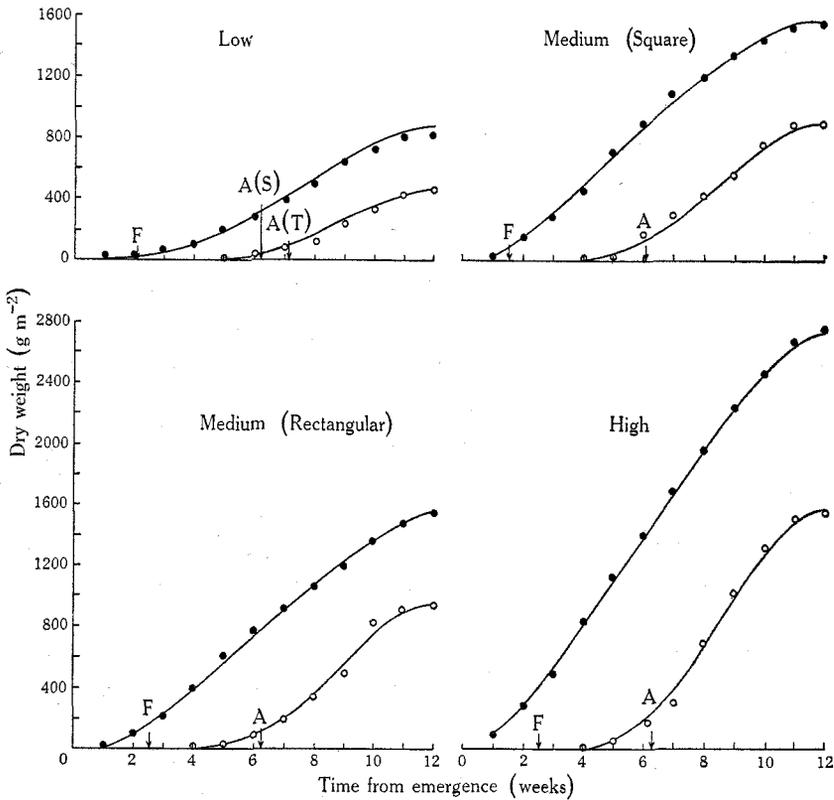


Fig. 1. Changes in total above-ground (shoot) (●) and inflorescence (○) dry weight yield over time for plants grown at low, medium (Square), medium (Rectangular) and high density populations. Floral initiation (F) and anthesis (A) dates are indicated, with a distinction between anthesis in main stems, A(S), and tillers, A(T), in the low population.

Values for R^2 . Low: shoot 0.98, inflorescence 0.97; medium (S): 0.98, 0.98; medium (R): 0.97, 0.94; high: 0.98, 0.97.

Floral initiation on the main stems occurred almost concurrently at all densities between 2 and 3 weeks after emergence and when nine leaves were fully expanded. Initiation on the main stems in the low population was slightly earlier, but was delayed 7–10 days in the tillers.

Anthesis commenced in the upper florets of the inflorescences on the main stems between weeks 6 and 7. Dry weight growth of grains (1000 grain weight) is shown in Fig. 2. Although the first measurement was made at week 8, the extrapolated growth

functions indicate a short interval after anthesis during which dry matter increased only slightly, but by this time (week 7) the grain had visibly increased in volume. Grain growth occurs in the cellular sense rather than in terms of dry matter accumulation during this period (Bingham 1967). After week 7, grain weights for the low, medium (R) and high densities increased linearly and at a similar rate to almost their maximum size by week 11. This pattern of growth is similar to that described by Kersting *et al.* (1961). Although the increase in grain weight for the medium (S) density crop commenced at a similar rate to the others, by week 9 it was less rapid and the final grain size was significantly less. For all densities, increase in dry weight ceased when the moisture content of the grain reached *c.* 35%. Values reported in the literature range from 23 to 32% (Kersting *et al.* 1961; Collier 1963) depending on variety and environment.

