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CROP PRODUCTIVITY IN RELATION TO INTERCEPTION OF PHOTOSYNTHETICALLY ACTIVE RADIATION*

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ABSTRACT

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The attenuation of photosynthetic photon flux density (PPFD) in maize, sorghum, pigeonpea, and a maize/pigeonpea intercrop in the operational research watersheds at ICRISAT Center in India was measured on a weekly basis throughout the growing season. A 2-m high frame covering an area of 3 m^2 was designed to accommodate four manually-operated traversing quantum sensors for the measurement of PPFD. The interception of PPFD by the crop canopies was found to be closely related to the leaf area index. The plots of the regression relationship between dry matter for different crops and cumulative intercepted PPFD (grams of dry matter/einstein intercepted) were used to define the efficiency of light interception by crops. The maize/pigeonpea intercrop proved to be most efficient, followed by maize, sorghum, and pigeonpea. The Bouguer—Lambert Law was used to compute the extinction coefficient of PPFD of plant canopies. The interception of PPFD could be accurately predicted for sorghum and maize using this law, but in the case of pigeonpea the law was not satisfactory for accurate prediction of PPFD interception.

INTRODUCTION

Agriculture is an exploitation of solar energy, made possible by an adequate supply of water and nutrients to maintain plant growth (Monteith, 1958). Although 99% of the solar radiation falls between limits of 0.2 and 4 microns, different wavelength bands show various biochemical effects. The wavelength band from 0.4 to 0.7 microns is photosynthetically active radiation (PAR). McCree (1972) showed that quantum flux was superior to energy flux as a measure of PAR. The photon flux density of PAR is defined as photosynthetic photon flux density or PPFD (Shibles, 1976).

Over the last two decades, there have been increasing research interests in the measurement of solar radiation in crop canopies and its use in the assessment of plant productivity (Allen and Brown, 1965; Monteith, 1965; Williams et al., 1965; Hesketh and Baker, 1967; Cowan, 1968; Szeicz, 1974a; Gallagher and Biscoe, 1978). However, most of the measurements of radiation in the

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canopy have been limited to total radiation using illumination meters (Williams et al., 1965), tube solarimeters (Szeicz et al., 1964), etc. Attempts to estimate the PAR were made by using tube solarimeters sensitive to the total spectrum and solarimeters fitted with filters sensitive to the infra-red spectrum only (Szeicz, 1974b) and from the measurements of solar radiation using tube solarimeters, and empirical reflection and transmission coefficients (Gallagher and Biscoe, 1978). Hatfield and Carlson (1978) used a quantum sensor (LAMBDA Instruments Corporation, Lincoln, NE) to measure PPFD in soybean canopies. However, the use of a stationary, small-diameter quantum sensor to measure PPFD in plant canopies results in considerable positional variability caused by shadows. Adams and Arkin (1977) used such a sensor traversing a 3-m track activated by a reversible AC motor to estimate the percent ground cover in sorghum. This equipment is effective in the measurement of PPFD.

Biscoe and Gallagher (1977), Monteith (1977), and Williams et al. (1965) showed that dry matter production early in the season is related to the amount of radiation intercepted by the crop. Gallagher and Biscoe (1978) then showed that for wheat and barley grown at Sutton Bonington and Rothamsted about 3 g dry matter were produced by each MJ of PAR absorbed until ear emergence. For the whole crop about 2.2 g dry matter were produced per MJ absorbed. Such measurements provide a useful index of the production efficiencies of different crops. No such indices have been computed for crops grown in the semi-arid tropics.

The objectives of the study were:

(1) To evaluate the attenuation of PPFD in different crop canopies in the operational research watersheds at ICRISAT Research Center.

(2) To relate the PPFD attenuation to canopy leaf area index (LAI) by using simple light models.

(3) To determine the efficiency of conversion of intercepted PPFD into dry matter in the crop canopies.

The crop canopies considered here are maize, sorghum, pigeonpea, and a maize/pigeonpea intercrop.

