Studies of Grain Production in *Sorghum bicolor* (L. Moench). VI*
Profiles of Photosynthesis, Illuminance and Foliage Arrangement

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Abstract

Grain sorghum was grown at two population densities in the field, and photosynthetic rates compared at noon. Profiles of photosynthesis were established by combining measurements of $^{12}CO_2$ exchange and $^{14}CO_2$ uptake. Canopy structure and light penetration were measured. Factors responsible for the superiority of the higher density population were evaluated.

Photosynthesis–radiation responses of leaves were similar between the populations and there was little difference in total light interception.

The high density population had leaves which were more vertically displayed, more uniformly dispersed, smaller in both length and width, and distributed over a greater height of canopy. Light was therefore more uniformly distributed down the profile, and coefficients of light extinction were lower. Associated with this was a higher leaf area index. The overall consequence was the distribution of intercepted radiation over a larger leaf surface, at a lower illuminance and therefore a higher efficiency of photosynthetic conversion, resulting in greater total photosynthesis.

Introduction

Fischer and Wilson (1975c) reported much higher crop growth rates in a high than in a medium density population of grain sorghum. The amount of solar radiation intercepted by both canopies was similar, and thus the higher density population was more efficient in energy conversion. The experiments reported here were designed to compare such canopies in closer detail, in particular to measure photosynthesis in the various height layers of these canopies, and to examine some features contributing to the performance of each layer.

Materials and Methods

Grain sorghum cv. RS 610 was grown at populations of 645,836 and 143,520 plants ha^{-1} (referred to respectively as high and medium density) in two field trials at Redland Bay, Qld., during the 1969–70 summer season. The planting arrangement and management of these trials, previously referred to as trials 2 and 3, have been described by Fischer and Wilson (1975a). Measurements of the profiles of photosynthesis, leaf area index and light were made only in trial 3. Mean leaf angles and light extinction coefficients were estimated for plants grown in both trials.

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Measurement of Photosynthesis by Canopy Layers

Diurnal measurements of photosynthesis in whole canopies in trial 3 were made on clear days during the period 5–15 days after anthesis. The contribution to photosynthesis by the various layers of the canopy was measured around noon. Only one assimilation chamber and therefore only one plot was used on any occasion for each of the two populations. Two replicates were obtained by making measurements on successive days.

Fischer and Wilson (1971) described a method to measure photosynthesis by the component parts of the canopy. It is based on the assumptions that in sorghum (a C_4 species), negligible respiratory carbon dioxide is released by above-ground parts in the light (and carbon dioxide does not leave the soil against the slight pressure which exists in the system used); that if plants are supplied for a very short period with an atmosphere containing $^{14}CO_2$, the ratio of rates of $^{12}CO_2$ and $^{14}CO_2$ assimilation is similar at all photosynthetic sites; and that during the period there is no significant movement of assimilates from those sites. Thus ^{14}C present in any photosynthetic site before translocation is directly related to photosynthesis by the ratio of ^{12}C to ^{14}C fixation. This ratio is the same as that of total ^{12}C to total ^{14}C fixed by the whole canopy. If both total canopy photosynthesis (^{12}C fixation) and ^{14}C fixation at various sites (whence total ^{14}C is obtained by summation) are measured, photosynthesis at each site may be calculated.

An open carbon dioxide assimilation system with an infrared gas analyser calibrated differentially was used to measure photosynthesis by the canopies. Ambient air, drawn into and mixed in a large vessel to reduce fluctuations in carbon dioxide concentration, was forced into the base of a transparent chamber which enclosed the plant canopy, and distributed evenly to the bottom of the canopy via perforated ducting. Assimilation rates, calculated from the difference in carbon dioxide concentrations between inlet and outlet (top of chamber) air streams, the air flow rate, and air temperature, were expressed in units of nanograms CO_2 cm^{-2} (of land surface) sec^{-1}, the same units as used for photosynthetic rates of leaves. The maximum carbon dioxide concentration drop was 20 μl l^{-1}.

