Radiation-Use Efficiency in Biomass Accumulation Prior to Grain-filling for Five Grain-Crop Species[1]

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ABSTRACT

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A commonly applied technique of modeling net increase in crop dry-matter in non-stress environments assumes that the amount of dry plant biomass produced is proportional to the intercepted photosynthetically active radiation (IPAR). The slope of this relationship or 'radiation-use efficiency' is often assumed to be constant for a non-stressed crop species. The objective of this study was to test the consistency of this slope both among and within grain-crop species. Published and unpublished data on sorghum (*Sorghum bicolor* (L.) Moench), rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), maize (*Zea mays* L.), and sunflower (*Helianthus annuus* L.) were analyzed in terms of amount of above-ground dry biomass produced per unit IPAR. Mean values for sunflower, rice, and wheat were 2.2, 2.2, and 2.8 g/MJ IPAR, respectively. For sorghum and maize the means were 2.8 and 3.5 g/MJ IPAR, respectively. The within-species variability in the values did not generally appear to be due to differences in temperature or incident solar radiation for the data sets examined.

INTRODUCTION

A relatively simple approach to modeling net increase in crop dry-matter is to assume that the dry weight produced per unit of intercepted photosynthetically active radiation (IPAR) is a constant in non-stress environments (Warren-Wilson, 1967; Monteith, 1977; Gosse et al., 1986). This method assumes that weight loss due to maintenance respiration and growth respiration is proportional to total gross photosynthesis (Charles-Edwards, 1982). This also

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assumes that the nonlinear response of photosynthetic rate to irradiance, seen in single-leaf measurements (Moss, 1963; Hesketh and Baker, 1967), is not present in leaf canopies. In canopies, leaves are rarely perpendicular to incoming radiation; therefore, most leaf area does not receive irradiance at levels high enough to saturate photosynthesis (Hesketh and Baker, 1967). Linearity in the response of photosynthetic rate to increasing solar radiation for leaf canopies is supported by the work of Hesketh and Moss (1963) and Louwerse (1980) with maize (*Zea mays* L.), Hesketh and Moss (1963) with sunflower (*Helianthus annus* L.), and Biscoe et al. (1975) with barley (*Hordeum vulgare* L.).

The energy required to produce a unit of dry-matter or radiation-use efficiency (RUE) may change if the chemical composition of the product changes. Biosynthesis of products high in proteins, lipids, or lignin require considerably more energy per unit dry weight than do components with low concentrations of these products (Penning de Vries et al., 1974); McDermitt and Loomis, 1981).). Therefore, RUE may change during grain-filling of crops producing seeds high in protein or oil (Williams et al., 1968; Bonhomme et al., 1982; Muchow et al., 1982). For our study, only growth occurring prior to grain-filling was considered.

The IPAR-to-biomass method of modeling biomass accumulation has been discussed in detail by Charles-Edwards (1982) and used in a number of plant-growth models (Stapper and Arkin, 1980; Williams et al., 1984; Ritchie, 1985; Jones and Kiniry, 1986). However, its validity has not been adequately investigated for the major crops. Our objective was to investigate RUE for sorghum (*Sorghum bicolor* (L.) Moench), rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), maize and sunflower. Field data from a number of published and unpublished data sets were used. Only data sets with no apparent nutrient, water, or low-temperature stress were included. Results from our work will assist modelers in applying this approach and will assist physiologists and agronomists in studying potential productivity of different grain-crop species.

MATERIALS AND METHODS

Data used in this study came from a number of sources and locations. Those from published sources are identified in Tables 1 and 2. Unpublished data came from field plots at Temple, Texas, Toulouse, France, and Los Baños, The Philippines. In these three cases, the experimental sites and techniques are described in detail. For all of the data sets, incoming solar radiation, leaf-area index (L), or fraction of light intercepted, and dry biomass were measured.