MATERIALS AND METHODS

Measurements were made on crops grown on a deep Vertisol during 1978—1979 at the ICRISAT Research Center, near Hyderabad. The soil, water, and crop management system developed for the deep Vertisol watersheds, described in detail by Krantz et al. (1978), utilizes a 150-cm broadbed-and-furrow system having a 0.4% slope. The width of the beds in this system is 120 cm, separated by 30-cm furrows. The broadbeds were tilled with a multipurpose tool bar immediately after harvesting the last crop. Seed-bed preparation was completed during the dry season, well ahead of planting time, with minimal tillage and soil compaction. Compound fertilizer (18-46-0) was applied at planting at 75 kg ha^{-1}, and 107 kg ha^{-1} N was sidedressed for the maize crop. Plant protection was minimal.

All the crops were sown on 12 June 1978. The maize (var. S5154)/ pigeonpea (var. ICRISAT-1) intercrop was planted on 150-cm wide beds, with two rows of maize to one of pigeonpea in the centre of each bed with an inter-row spacing of 45 cm. In an adjacent field, two rows of maize (var. SB-23) were planted on each bed with an inter-row spacing of 75 cm. Pigeonpea (var. ICRISAT-1) was sown on the broadbed with an inter-row spacing of 75 cm in a nearby field. Final plant populations established for maize were about 80 000 plants/ha in both the intercrop and sole crop fields, whereas those for sole and intercropped pigeonpea were 80 000 and 40 000 plants/ha respectively. In order to permit more light penetration to the intercrop pigeonpea after the maize reached its physiological maturity the maize tops were cut just above ear level by 15 September. Sorghum (Hybrid CSH-6) was planted in a 1500-m^2 plot with 75-cm distance between rows giving a final plant population of about 150 000 plants/ha. Land preparation, sowing, fertilization, weeding, etc., were conducted as outlined by Krantz et al. (1978). A manually-operated traversing quantum sensor was constructed to measure PPFD at different heights within the crop canopies grown in the broadbed-and-furrow system using four quantum sensors (LAMBDA Instruments Corporation) mounted on horizontal bars in a portable framework 150 x 200 cm (Fig. 1). The frame was placed horizontally and level at different heights in each canopy so that the crop rows in a 150-cm wide bed were centered in the frame, siting the frame under the most uniform stand

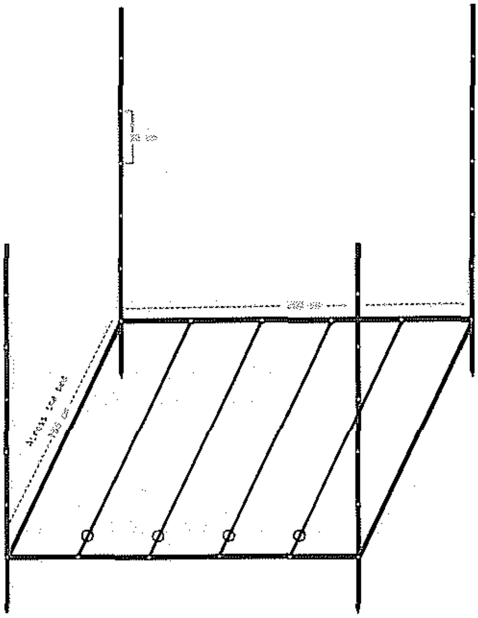


Fig. 1. Diagrammatic sketch of PPFD measurement framework. Circles represent the PPFD sensors.

of plants available. Each sensor was then moved across the crop row on the horizontal track provided by the 150-cm steel bar, which was marked at 10-cm intervals so that the sensor could be moved manually from one end to the other in 150 s by positioning it for 10 s at each mark. Each sensor was attached to a read-out integrator (LI-510, LAMBDA Instruments Corporation); after 150 s the integrated reading was noted and the sensor moved back to its original position. Data for PPFD transmission to the soil surface on any given day under any given canopy represent the average of forty readings, i.e., from the four sensors, each replicated ten times. One quantum sensor was mounted above the crop canopy to record the PPFD incident on the canopy (I_0) and interception of PPFD was calculated using the I_0 and PPFD transmission values. Using the framework, canopy interception of PPFD was measured at several spots in the field throughout the growing season. To eliminate the effect of solar altitude on the interception measurements, PPFD measurements were confined to the midday period. Measurements were not made when the sky was overcast. PPFD interception data, taken at 7—10-day intervals during the growing season, were plotted and interception for each day calculated. Daily solar radiation data for ICRISAT were used to calculate PAR values for each day from the relationship between solar radiation and local PAR (Sivakumar, 1984). The PPFD intercepted each day and cumulative intercepted PPFD for the growing season for each canopy were calculated from daily PPFD and data for canopy interception.