Air flow was measured with an orifice flow meter (constructed to the specifications of the British Standards Institution (1964)) placed in the air line to the chamber. Thermometers were mounted in both inlet and outlet ducts.

Assimilation chambers to enclose 2·08 m^2 and 1·11 m^2 of the canopy of the medium and high density plantings respectively were constructed. They comprised a demountable rectangular metal base plate (with the perforated air ducting) which supported the transparent chamber. The detachable sites and top of the chamber were made from 1·92 cm wide aluminium insect-screening frame and polypropylene-C transparent film. The top of the chamber was perforated (1·6 cm diameter holes) on a 15 cm square pattern. The frames were temporarily sealed together and to the base with adhesive tape to prevent air leakage. The chambers, including the sections of the base, were assembled in the plant stands with minimum disturbance of the canopy, on sites selected at random within the plots.

To measure photosynthesis by layers, carbon dioxide labelled with ^{14}C was injected into the large air-mixing vessel, which thus exposed the canopy to $^{14}CO_2$ while $^{12}CO_2$ uptake was being measured. A total of 0·15 mCi was used at a constant rate by regulating the flow of 1N hydrochloric acid into a glass chamber containing a mixture

of $Ba^{12}CO_3$ and $Ba^{14}CO_3$. After 5 minutes of exposure, the assimilation chambers were flushed with ambient air and quickly dismantled. The border row and end plants were removed. A frame of adjustable height was placed over the remaining treated area, and the canopy was harvested in 20 cm height layers and immediately stored at low temperature until the next steps.

After drying to constant weight, the material was ground and ^{14}C counts were made on three 50 mg samples. Plant material was counted in two fractions, the water-soluble and the residue. Ten millilitres of the filtrate was mixed with an equal volume of a 1/1 mixture of toluene and Triton X-100 containing $0 \cdot 5\%$ w/v 2,5-diphenyloxazole for liquid scintillation counting. The residue on the filter was dried, and 30 mg was placed in the counting vial with 3 ml of chlorinated water and allowed to stand for 8 hr. Chlorine water decolorizes pigments and thereby reduces quenching (Shneour *et al.* 1962). After decoloration, a further 6 ml of water was added and 11 ml of a mixture of toluene (with fluor) and Triton X-100 (1/35). The mixture formed a gel which suspended the plant material in the scintillating solvent. Both fractions were counted for 10 min or until 10,000 counts had accumulated. Activity recovered by this method was significantly correlated with that from oxygen combustion ($r = 0 \cdot 91$).

Measurement of Canopy Arrangement

The area of leaf in each stratum in trials 2 and 3 was calculated from the total leaf dry weight and the ratio of leaf area to leaf weight determined for a sample. The leaf area of the sample was measured by air-flow planimeter.

The mean leaf angles (α) of plants grown in trials 2 and 3 were determined by point quadrat analysis, as described by Warren Wilson (1963). An instrument described by Heslehurst (1966) was used. Measurements were made after anthesis, and initially each 20 cm layer was considered. However, because too few contacts were made for each 20 cm stratum, data were pooled to describe the canopies in two layers only, 0–60 and 60–140 cm in the medium and 0–80 and 80–160 cm in the high density population. These are referred to hereafter as upper and lower canopies. Even so, only about 200 contacts for each layer were recorded. Thus the error in quantification may be high and the data obtained were not statistically analysed.

Measurements of Light

Canopy light profiles were measured with an instrument based on cadmium sulphide sensors, consisting of six photo-resistors surmounted by diffusing tape and filters, linked in parallel and mounted in a probe 1 m in length. This instrument was satisfactory for relative measurements of photosynthetically active radiation. In trial 2, such measurements were combined with leaf area index (F_A) data to provide estimates of light extinction coefficients (K).

Measurement of Photosynthetic Responses of Individual Leaves to Light

One week after anthesis, two plants were taken from each population in trial 3, and together with large volumes of soil in plastic bags were transported in a covered van to the laboratory. The flag leaf, and leaves 3 and 5, attached to the plants were placed separately and in turn in a controlled environment leaf chamber, and the photosynthetic response to illumination (quartz iodine 2000 W, filtered through 10 cm

water) was recorded. The equipment used was that described by Ludlow and Wilson (1971a).