General approach

Total plant dry-matter data ideally included both root and shoot weights sampled several times during crop growth. Unfortunately, root dry weight is

TABLE 1

Radiation-use efficiency (RUE) for above-ground biomass accumulation for sunflower, rice, and wheat

Crop		Source of data	RUE [1] (g MJ^{-1})	SR [1] (MJ m^{-2} day^{-1})	TMEAN [1] (°C)
Sunflower		Blanchet (see text)			
		normal hybrid	4.8	20	17.5
		dwarf hybrid	5.0	20	20
		Warren-Wilson (1967	2.6		
		Kiniry [2] (see text)	2.2	17	24
		Connor et al. (1985)			
		1980/1981	2.1	28	24
		1981/1982	1.9	27	22
		Mean	3.1		
	w/o	Blanchet			
		Mean	2.2		
		SD	0.3		
		CV	13%		
Rice		Warren-Wilson (1967)	4.1	—	—
		Charles-Edwards (1982)	2.4	—	—
		M. Dingkuhn, E. Wijanco, C. Javellana and S. K. de Datta, personal communication			
		(1986)	2.1	18	26
		O'Toole (see text) [3]	2.0	16	26
		Mean	2.7		
	w/o	largest value			
		Mean	2.2		
		SD	0.2		
		CV	10%		
Wheat		Stapper (1984)	3.0	—	—
		Monteith (1977)	2.8	—	—
		Biscoe and Gallagher (1977) [3]	2.7	—	—
		Aase (1978) [4]			
		1972	2.6	9.5	17.5
		1978	3.1	10	19
		Mean	2.8		
		SD	0.2		
		CV	7		

[1] Mean daily solar radiation (SR) and mean daily air temperature (TMEAN) are given when available. Unless otherwise noted, light interception was estimated from the leaf-area index with a Beer's law equation.

[2] Fraction of incoming PAR which was intercepted was measured directly.

[3] Above-ground biomass was estimated from total biomass assuming 10% of the total dry weight was in the roots at anthesis.

[4] Data from periods when the temperature stayed above 5°C for all but one or two nights.

TABLE 2

Radiation-use efficiency (RUE) for above-ground biomass accumulation for maize and sorghum

Crop	Source of data	RUE (g MJ^{-1})	SR[1] (MJ m^{-2} day^{-1})	TMEAN[1] (°C)
Maize	Jones (see text)			
	6 plants/m²	4.5	20	24
	4 plants/m²	3.6		
	Griffin (1980)	4.4	21	23
	Cabelguenne (see text)			
	1987	4.1	19	19
	Sivakumar and Virmani (1984)[2]	3.8	15.5	26
	Warren-Wilson (1967)[2]	3.4	—	—
	Kiniry[2] (see text)			
	3.9 plants m^{-2}	2.1	20	25
	6.4 plants m^{-2}	3.9	20	25
	10.4 plants m^{-2}	3.4	20	25
	Yao (1980)	3.2	18.5	19
	Bonhomme et al. (1982)	3.2	—	—
	Williams et al. (1965)	2.9	31	22
	Mean	3.5		
	SD	0.7		
	CV	19%		
Sorghum	Cabelguenne (see text)			
	1986	3.8	21	19
	1987	3.3	18	20
	Soza[2] (1973)			
	1971	3.2	22	20
	1972	2.7	20	22
	Howell and Musik (1985)	3.1	—	—
	Steiner[2] (1986)	3.0	23	23
	Reeves (1971)			
	1965	3.0	20	25
	1966	2.7	22	27
	Sivakumar and Virmani (1984)[2]	2.9	15.5	26
	Sivakumar and Huda (1985)[2]	2.7	18	—
	Natarajan and Willey (1980)[3]	2.4	—	—
	Muchow and Coates (1986)[2]	2.4	19	27
	Gibson and Schertz (1977)	2.4	21	24
	Abetunge (1983)	2.1	18	24
	Mean	2.8		
	SD	0.4		
	CV	16%		