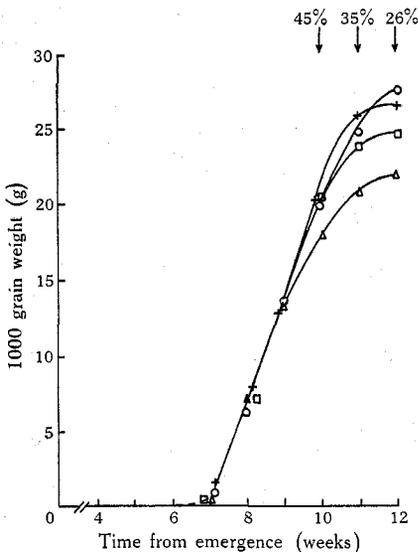


Fig. 2. Increase in grain size (1000 grain weight) over time in plants grown at low (□), medium (Square) (△), medium (Rectangular) (+) and high (○) density populations. (Percentage moisture contents are indicated.)

Inflorescence weights from 1 week after anthesis onwards tended to parallel the total shoot weights (Fig. 1). The difference between shoot and inflorescence weights is stem plus leaf dry weight. This increased up to week 7 (commencement of substantial grain dry weight increase) and decreased during grain filling. Towards the end of grain filling, stem plus leaf weight remained constant or began to increase in all treatments except the low density.

The development of leaf area index is shown in Fig. 3. In the medium and high density populations, leaf area increased until full emergence of the flag leaf and then declined, the loss of leaf area being more rapid in the later stages of grain filling. In the low density population, tiller leaves were a major component of the leaf area index, and because tiller development lagged behind that of the main stem, maximum leaf area occurred at a later stage than at the other densities. Leaf area values were significantly larger in the high population and smaller in the low population. The medium (S) population tended to have a higher leaf area index than the medium (R) in the early growth stages, but because of tiller loss prior to heading in the former, values were similar during grain filling.

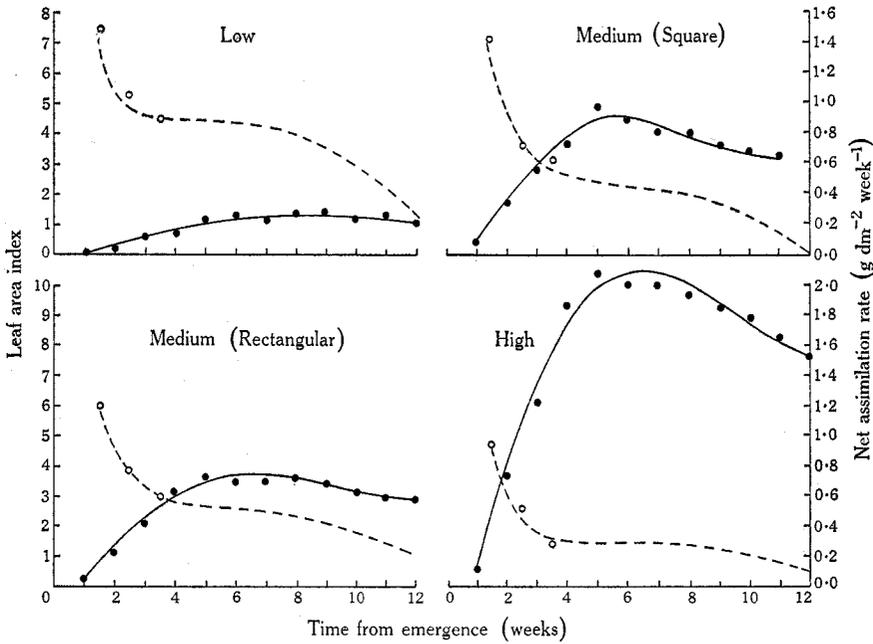


Fig. 3. Changes in leaf area index (● and unbroken lines) and net assimilation rate (broken lines) over time for plants grown at low, medium (Square), medium (Rectangular) and high population densities. The curve showing net assimilation rate was derived from equations describing total dry weight and leaf area index. Data points indicated, (○), were calculated according to Watson (1952). Standard errors of the treatment means for net assimilation rate are 0.05, 0.04 and 0.09 at 3, 7 and 11 weeks respectively.

Values for R^2 . Low: 0.87; medium (S): 0.90; medium (R): 0.95; high: 0.94.