Results and Discussion

The daily patterns of solar radiation and of photosynthesis for the canopies are shown in Fig. 1. Measurements were made on a clear day, 1 week after anthesis. Photosynthesis in the high density population canopy was greater than for the medium density canopy during the period 0900 to 1600 hours (over 44% more photosynthesis at noon), but equal to or less than in the medium density canopy at other times. Maximum rates for both densities were at noon.
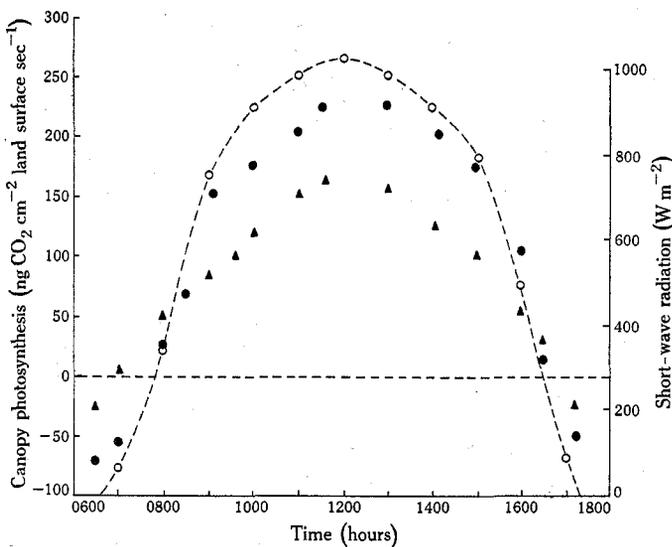

Fig. 1. Diurnal pattern of net carbon dioxide exchange of canopies of medium (143,520 plants ha^{-1}, ▲) and high (645,836 plants ha^{-1}, ●) population sorghum canopies, and solar radiation (○), on a clear day 1 week after anthesis. (Trial 3; total daily short-wave radiation, 20·1 MJ m^{-2}.)

The ^{14}C measurements of photosynthesis of the whole canopy at noon in the period 5–15 days after anthesis (Fig. 2) also showed that of the high density canopy to be greater ($P < 0.05$) (277 cf. 195 ng cm^{-2} land surface sec^{-1}). Of these rates, 46 and 28 ng cm^{-2} sec^{-1} respectively were due to the inflorescences, but this accounts for only 18 of the 82 ng difference between the stands. Thus most of the difference was attributable to the vegetative parts. Contrary to the earlier work (Fischer and Wilson 1975c) where stands of the same population density differed greatly in dry matter accumulation while intercepting the same amounts of radiation, the present stands did differ somewhat in interception; viz. 93 and 87% for high and medium density stands respectively. However, this cannot account for the differences in photosynthesis, and therefore these data confirm the previous observation that the high density planting was a more efficient converter of intercepted radiation.

The higher efficiency of the dense population canopy was not due to a higher photosynthetic potential of the leaves. There was little difference between the photosynthesis–radiation response curves for leaves taken from the two populations, with either the flag leaf or leaf 3. In the case of leaf 5, rates were in fact lower for the dense population (data not shown). In any case, one might anticipate higher photosynthetic rates in leaves with a history of higher illumination (Ludlow and Wilson 1971b), viz. from the lower density planting.
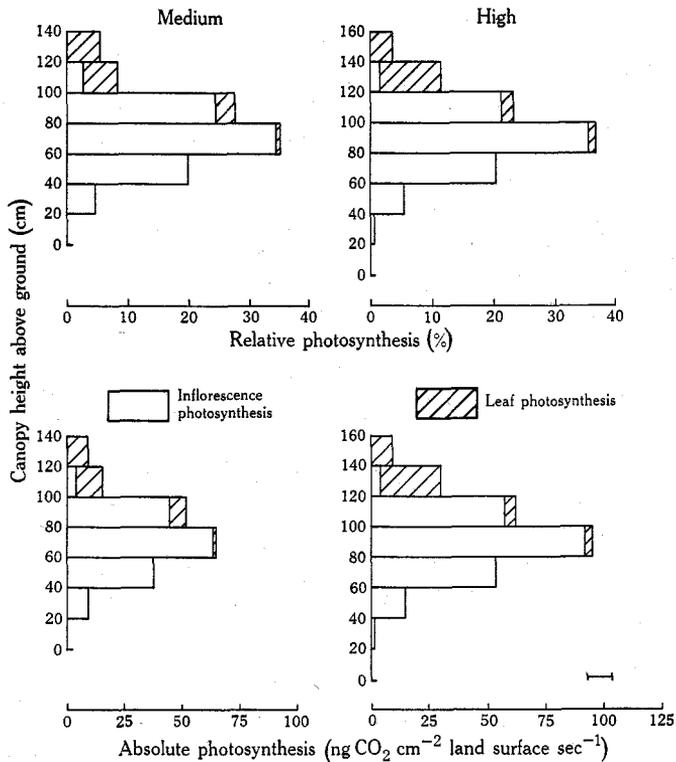