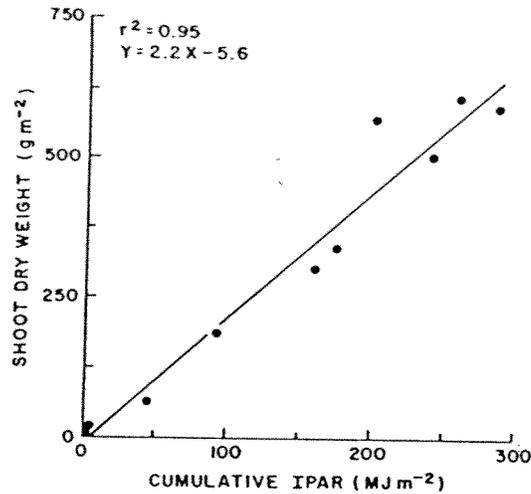For explanation of footnotes, see Table 1.

Fig. 1. Shoot dry weight as a function of cumulative intercepted PAR for sunflower (see text).

difficult to measure and was not reported in most of the studies considered. In the present study, we considered only above-ground dry weight. In the three cases where only combined root and shoot weights were available, we assumed 10% of the total plant dry biomass at anthesis was in the roots. This was similar to values reported for maize (Foth, 1962) and wheat and barley (Gallagher and Biscoe, 1978).

When analyzing studies which did not include direct measurements of IPAR, Beer's law (Monsi and Saeki, 1953) was used to estimate it from incoming photosynthetically active radiation (PAR) and L:

$$IPAR = PAR(1 - \exp(-k*L)) \tag{1}$$

Extinction coefficients (k) of 0.65 were used for maize, wheat, and rice, and 0.90 was used for sunflower (Monteith, 1969). Linear interpolations of L were used for days between dates of measurement of L.

Total incoming solar radiation (cal cm^{-2} day^{-1}) was converted to PAR (MJ m^{-2} day^{-1}) using a conversion constant of 0.042, and assuming 45% of incoming radiation energy was PAR (Monteith, 1965; Meek et al., 1984).

Above-ground biomass at different dates prior to anthesis was plotted against cumulative IPAR as shown for sunflower in Temple, Texas. (Fig. 1). The line fitted by least-squares regression had a slope equal to the RUE in units of g dry biomass per MJ of IPAR.

Maize (Jones) Temple, Texas, 1981

Maize hybrid McCurdy 67-14 was sown on a Siliwa sandy clay (fine-loamy, mixed, thermic Typic Haplustalf) near Temple, Texas (lat. 31° 06′ N, long.

$97° 20'$ W) on 27 and 28 April in 0.60-m rows, and was thinned to 4 or 6 plants m^{-2} on 11 May. There were five replications on a randomized complete-block design with plant population and amount of nitrogen applied as the two treatments. Only the high-N treatment was analyzed here. Nitrogen was applied as urea (46-0-0) at a rate of 120 kg N ha^{-1} on 3 March. Additional urea (120 kg N ha^{-1}) was applied on 2 June. Furadan (11 kg ha^{-1}) was applied on 27 April for insect control. Furadan (9 kg ha^{-1}) was also applied as a side-dress on 11 and 12 May. Plots were drip-irrigated based on estimated soil moisture to prevent drought stress. Weeds were controlled by periodic hand cultivation.

There were four sample dates from seedling emergence to silking: 18 May; 28 May; 9 and 10 June; and 18 and 19 June. The above-ground portions of four competitive plants per replication were harvested each date. Leaf area of one of the four plants was measured for L determination. Thus, plant dry weight and leaf area were measured on 20 and 5 plants per date, respectively.