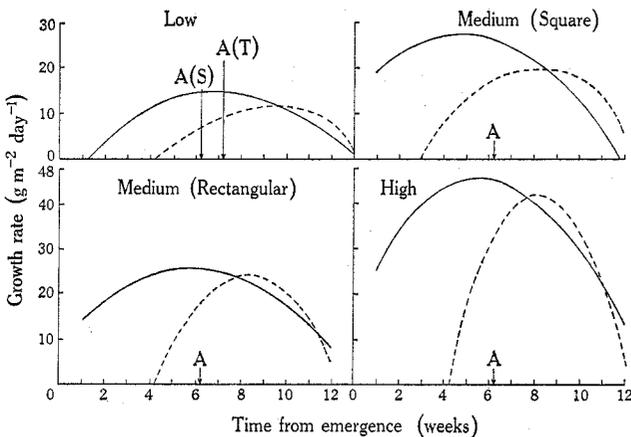


Fig. 4. Crop (solid line) and inflorescence (broken line) growth rates of plants grown at low, medium (Square), medium (Rectangular) and high population densities. Dates of anthesis (A) are shown with a distinction between anthesis in main stem, A(S), and tillers, A(T), in the low population. Standard errors of the treatment means for crop growth rate are 1.65, 1.5 and 2.9 at 3, 7 and 11 weeks respectively; and for inflorescence growth rate the error is 2.4 at 8 weeks.

Growth Analysis

The fitted equations for dry matter and leaf area growth over time were differentiated to provide estimates of crop growth rate (Fig. 4), inflorescence growth rate (Fig. 4), net assimilation rate (Fig. 3) and relative leaf growth rate (data not shown). The smooth time trends of the values calculated from growth functions are to be distinguished from the actual fluctuating values measured at each harvest. As response to the one environment by the different plant populations is being considered fluctuations caused by the weather are ignored. In Fig. 3, some values of net assimilation rate calculated from the untreated data in accordance with Watson (1952) are shown for comparison.

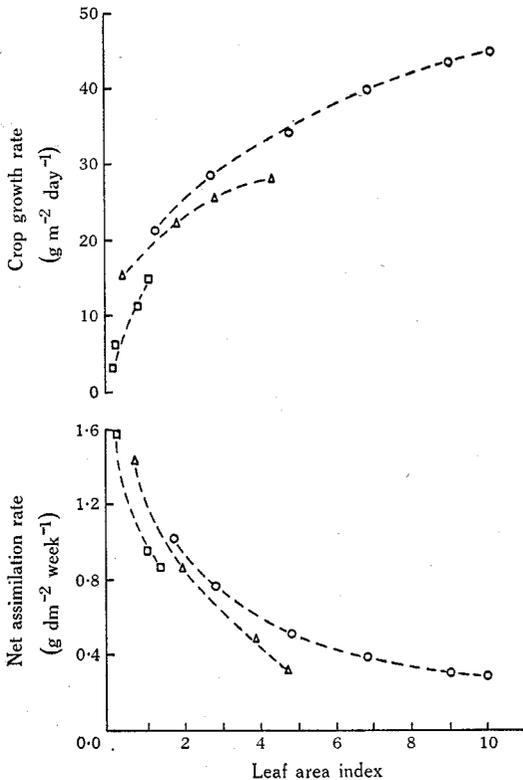


Fig. 5. The relationship between leaf area index and both crop growth rate and net assimilation rate for plants grown at low (\square), medium (Square) (Δ) and high (\circ) population densities.

Crop growth rates (Fig. 4) for all densities increased to a maximum around heading and then declined during the grain-filling period. At all stages of growth the crop growth rate was highest for the high density and lowest for the low population. Prior to heading, values for the medium (S) density tended to be greater than for the medium (R) density, but in the later stages this order was reversed.

Inflorescence growth rates are shown together with crop growth rates in Fig. 4. Where the rate of growth of the crop exceeds the inflorescence growth rate, either further growth of other plant parts or storage of dry matter other than in the head (probably in the stem) is proceeding. However, where inflorescence growth is in

excess of crop growth, material stored previously is being translocated to the inflorescence. Prior to and for a period after anthesis, crop growth was greater than inflorescence growth rate at all densities. In the later stages of grain filling, inflorescence growth rate exceeded crop growth at all densities, although the amount of retranslocation would appear small, and of greatest importance in the medium (S) population.