Fig. 2. Profiles of relative (upper figures) and absolute (lower figures) photosynthesis in canopies of medium (143,520 plants ha^{-1}) and high (645,836 plants ha^{-1}) populations of sorghum at noon. Data are means of two replicates measured 5 and 10 days after anthesis. LSD ($P = 0.05$) indicated for absolute photosynthesis is applicable to both populations. Height axes are placed so that comparisons can be made between populations on basis of distance from tops of canopies.

It might be suggested that higher photosynthetic rates measured in the field were attributable to larger sinks for assimilate in the high density population, because of higher grain yield. However, there was not a higher yield per unit of leaf area; the measurements referred to above were made in the presence of these sinks; and a fairly detailed study of yield characteristics in this variety in the same experimental series could not identify an effect of this kind (Fischer and Wilson 1975b).

The explanation is then to be sought in radiation distribution over photosynthetic surfaces. Higher efficiency of conversion occurs at low radiation in *Sorghum almum*

(Ludlow and Wilson 1971a) and is known to occur in a wide range of species. Thus a canopy in which the available radiation is distributed uniformly at a low level over a large leaf area may be expected to be more productive than one in which it is intercepted by some or all leaves at a higher and less efficient level. Canopies providing the former conditions are associated with low light extinction coefficients and high leaf area indices.

Light profiles for trial 3 are shown in Fig. 3 and coefficients of light extinction (K) for both trials in Table 1. Values of K were higher in the upper layer of both populations in both trials and the overall values for the whole canopies were higher in the

Table 1. Foliage characteristics of the canopies of plants grown at medium (143,520 plants ha^{-1}) and high (645,836 plants ha^{-1}) populations in the field (trials 2 and 3)

Parameter	Canopy layer	Medium density Trial 2	Medium density Trial 3	High density Trial 2	High density Trial 3
Light extinction	Upper[A]	0·80	0·58	0·32	0·29
coefficient (K)	Lower[A]	0·35	0·39	0·40	0·34
	Total	0·55	0·55	0·36	0·33
Mean leaf	Upper	14	28	44	32
angle (α) (deg)	Lower	52	44	54	55
Variance ratio (90° quadrat)	Total	1·1	0·91	0·87	0·66
Mean leaf length (cm)	Total	68		56	
Mean leaf breath (cm)	Total	7·3		4·9	

[A] Upper strata, 0–60 and 0–80 cm for medium and high densities respectively; lower strata, 60–120 and 80–140 cm for medium and high densities respectively.

[B] Significantly $<1\cdot0$ at $P \leqslant 0\cdot05$.

medium density planting, mainly because of relatively high coefficients in the upper layer. A similar effect of population in sorghum has been shown by Goldsworthy (1970). His values of s (the percentage of incident radiation transmitted by unit leaf area index) increased—corresponding to a decrease in K—as the population increased.