Maize and sunflower (Kiniry), Temple, Texas, 1987

Maize hybrid DeKalb XL72AA was sown on 9 March 1987 and resown on 1 and 2 April 1987 on a Houston black clay (fine montmorillonitic, thermic Udic Pellustert) at the Grassland, Soil and Water Research Laboratory near Temple, Texas. Plots were 22 rows, 8.5-m long, with seeds sown 0.25-m apart in 0.80, 0.40, or 0.27-m rows for target populations of 5, 10, and 15 plants m^{-2}. Actual plant populations were 3.9, 6.4, and 10.5 plants m^{-2}, with replication 1 of the medium population deleted. There were 3 replications of a split-plot design. On 5 March, 56 kg N ha^{-1} as urea and 67 kg P_2O_5 ha^{-1} were applied. A side dressing of 56 kg N ha^{-1} as urea was applied on 7 May. Eradicane 6.7-E^1 (Stauffer Chem. Co., Westport, CT 06881-854) was applied at a rate of 6.8 kg ha^{-1} on 13 March for weed control.

Light-interception measurements were made at approximately 5-day intervals using a LI-COR line quantum sensor. Measurements were taken between 09:30 and 13:30 C.S.T. For each replication of each treatment, 2–4 measurements were taken above the canopy and 4 below. For each measurement, the sensor was positioned randomly below the canopy. The fraction of light intercepted was taken as the mean for all measurements for a population.

Dry-matter harvests consisted of the above-ground portions of all plants in a 1-m length of row for each replication of a population, taken on 8 dates, ending 8 days after 50% silking. Mean sample size was 3 plants per replication.

Dwarf sunflower hybrid 'Sigco 471D' was sown in the same soil as was maize, on 25 March in 0.60-m rows with a final plant density of 5.5 plants m^{-2}. There were 10 rows, 8 m long in each of 4 replications. Plants were fertilized similarly

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[1] Mention of a proprietary name is for readers' information only, and endorsement by the USDA, nor does it imply its approval to the exclusion of other products which may also be suitable.

to the maize plots, except that the side dressing was 112 kg N ha^{-1}. Weed control was done by hand. Light-interception measurements and dry-matter harvests were identical to those for maize, except there were 10 dates of dry-matter harvests, ending prior to anthesis. Mean sample size was 3 plants per replication.

Rice (O'Toole), Los Baños, The Philippines, 1984

The experiment was conducted at the International Rice Research Institute (lat. 14° 13′ N, long. 121 ° 15′ E). Rice cultivar IR54, a modern semi-dwarf plant type, was seeded 13 January 1984 in the field and transplanted 7 February 1984. Plants were equally spaced on a 0.2-m × 0.2-m grid. The soil was a montmorillonitic clay (Andaqueptic Haplaquoll) which was plowed once with a narrow-gauge moldboard plow and harrowed twice to achieve soil puddling to a depth of 0.25 m. During the last harrowing, 60 kg N ha^{-1} as urea, 30 kg P ha^{-1} as P_2O_5 and 30 kg K ha^{-1} as K_2O were broadcast and incorporated. During crop growth, high levels of pest control assured weed, disease, and insect-free conditions. After transplanting, the field was flooded to a depth of 0.07–0.10 m, and remained flooded until 2 weeks before final harvest. A 1-m^2 sample area with 25 'hills' was sampled for shoot dry-weight determination. The root system was sampled using a soil sampler (Thangaraj and O'Toole, 1986) on a single hill at the center of the 1-m^2 shoot sample area. Roots were washed free of soil and decaying organic matter then oven-dried for dry-weight determination. Leaf area was determined on 4 of the 25 hills sampled using an electronic leaf-area meter (Hayashi Denkoh Co., Tokyo, Japan). Four replications in a randomized complete-block design were sampled on 8 dates during the crop development period.