The high crop growth rate of the high population was associated with a large leaf area index (Fig. 2). Leaf area development was more rapid at high density, not because of any difference in relative leaf growth rate, but because there were more seedlings.

Initially, the net assimilation rate (Fig. 3) was similar at the low and medium densities and higher than for the high population. Values declined rapidly at all densities, and then gradually from about week 2 at the low density. The decline started somewhat later in both the medium and the high density populations. In the final stage of growth there was a marked reduction at all densities. Values for the low population were consistently higher than for either the medium or high populations.

The relationships between crop growth rate and leaf area index, and between leaf area index and net assimilation rate are shown in Fig. 5 for low, medium (S) and high densities. Even when the leaf area index fell below 1, the crop growth rate per unit increment in leaf area index at low density was less than at higher densities, presumably because the leaves of the plants at higher densities were more uniformly dispersed horizontally since much of the leaf area is clumped around the stems. However, there was also a difference in response between medium (S) and high density plants at comparable leaf area indices above 3: the values of net assimilation rate and therefore of crop growth rate were higher at high density. At lower leaf area index values, the net assimilation rates in medium and high density populations were more nearly equal, and therefore this differential response did not occur.

Discussion

The highest grain yield of $14,250 \text{ kg ha}^{-1}$ (12% moisture) from the high density planting can be compared with the maximum yield of $16,500 \text{ kg ha}^{-1}$ recorded in the literature (Pickett and Fredricks 1959). The yield in our experiment was achieved with a crop duration of 91 days. This represents a production rate of $15.5 \text{ g m}^{-2} \text{ day}^{-1}$ of crop life and exceeds the rates recorded for rice and maize (Stewart 1970). Grain yield per unit of radiation was $2.5 \times 10^{-6} \text{ g cal}^{-1}$, exceeding a value of $2.0 \times 10^{-6} \text{ g cal}^{-1}$ for rice (Stewart 1970).

The superior yield of the high density plants resulted from their greater production of total dry matter, while the harvest index was almost as high as that of the other densities. Kira *et al.* (1953) demonstrated a relationship between seed number and plant weight at maturity in which a critical plant size is required before reproductive development occurs. Furthermore, competition increases the variability of relative growth rate, resulting in a skewed distribution of plant weights (Koyama and Kira 1956). Thus in the high density plots a number of plants (*c.* 10%) were rendered infertile through competition, and this reduced the harvest index. In our high density plots this effect was probably minimized by the precise planting methods which would have produced more uniform early competition. Probably in commercial

plantings, where placement of seed is less precise, this density would be less productive in grain yield.

The similarity of yields from plants grown in either narrow or wide rows (and correspondingly closer spacing within rows) at the same population density does not agree with other workers' findings obtained when sorghum was grown under favourable moisture conditions, as in our experiment. Stickler and Wearden (1965) measured consistently higher yields from square plantings over a range of densities. This was associated with greater tiller production. In our experiments, the greater initial tillering of individually isolated plants in the square pattern was a disadvantage in that dry matter was lost from the grain-producing system through subsequent competitive suppression which resulted in death of the tillers.

In another trial (not reported here) in which sorghum was grown under conditions of low radiation (averaging $14.3 \text{ MJ m}^{-2} \text{ day}^{-1}$) from emergence to initiation, tiller production appeared to be an advantage in that it contributed to grain number per land area. Under higher radiation and with the more rapid increase in leaf area index realized in the trial discussed here, early shading suppressed these tillers.

Growth analysis techniques were successfully used to analyse differences in dry matter production between plants grown at various densities. The mathematical treatment of the growth indices (dry weight and leaf area) allowed an interpretation of the effects of time and density on crop growth rate, leaf area index and net assimilation rate by removing the fluctuations caused by short-term changes in the weather.