The profiles of leaf area index (F_A) for trial 3 only are shown in Fig. 3. There was more leaf (total F_A of 3·5 and 6·2 for medium and high density populations respectively) and a greater depth of leaf canopy in the high density population. There was a significant planting density × height interaction when the canopy was stratified from the top of the canopy downward. For each of the upper three strata, F_A values did not differ between populations, but there was more leaf lower in the high density canopy.

Fig. 2 shows the relative and absolute photosynthesis by each 20 cm height layer of the two canopies at noon. There was no significant interaction between density and either absolute or relative photosynthesis of each layer of the canopy when stratified from the top of the canopy downward; that is, the photosynthetic profiles are of the same shape. Activity in the upper two layers in both canopies was due largely to the inflorescences, with some contribution from this site in lower layers. Maximum photosynthesis was in the 60–80 cm and 80–100 cm strata for the medium and high

density populations respectively (i.e. at the same depth in both canopies), and at both densities the canopy below these layers contributed only 25% of the total photosynthesis.

There were differences in carbon dioxide exchange of the leaf canopies, both in the upper layer (rates of 162 and 120 ng CO_2 cm^{-2} sec^{-1} for the high and medium density populations respectively), where leaf area indices were similar (F_A 1·55 and 1·50 respectively, Fig. 3), and in the lower part (rates of 68 and 46 ng respectively) where there was a greater F_A in the high density population. Thus, although less radiation was intercepted by the leaves in the upper layer of the high density population (smaller K values), photosynthesis per unit leaf area was higher than for corresponding leaves of the medium population. This was not due to a higher response to light by the individual leaves, as discussed earlier for whole canopies. The greater photosynthesis
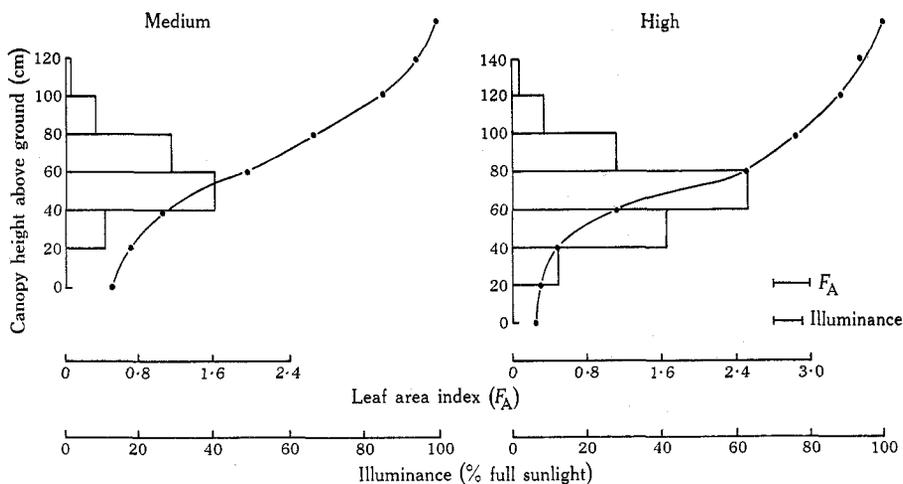

Fig. 3. Profiles of leaf area index (F_A) (histograms) and light intensity (curves) at noon in canopies of medium (143,520 plants ha^{-1}) and high (645,836 plants ha^{-1}) populations of sorghum (trial 3). Measurements were made 5–15 days after anthesis. LSD ($P = 0·05$) is applicable to both populations. Height axes replaced so that comparisons can be made between populations on basis of distance from top of canopies.

in the lower leaf canopy of the high density population was due in part to more illumination arising from less interception by the upper layers, and partly to higher leaf area indices, adequate to intercept almost all of the radiation which did reach it. However, most of the advantage in the high density population occurred in the upper canopy.

Fig. 4 shows the relationship between photosynthetic rate per unit of land surface and F_A as it accumulates down the canopy. From equations fitted to these data, photosynthetic rates on a leaf area basis were calculated and are shown in the figure. A consistent 30% superiority of rate in the dense population occurred at all values of F_A.

These data indicated, therefore, that a more efficient conversion of intercepted radiation occurred in the high density population as a result of improved light and leaf area distribution. Some of the determinants of such distribution are now examined, viz. leaf orientation, leaf dispersion and the size and shape of leaves.