Sunflower (Blanchet), Toulouse, France, 1985 and 1986

Two hybrids of sunflower, Topflor (a normal-height hybrid) in 1985 and SPDN 100 (a dwarf hybrid) in 1986, were grown at Toulouse, France, (lat. 43° 37′ N, long. 1° 27′ E) on a soil characterized as a fine, mixed, mesic Udic Haplustalf (O.Rice, personal communication, 1986). Topflor was planted 1 April at 8 plants m^{-2}, and SPDN 100 was sown 16 April at 5.3, 7.6, and 10.0 plants m^{-2}. In both years 170 kg N ha^{-1} as urea was applied prior to sowing. Plots were 3 m long and consisted of four 0.50-m rows. In 1985, respective irrigation dates and amounts (mm) were: 13 June, 30: 15 June, 25; 22 July, 25; 30 July, 20, and in 1986; 17 June, 30; 29 June, 40; 1 July, 40; 11 July, 40; 16 July, 30; 27 July, 40; 30 July, 30; 6 August, 40. Length and width of the largest green leaf (area-S1), the lowest green leaf (area-S2), and the smallest of the uppermost two leaves (area-S3) were measured repeatedly on the same 6 representative plants with a meter stick. Leaf length and width were converted to

area by multiplying by 0.75. Total leaf area of a plant (LA) was calculated (Pouzet and Bugat, 1985) as:

$$LA = (NI(S1 + S2) / 2) + (NS(S1 + S3) / 2) \qquad (2)$$

where NI is the number of green leaves below the largest and NS is the number of green leaves from the largest upwards. Sampling for dry matter consisted of harvesting 4 representative plants on 4–6 dates prior to anthesis, drying, and weighing.

Sorghum and maize (Cabelguenne), Toulouse, France, 1986 and 1987

Sorghum hybrid Argence was grown in 1986 and 1987 and maize hybrid Eva was grown in 1987 on the same soil described above for sunflower. Sorghum was sown 5 May 1986 in 0.50-m rows at 36 plants m^{-2}. Plots received 190 kg N ha^{-1} as ammonium nitrate prior to planting. Plots were irrigated with 40 mm of water on 8, 24, and 28 July, and 18 and 28 August. Plants were sampled for dry matter 4 times prior to anthesis.

Two sets of plants, each from 1 m of row, were harvested each date. Height of each of the 10 representative plants was measured, and the 5 median-height plants were selected for measurement of leaf area with an electronic leaf-area meter (Hayashi Denkoh Co., Tokyo, Japan). All 10 plants were than dried and weighed.

In 1987, sorghum was sown 11 May in 0.50-m rows with a plant population of 27.9 plants m^{-2}. Plots received 190 kg N ha^{-1} as ammonium nitrate prior to planting. Plots were irrigated with 40 mm of water on 5, 12, and 19 August. Potassium was applied 11 May at a rate of 60 kg ha^{-1}, and phosphorus was applied 14 October 1986 at a rate of 220 kg ha^{-1}. Data for four dates of harvest were used for this analysis. The techniques of sampling of both sorghum and maize in 1987 were identical to those described above for 1986.

Maize in 1987 was sown on 28 April and had a plant population of 8.1 plants m^{-2}. Plots received 250 kg N ha^{-1} as urea on 27 April. Phosphorus was applied on 28 April at a rate of 60 kg ha^{-1}. Plots were irrigated 40 mm on 1 July, 30 mm on 28 July, 40 mm on 12 August, and 40 mm on 19 August. Data for four dates of harvest were used for this analysis.

RESULTS AND DISCUSSION

In temperate regions, RUE should decrease as crops develop due to two factors, increasing biomass and increasing temperatures, both causing increased maintenance respiration (McCree and Silsbury, 1978). Therefore, one would expect the slope of the dry-matter : IPAR relationship to decrease as one approaches anthesis. In no case did this occur for the data in the present study. As typified by the sunflower data from Temple, Texas (Fig. 1), in the absence

of prolonged cool weather early in the season, there was no obvious nonlinearity throughout the range of measured data. Thus, total energy loss due to all respiration appeared to be proportional to plant growth.

The linear equations for dry weight as a function of IPAR fit exceptionally well for all the unpublished data (Table 3). Attempts at fitting a squared term failed to show significance in all cases except for the normal sunflower hybrid of Blanchet. In that case, there was a slight tendency for the efficiency to increase in the later samplings. Values of r^2 were 0.95 or greater in all cases but two; however, there were noticeable differences among values of RUE within each species (Tables 1 and 2).