After the PPFD measurements were made the leaves within the frame were harvested in 30-cm strata.

Leaf area for all crops was measured with an electronic foliometer (LAMBDA Instruments Corporation). The dry weight was measured after drying in a forced air oven at 65°C for 48 h. Use of the framework facilitated the measurement of PPFD and leaf area sampling in an area always covering 3 m^2.

RESULTS

A summary of the meteorological data for the growing season is presented in Table I. Rainfall during June, July, and August was high. August was wet (516 mm) and average daily solar radiation was also low (13.73 MJ m^{-2} day^{-1}) during that month. The soil profile was fully recharged and pigeonpea was rarely under moisture stress during November, December and January.

Canopy growth and interception of PPFD

Seasonal variations in the PPFD interception patterns and leaf area index (LAI) were similar for maize and sorghum (Fig. 2).

The interception of PPFD by maize reached the highest level between 50 and 60 days after planting when the LAI was at its maximum. Afterwards, with leaf senescence, the LAI dropped and the PPFD interception

TABLE I

Meteorological parameters during the growing season at the ICRISAT Research Centre

Month	Average temp.		Total precipitation (cm)	Average 24 h winds (km h^{-1})	Average solar radiation (MJ m^{-2} day^{-1})	Average pan evaporation (cm day^{-1})
	Max. (°C)	Min. (°C)				
June	33.1	23.2	18.1	20.3	17.96	0.36
July	28.9	22.1	22.8	14.9	14.69	0.45
August	28.0	21.7	51.6	14.3	13.73	0.36
September	29.6	21.6	8.2	8.7	18.00	0.42
October	30.5	20.0	7.1	7.2	20.80	0.52
November	29.2	18.6	1.0	8.4	18.12	0.43
December	27.2	15.2	0.1	7.9	16.78	0.47
January	28.5	16.2	0	9.6	18.04	0.53
February	30.2	18.7	4.1	11.6	17.79	0.61

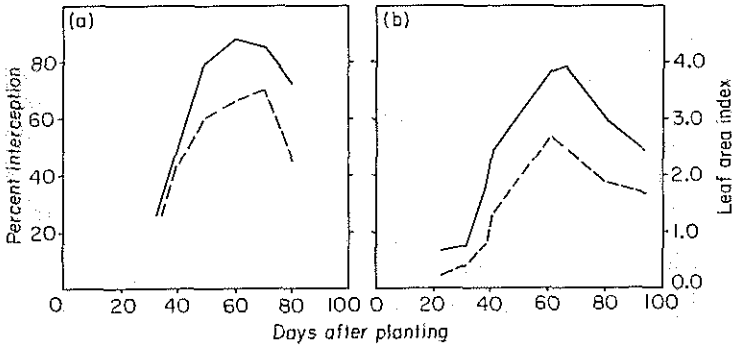


Fig. 2. Seasonal variation in the interception of PPFD (——) and LAI (------) for (a) maize and (b) sorghum.

decreased. The LAI and PPFD interception of sorghum, in general, were lower than those of maize.

The seasonal pattern of variations in the interception of PPFD for a long-duration crop such as sole pigeonpea (Fig. 3a) presented patterns that were different from those of maize and sorghum. During the first 90 days after planting, growth and the increase in LAI of pigeonpea was slow. During the next 40 days, leaf area expansion and dry matter accumulation occurred at higher rates. Subsequently, as more leaves in the bottom 90—120 cm of the crop senesced, the LAI and interception of PPFD declined progressively.