Mean leaf angles (Table 1) vary between trials, but there is a consistent pattern in that angles were always higher (that is, leaves more vertical) in the high than in the medium density population, in both upper and lower canopy layers in both trials. Also, mean angles were always higher in the lower than in the upper canopy layer at both densities. Light extinction coefficients (Table 1) are associated with angles such that higher angles accompany lower K values. Differences in leaf angles were considered by Goldsworthy (1970) to have caused different s values in sorghum and have been shown to influence K in other species.
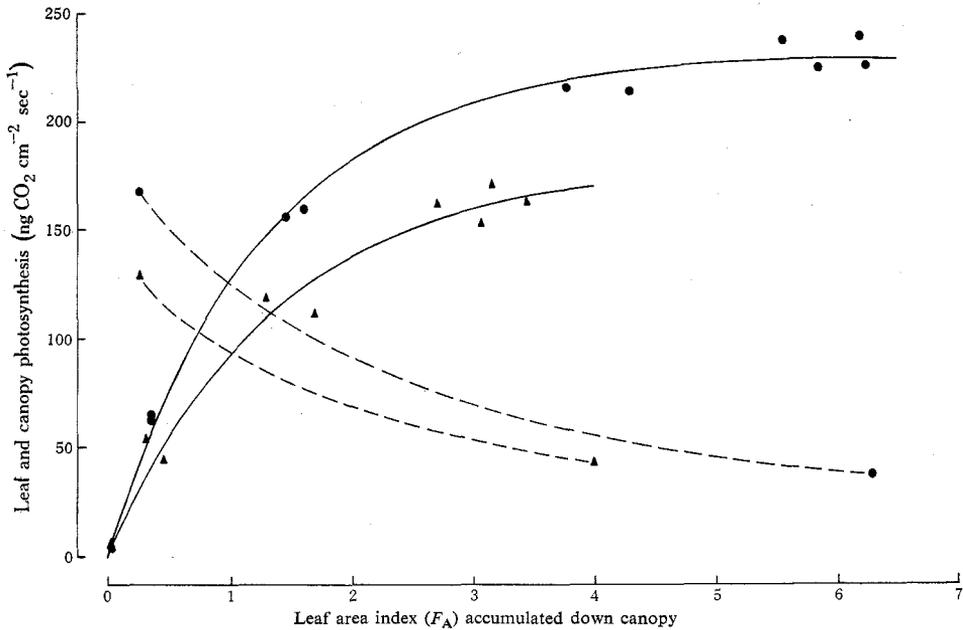

Fig. 4. Relationship between photosynthetic rates and cumulative leaf area index down the profile, for medium (143,520 plants ha^{-1}, ▲) and high (645,836 plants ha^{-1}, ●) density population of sorghum. Continuous lines, per unit land area; broken lines, per unit leaf area.

Light penetration into canopies is influenced by dispersion of leaf. Variance ratios (Warren Wilson 1965) calculated for 90° quadrat data, corresponding to horizontal dispersion, are shown in Table 1. Ratios of unity indicate random dispersion; less than unity, regular dispersion. The variance ratios for the medium density population in both trials were not significantly different from and approximated to 1, which indicated random dispersion. In the high density population, the ratio in trial 3 was significantly less than 1, which indicated regular dispersion of leaf. The differences in variance ratios between densities (in both trials) were not significant, but there was a consistent trend towards random dispersion in the medium density and more regular dispersion in the high density population.

Regular dispersion of leaves should be more efficient photosynthetically than random or clumped leaves because of more uniform illumination (Warren Wilson 1960), although Acock *et al.* (1970), in a model treating non-random leaf dispersion, suggest that this character may be important only for canopies of low leaf area index where a substantial proportion of the incident light is not intercepted. However, most models

simulating plant production assume random leaf dispersion, and the effects of this character have not been thoroughly evaluated. The more regular dispersion of leaves in the denser population should lead to higher K values than the randomly dispersed leaves of the other. However, this tendency to increase K is counteracted by leaf orientation, which has already been discussed, and perhaps also by the shape and size of the leaves which, together with vertical height of the canopy, affect light penetration.