Sunflower is the only dicotyledon in this study. Not only are leaves of sunflower more horizontal than those of the common monocotyledon crop species, but they are phototropic and one might expect the leaves to light-saturate. As

TABLE 3

Parameters of filled regression lines for plant dry weight[1] as a function of cumulative intercepted PAR

Crop	Source of data	Slope (g MJ^{-1})	n	r^2
Sunflower	Blanchet			
	normal hybrid	4.8	6	0.98
	dwarf hybrid	5.0	6	0.95
	Kiniry	2.2	10	0.95
	Connor et al. (1985)			
	1980/81	2.1	6	0.97
	1981/21	1.9	6	0.998
Rice	O'Toole	2.2	4	0.997
Wheat	Aase			
	1972	2.6	5	0.99
	1978	3.1	6	0.99
Maize	Jones			—
	6 plants m^{-2}	4.5	4	0.97
	4 plants m^{-2}	3.6	4	0.99
	Cabelguenne	4.1	5	0.97
	Kiniry			
	3.9 plants m^{-2}	2.1	8	0.93
	6.4 plants m^{-2}	3.9	8	0.91
	10.4 plants m^{-2}	3.4	8	0.95
Sorghum	Cabelguenne			
	1986	3.8	4	0.99
	1987	3.3	4	0.95
	Gibson and Schertz (1977)	2.4	32	0.99

[1]Weight was for the above-ground plant in all cases except for rice, where roots were also included.

discussed above, however, photosynthetic rate of sunflower behaves more like maize, with no tendency to light-saturate, even at full sunlight (Hesketh and Moss, 1963).

Results obtained from Blanchet's (unpublished) data for sunflower shows that RUE was considerably greater in southern France than for any of the other locations (Table 1). The mean value for RUE was 3.2 g MJ^{-2} with all the data, while it was 2.2 with only the last four data-sets. Mean solar radiation (SR) did not appear to be related to be large values for France in that SR was between values of Connor et al. (1985) and those of Kiniry (Table 1). Lower temperature for the French experiments may have contributed to the high RUE (see Table 2).

The relatively large value for RUE of sunflower, when data of Blanchet were included, was supported by the results of Warren-Wilson (1966). He found that, under certain conditions, both rate of net assimilation and rate of dry-matter increase of sunflower were twice as great as values previously reported as maximums.

Without the results from France, the SD among experiments was low (0.3 g MJ^{-1}), and the CV was 13%; thus the mean value of 2.2 g MJ^{-1} is probably appropriate over a wide range of SR, unless daily mean air temperatures are below 20°C for long periods of time.

Rice data also showed that RUE could vary between locations, the largest value being twice as great as the smallest. This great range did not appear to be due to differences between indica and japonica rice. Charles-Edwards (1982), working with data of Vong and Murata (1978), found mean values of RUE for indica and japonica rice differed by only 4%. Deleting the largest value for RUE in the present study, the mean was 2.2 g MJ^{-1}, and the CV was 10%.

Wheat had a similar variation in RUE, the mean being 2.8 g MJ^{-1} and the CV 7%. However, one should be careful in applying this number to winter wheat in the late fall or early spring when low temperatures restrict growth; values under such conditions can be more than 30% smaller (Howell and Musick, 1985).

Data-sets for maize were more numerous than for the C_3 plants (Table 3). Locations were as far north as State College, Pennsylvania (Yao, 1980) at 40° 5'N and Peronne, France (Bonhomme et al., 1982) at 50°N to as far south as Hyderabad, India (Sivakumar and Virmani, 1984) at 17° 5'N.

Mean RUE of maize was greater than for any other species, with values more nearly normally distributed than those for the three previously discussed species; RUE was intermediate for the data-set having the lowest SR, whereas it was lowest for the data-set with the greatest SR. Maize does not exhibit light saturation even at full sunlight (Hesketh and Moss, 1963), so one would not expect a decrease in RUE at high SR. The lowest values of RUE were found by Kiniry and by Williams et al. (1965). The effects of low population densities

in Kiniry's data are unexplained, but inadequate irrigation in a California location with high evaporative demand may explain the results obtained by Williams et al. (1965).