Differences in crop growth rate between populations in the early stages of ontogeny were attributed to leaf area development and its influence on the amount of radiation intercepted. The reduction in crop growth rate after heading was associated with both a loss in leaf area and a reduction in the net assimilation rate. Mean daily radiation for the grain-filling period was 10% lower than for the period of maximum crop growth and this may have contributed to the lower rate of assimilation. However, reduction in the photosynthetic capacity of the leaves with ageing is likely to have been a more important influence. This effect has been demonstrated by Ludlow and Wilson (1971*b*). In addition, the activity of plant parts other than the leaves, both photosynthetically and metabolically, would affect net assimilation values (Ludlow and Wilson 1970). Eastin and Sullivan (1968) measured a reduction in the net carbon dioxide uptake of sorghum inflorescences from anthesis onwards, and at a later stage of development carbon dioxide was released.

At later stages differences in crop growth rates between the high and medium (S) population densities were not caused by differences in the amount of radiation intercepted. Peak crop growth rates of $26.8 \text{ g m}^{-2} \text{ day}^{-1}$ for the medium and $43.6 \text{ g m}^{-2} \text{ day}^{-1}$ for the high population were obtained when both canopies were intercepting similar amounts of radiation, although leaf area indices for the medium density were almost half those of the high population. It follows then that the high density was more efficient in the conversion of radiation. Measurements of photosynthesis by the canopy will be reported in a later paper, but they support this.

It is unlikely that the superiority of the high density stand arose from more efficient conversion, per unit of leaf surface, of radiation at any one level of leaf irradiance. In so far as the leaves in the higher density might have been adjusted to somewhat lower radiation environments, one would expect from the work of Woolhouse (1968) and Ludlow and Wilson (1971*a*) that their efficiency would be lower. The superiority

presumably arose from characteristics of the canopy which are associated with the distribution of light and its manner of interception by the foliage.

Light extinction coefficients (Monsi and Saeki 1953) for the canopies of the medium and high density stands at harvest 6 (peak leaf area indices of 4.6 and 10.2 respectively) were 0.45 and 0.29. Monteith's (1965) s values (s is the fraction of light not intercepted by a unit of leaf area index) were 0.55 and 0.79 for the medium and high densities respectively. Thus at the lower plant density 45% of the incident radiation was intercepted by each unit of leaf area, but only 21% was intercepted at the higher density. In grain sorghum populations of 10,000 and 100,000 plants per acre, Goldsworthy (1970) measured s values of 0.51 and 0.58 respectively, and for these two populations Monteith (1969) calculated a mean light extinction coefficient of 0.46. Our results agree with these workers' findings. Goldsworthy's s values also increased with increasing population density and the value for the medium population in our experiment is similar to his values. The s values and light extinction coefficients calculated for the high density stand of sorghum are not uncommon for grasses. Stern and Donald (1962) and Monteith (1965) found s to be 0.75 and the light extinction coefficient to be 0.27 for *Wimmera* ryegrass. Values of 0.77 and 0.24 have been recorded for perennial ryegrass (Monteith 1969).

Differences in leaf inclination were considered by Goldsworthy (1970) to have caused different s values. The data in this paper do not include any measurements of canopy structure other than leaf areas. However, leaves of the high density plants were narrower relative to length and less 'droopy', and the plants themselves were taller than in the medium population. Such features of the canopy are more favourable to light penetration per unit leaf area (Loomis and Williams 1969). Canopy structure was considered in another trial involving these two populations and will be discussed in another paper.

The dry weight of stem plus leaf increased until week 7 (commencement of substantial increase in the dry matter content of the grain), but decreased during grain filling. Part of the loss in stem plus leaf weight after anthesis represents transfer to the grain, as the inflorescence growth rate was greater than crop growth rate during this period. Goldsworthy and Tayler (1970) measured such a decrease in stem weight in this species. From studies on individual plants, Fischer and Wilson (1971) could account for 12% of the final dry matter content of the grain as material produced prior to anthesis. The amount of such retranslocation that occurred in the present trial, as indicated by the area between the curves of inflorescence growth rate and crop growth rate, is of a similar magnitude.

The close association between inflorescence growth rate and crop growth rate, and the indication that after anthesis there is minimal net storage of dry matter in parts other than the inflorescence, suggest that grain yields are dependent on assimilate supply. This concurs with previously reported findings (Fischer and Wilson 1975) for these same populations.

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