The inefficiency of pigeonpeas in the utilization of solar radiation during the first 90 days after planting led to the introduction of a short-duration maize (85—95 days) crop as an intercrop. Two rows of maize with a pigeonpea row in the center were planted on each bed of 150-cm width (Krantz et al., 1978). Canopy PPFD interception and LAI patterns in the maize/

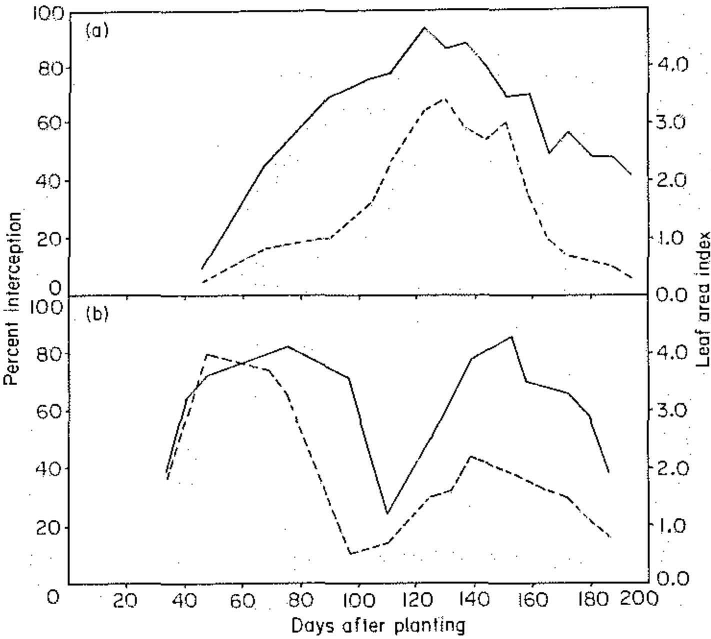


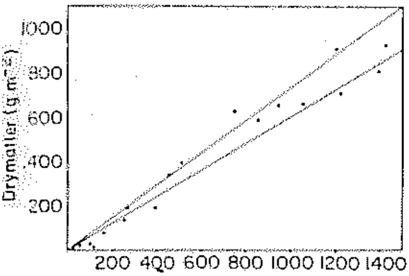
Fig. 3. Seasonal variation in the interception of PPFD (——) and LAI (------) for (a) sole pigeonpea and (b) maize/pigeonpea intercrop.

pigeonpea intercrop (Fig. 3b) reveal the increased efficiencies over those of pigeonpea grown in pure stands. The apparent anomaly in the patterns of PPFD interception and LAI between 90 and 110 days after planting was due to the fact that at physiological maturity the tops of maize plants were cut just above the ear level. The maize ears were allowed to dry in the field on the stalks and were harvested whenever convenient. The LAI of 0.5 for the intercrop at 97 days after planting was measured for the pigeonpeas only, though the post-harvest maize stalks were still in the field. After the maize stalks were removed at 110 days after planting, the PPFD interception and LAI showed similar trends.

The intercrop pigeonpeas appear to have suffered some competition, indicated by a lower LAI than that of the sole pigeonpeas. However, the intercrop and sole pigeonpeas reached the same level of PPFD interception by 143 days after planting. The dry matter produced by intercrop pigeonpea was 606 g m^{-2}, whereas sole pigeonpea produced 787 g m^{-2}.

Efficiency of utilisation of PPFD

The absolute value of maximum quantum yield averaged over a number of crop species was given as 0.065 mol carbohydrate per einstein by McCree (1972). If the energy released by respiration is assumed to be 33% of net CO_2 assimilation (Loomis and Williams, 1963) then the net quantum yield



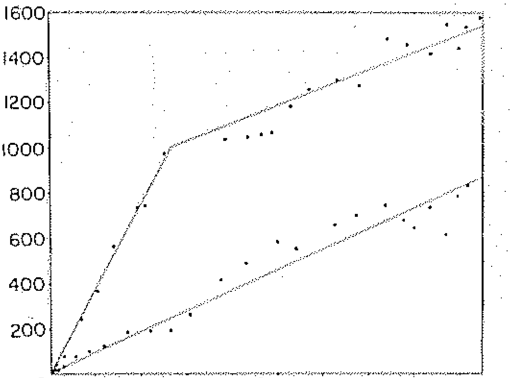


Fig. 4. Relationship between cumulative intercepted PPFD and dry matter produced for maize (●) and sorghum (○).

Fig. 5. Relationship between cumulative intercepted PPFD and dry matter produced for maize/pigeonpea (●) and pigeonpea (○).

could be taken as 0.043 mol CH_2O per einstein or 1.29 g dry matter per einstein. This would mean that for each einstein of PPFD absorbed, it is possible to produce 1.29 g dry matter.