The means of both lengths and maximum breadths of the upper five leaves for each density are shown in Table 1. Leaves from the high density population were respectively 68 and 82% of the widths and lengths of those in the medium density population; that is, they were smaller in both dimensions. Although there is no published theory capable of describing the influence of leaf size, there is recorded evidence that smaller leaves are associated with lower K values. Newton and Blackman (1970) showed that for *Gladiolus*, increasing plant density did not affect leaf orientation but resulted in longer, narrower and smaller leaves, while K decreased from $0 \cdot 30$ to $0 \cdot 16$. In the present work, increased density resulted in reduction of leaf width and size. Moreover, the narrower leaves of the high density population would have had a greater vertical distance between them because the plants were taller, and therefore a reduced ratio of leaf width to vertical separation (w/d). Although current mathematical models do not consider the size and shape of individual leaves (Ross 1970), leaf dimensions influence canopy photosynthesis by influencing the extent of penumbra (Nichiporovich 1960). Some area of the laminae may have been occluded permanently from skylight in the medium density population because of the increased w/d ratio. Loomis and Williams (1969) have suggested that dwarf type sorghums would have a 'poor type canopy' because the occlusion of skylight from parts of the foliage in canopies of large w/d ratios effectively reduces the productive leaf area.

Acknowledgment

References

Acock, B., Thornley, J. H. M., and Warren Wilson, J. (1970). *In* 'Prediction and Measurement of Photosynthetic Productivity'. (PUDOC: Wageningen.)

British Standards Institution (1964). B.S.1042. Part 1 (1964).

Fischer, K. S., and Wilson, G. L. (1971). *Nature (Lond.) New Biol.* **229**, 30.

Fischer, K. S., and Wilson, G. L. (1975*a*). *Aust. J. Agric. Res.* **26**, 11–23.

Fischer, K. S., and Wilson, G. L. (1975*b*). *Aust. J. Agric. Res.* **26**, 25–30.

Fischer, K. S., and Wilson, G. L. (1975*c*). *Aust. J. Agric. Res.* **26**, 31–41.

Goldsworthy, P. G. (1970). *J. Agric. Sci.* **75**, 123–31.

Heslehurst, M. R. (1966). *In* 'Instrumentation for Plant Environment Measurements'. Conf. Aust. Soc. Instrum. Technol., CSIRO Aust., Aspendale, Sept. 1966, p. 1.

Loomis, R. S., and Williams, W. A. (1969). *In* 'Physiological Aspects of Crop Yield', ed. J. D. Eastin, F. A. Haskins, C. Y. Sullivan, and C. H. M. van Bavel, pp. 27–45. (Am. Soc. Agron. and Crop Sci. Soc. Am.: Madison, Wis.)

Ludlow, M. M., and Wilson, G. L. (1971*a*). *Aust. J. Biol. Sci.* **24**, 449–70.

Ludlow, M. M., and Wilson, G. L. (1971*b*). *Aust. J. Biol. Sci.* **24**, 1077–87.

Newton, J. E., and Blackman, G. E. (1970). *Ann. Bot. (Lond.)* **34**, 329–47.

Nichiporovich, A. A. (1960). *In* 'Photosynthesis of Productive Systems', ed. A. A. Nichiporovich. (Transl. ed. Israel Prog. Sci. Transl.: Jerusalem.)

Ross, J. (1970).   *In* 'Prediction and Measurement of Photosynthetic Productivity'. (PUDOC: Wageningen.)
Shneour, E. A., Aranoff, S., and Kirk, M. R. (1962). *Int. J. Appl. Radiat. Isot.* **13**, 623–7.
Warren Wilson, J. (1960). Proc. 8th Int. Grassld. Congr., Reading, 1960, p. 275.
Warren Wilson, J. (1963). *Aust. J. Bot.* **11**, 95–105.
Warren Wilson, J. (1965). *J. Appl. Ecol.* **2**, 383–90.