Temperature did not appear to affect RUE, the data-sets with the smallest and greatest TMEAN values having intermediate values for RUE.

Sorghum also had an extensive group of data-sets: Mead, Nebraska (Soza, 1973) at 40° 5′N: Hyderabad, India (Natarajan and Willey, 1980; Sivakumar and Virmani, 1984; Sivakumar and Huda, 1985) at 17° 5′N; northern Western Australia (Muchow and Coates, 1986) at 16°S; and Perth, Australia (Abetunge, 1983) at 32°S.

Mean RUE of sorghum was similar to maize and was greater than the means for rice and sunflower, values being approximately normally distributed. The CV was slightly less than for maize, but greater than for the C_3 species, whereas SR had no apparent relationship with RUE in that the data-sets with both the greatest and the smallest SR had intermediate values for RUE. However, as with sunflower, RUE was greatest for the data with the lowest mean temperature.

In conclusion, deleting the two high values for sunflower and the greatest value for rice gives mean values for RUE for sunflower, rice, and wheat of 2.2, 2.2, and 2.8 g MJ^{-1}, respectively. Likewise for maize and sorghum, means were 3.5 and 2.8; these values are nearly identical to the 3.56 and 2.78, respectively, reported by Muchow and Davis (1988). Values measured in cool temperatures may be much different from these. There was a trend for C_4 species to have greater values than C_3 species, as discussed by Monteith (1978); however, these differences did not appear to be as distinct as previously thought.

Estimates of solar-enery utilization efficiency (Murata, 1981) of most of these crops showed a relative ranking similar to the mean RUE reported here. With maize as the standard, sorghum, wheat, and indica and japonica rice were 82.5, 70, 103, and 70% as efficient in using solar energy. In the present study, mean RUE for sorghum, wheat, and rice were 80, 80, and 63% as great as for maize. The ranking of the rice value in the present study was closer to Murata's value for japonica rice. However, as discussed above, values of RUE for indica and japonica rice have been shown to differ by only 4% (Charles-Edwards, 1982).

The magnitude of the variability in RUE within each species was great. With this in mind, three assumptions need further investigation. First, estimation of light interception with Beer's law, with one value for the extinction coefficient (k) of a crop, may have caused some errors, especially at low L; however, the authors feel that since most biomass accumulation occurs at L large enough for light interception to be fairly insensitive to k, this sould not have caused differences in RUE of the magnitude experienced here. This was supported by the fact that data-sets with percent light interception measured directly (Soza, 1973; Natarajan and Willey, 1980; Kiniry unpublished; Sivakumar and Virmani, 1984; Sivakumar and Huda, 1985; Muchow and Coates, 1986; Steiner,

1986) generally had intermediate values of RUE. In addition, these groups of data-sets still had great within-species differences: 2.1–3.9 for maize, and 2.4–3.2 for sorghum.

The second critical assumption, that the above-ground biomass was a suitable measure of total plant biomass, was more difficult to evaluate for this study; for this to be true, the fraction of total biomass partitioned to roots would have to have been stable across the data-sets. Only three sets had measurements of root weight: O'Toole (unpublished) for rice; Biscoe and Gallagher (1977) for wheat; and Natarajan and Willey (1980) for sorghum. Calculation of above-ground biomass, assuming 10% was in the roots at anthesis, resulted in two of these three data-sets having low values for RUE; this would imply that the 10% estimate was not too low. Future research may reveal that variability of the shoot:root ratio is a major factor contributing to the variability of such estimates of RUE.

Finally, this radiation-use-efficiency approach for modeling biomass accumulation assumes that leaf photosynthetic rates behave similarly among data-sets for a species, the importance of which was discussed by Monteith (1977). Thus, it assumes variability due to genotype, CO_2 concentration, and leaf angle in the field are minimal compared to variability in incident solar radiation and the fraction intercepted by the leaf canopy.

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