From the measured interception values throughout the growing season in each crop canopy, the cumulative intercepted PPFD was calculated and plotted against the dry matter produced throughout the season. The slope of the regression line between the cumulative intercepted PPFD and dry matter, i.e., grams of dry matter/einstein intercepted, is taken as the production efficiency of the canopy.

The relationship between cumulative intercepted PPFD and dry matter for maize and sorghum (Fig. 4) suggests that during the growing season, maize was more efficient in the conversion of intercepted PPFD into dry matter than was sorghum.

The higher production efficiency of the maize/pigeonpea intercrop system in the conversion of intercepted PPFD into dry matter over the sole pigeonpea crop is evident from Fig. 5. It reflects the increase in leaf area duration and PPFD interception of the intercrop and the higher photosynthetic efficiency of the C_4 crop (maize). Up to harvesting of the maize, the maize/pigeonpea intercrop system produced 0.93 g/einstein whereas the sole pigeonpea crop could produce only 0.23 g/einstein. The corresponding values for maize and sorghum grown as monocrops were 0.82 and 0.62 g/einstein, respectively.

Profiles of PPFD and prediction of intercepted radiation

The quantity of PPFD intercepted at different heights within the crop canopy is used in the computation of potential photosynthesis in some

TABLE II

Leaf area index (LAI) and extinction coefficient (K) for different canopies

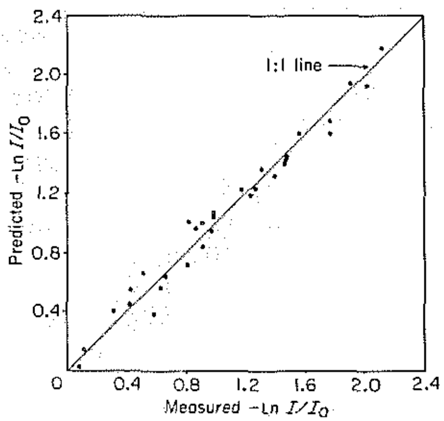
Crop	Date of measurement	LAI	K	S.E. of K	R^2
Maize	24 Aug.	2.77	0.64	0.11	0.99
Sorghum	30 Aug.	2.84	0.53	0.12	0.96
Maize/P.pea	26 Aug.	2.45	0.66	0.07	0.99
Intercrop P.pea	29 Sep.	0.79	0.28	0.04	0.94
Intercrop P.pea	28 Oct.	2.40	0.51	0.20	0.96
Sole Pigeonpea	12 Oct.	3.71	0.69	0.26	0.99

simulation models. From the fraction of intercepted PPFD (I/I_0) and LAI measurements at different heights, the Bouguer—Lambert Law as proposed by Monsi and Saeki (1953) was used to compute the extinction coefficient (K) of PPFD of the plant canopy.

$$-\ln(I/I_0) = K\,\mathrm{LAI} \tag{1}$$

Calculated extinction coefficients and the corresponding LAI values for selected dates are shown in Table II. The extinction coefficient for maize was 0.64, whereas for sorghum it was 0.53. In both crops the regression accounted for more than 90% of the variation in the data. The standard error of estimate for K also shows that the predictability was fairly accurate. It is evident from a plot of the measured $-\ln(I/I_0)$ against predicted $-\ln(I/I_0)$ (Fig. 6) for maize and sorghum, that the Bouguer—Lambert Law could be used fairly accurately to predict the PPFD intercepted at any given height.

Extinction coefficients measured for intercropped pigeonpea increased



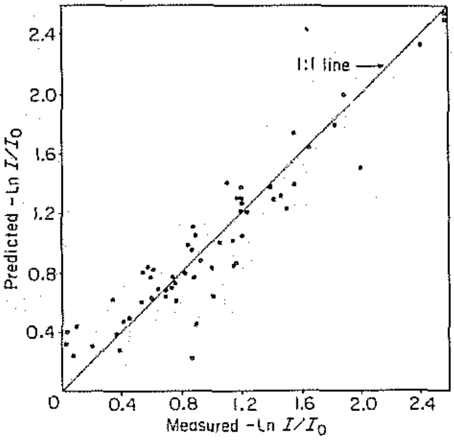


Fig. 6. Relationship between measured Y and predicted Y for maize (●) and sorghum (○).

Fig. 7. Relationship between measured Y and predicted Y for intercropped pigeonpea (●) and sole pigeonpea (○).

from 0.28 to 0.51 during a 30-day period from 29 September to 28 October. On 12 October the extinction coefficient for sole pigeonpea was 0.69 (Table II). The reason for this difference in the size of the extinction coefficient may be due to higher plant population and better growth patterns in the sole pigeonpea. The standard error of estimate for K was about 0.20 on average, which indicates that the Bouguer—Lambert Law as used in its present form may not be suitable to describe PPFD attenuation for the pigeonpea crop. Figure 7 shows a plot of the measured $-\ln(I/I_0)$ against predicted $-\ln(I/I_0)$ for sole pigeonpea and intercropped pigeonpea. There is a wide scatter of data along the 1 : 1 line.

DISCUSSION

Data presented here emphasise the importance of the use of detailed studies on the relationship between intercepted radiation and dry matter in an analysis of the relative efficiencies of different crops and cropping systems. This approach has recently been recognised as a more rational means of analysis of growth than the traditional growth analysis techniques (Monteith, 1977). In the present study, this point is amply illustrated by the differences in the calculated production efficiencies of maize, sorghum, pigeonpea, and the maize/pigeonpea intercrop, all grown in operational research watersheds under a uniform agronomic management. Apart from measured growth indices such as LAI and final yields, a useful index of crop productivity can be obtained by computing the production efficiency as shown in this study.

Analysis of the relationship between dry matter and cumulative intercepted PPFD for different crops showed that maize proved superior to sorghum in the conversion of intercepted PPFD into dry matter. Trenbath (1979) also showed that the leaf and canopy properties measured for maize are closest to the predicted optimum for the upper canopy.

One obvious advantage of intercropping pigeonpea with a fast growing, short duration cereal crop like maize lies in a better resource use, especially of radiation. Greater light interception in the intercrop could be associated with complementarity in time and higher plant population pressure as shown by Willey and Natarajan (1978) in their study with a sorghum/pigeonpea intercrop and by Sivakumar and Virmani (1980). The efficiency of conversion of intercepted PPFD into dry matter was superior in the maize/pigeonpea intercrop than in sole pigeonpea. It is important to remember, however, that two factors play a very important role in the conversion of intercepted radiation into dry matter: (1) the changes in photosynthesis with irradiance and temperature; and (2) the fraction of carbon fixed by photosynthesis that is respired (Gallagher and Biscoe, 1978).

Data sets presented here show that canopy light interception was very closely related to the changes in LAI. This is expected because the amount of radiation intercepted by a crop depends on the distribution of leaf area in time and space in relation to solar radiation. The purpose of light interception measurements at different heights in the crop canopy is to compute extinction coefficients that would enable the prediction of intercepted light from canopy LAI data. Using a single extinction coefficient to predict the PPFD interception, Kanemasu and Arkin (1974) found that, over the midday period, actual field measurements and computed values showed little change over a significant portion of the midday period. In this study also the light interception measurements were confined to the midday period. Computed extinction coefficients for maize and sorghum in this study (0.64 and 0.53, respectively) are comparable to the values of 0.46 for wheat and 0.64 for barley obtained by Szeicz (1974b) for extinction coefficients from PPFD measurements. Extinction coefficients for intercrop and sole pigeonpea decreased with an increase in leaf area index, a trend that was reported earlier by Szeicz (1974b) and more recently by Fasheun and Dennett (1982) for field beans.

The Bouguer—Lambert Law provided an adequate description of the PAR penetration into the canopies because the radiative transfer closely follows to assumptions of this law. Earlier, Sakamoto and Shaw (1967), Singh et al. (1968), Luxmoore et al. (1971), Hatfield (1975) and Sivakumar and Shaw (1979) applied this law to describe the light penetration in field crops. Arkin et al. (1976) used the Bouguer—Lambert Law for the calculation of PPFD in the canopy light interception submodel incorporated in a dynamic sorghum growth model.

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