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Predicting growth and development of pigeonpea: biomass accumulation and partitioning

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Abstract

Examining physiological relationships that quantify the processes of interception of radiation and biomass accumulation and partitioning provide one avenue for understanding limits to pigeonpea productivity. The radiation extinction coefficient (k), radiation use efficiency (RUE), partitioning of biomass between leaf and stem before flowering, and the rate of linear increase in harvest index (HI) during pod-filling were determined for nine cultivars in water and nutrient non-limiting conditions at ICRISAT Centre, Patancheru, India. The nine cultivars comprised three each from the cultivar duration classes extra-short (100 days to maturity), short (115 days) and medium (170 days). Values of k and RUE were consistent across duration groups, with mean values of 0.53 and ca. 0.9 g MJ⁻¹, respectively. RUE remained at its maximum value almost until maturity. Partitioning between leaf and stem prior to flowering was also consistent across groups, in the ratio of 1:1.03 to 1:1.14. The rate of linear increase in HI and final HI varied across groups, with lower rates of partitioning to grain and final HI in the later maturing groups. When adjusted for fallen leaf, the HI increase was ca. 0.08, 0.075 and 0.04 per day, and maximum HI was ca. 0.35, 0.32 and 0.19 for extra-short, short and medium-duration groups, respectively. The association of lower HI increase with indeterminate growth provides a convenient framework to simulate concurrent reproductive and vegetative growth during pod-filling. © 2001 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: *Cajanus cajan*; Pigeonpea; Biomass accumulation and partitioning

1. Introduction

Diversification of pigeonpea into new production systems requires knowledge of its yield potential, production risks and returns in diverse climatic environments. Likewise, the shift from low- to high-input systems necessitates an understanding of the produc-

tion potential of the crop and limits to productivity. In previous papers, functional relationships quantifying phenological development (Carberry et al., 2001) and leaf area development (Ranganathan et al., 2001) in pigeonpea were described. This paper quantifies the functional relationships that describe biomass accumulation and partitioning in pigeonpea in water and nutrient non-limiting conditions.

Key determinants of biomass accumulation are the interception of solar radiation by the crop leaf canopy and the use of this intercepted radiation to grow biomass. The radiation extinction coefficient (k) quan-

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tifies the effectiveness with which a crop canopy, of a given leaf area index, intercepts radiation. Radiation use efficiency (RUE) describes how efficiently intercepted radiation is converted to biomass. Both k and RUE are key parameters in many crop growth models. In order to use crop growth models confidently over a range of situations, some understanding of the variation of k and RUE with cultivar, and within and between seasons, is necessary. While k and RUE for pigeonpea have been determined by a number of authors (Natarajan and Willey, 1980; Sivakumar and Virmani, 1980; Rowden et al., 1981; Hughes and Keatinge, 1983; Nam et al., 1998), there has been no systematic comparison of cultivars that vary in time to flowering and maturity. Pigeonpea genotypes are typically grouped into different maturity (duration) classes of extra-short, short, medium and long based on the number of days to flowering at Patancheru, India (Carberry et al., 2001), a low-latitude tropical environment, and whether they have determinate (DT) or non-determinate (NDT) growth habit.

The linear change in harvest index (HI) with time has been shown to be a common feature for a number of species, including soybean (Spaeth and Sinclair, 1985), peanut (Hammer et al., 1996; Bennett et al., 1993) and pea (Bindi et al., 1999). Defining a constant rate of increase in HI is desirable in modelling crop growth and yield, as it has proved effective and robust in a number of modelling efforts including simulations of soybean (Sinclair, 1986). The rate of increase in HI during seed growth has not been quantified for pigeonpea. The wide range in crop duration that exists in pigeonpea also permits some examination of the variation in HI with duration. It is unclear to what

extent the rate of increase in HI will vary across duration groups in pigeonpea as a greater degree of vegetative growth concurrent with reproductive growth occurs as growth duration of a genotype increases.

This paper reports results from field experiments conducted at ICRISAT, Patancheru, India that examined growth analysis of cultivars from the main growth-duration groups. The data are analysed in terms of the following key relationships: (1) between leaf area index and the fraction of radiation intercepted, (2) between cumulative intercepted radiation and biomass accumulation, (3) partitioning of biomass to different plant organs before flowering, and (4) the increase in HI during pod-filling. These relationships are examined with a view to the development of a simulation model for pigeonpea development, growth, and yield.

2. Materials and methods

2.1. Data sources

Two experiments were conducted in the rainy seasons of 1990–1991 and 1991–1992 at ICRISAT, Patancheru, India (17°N, 78°E, 500 m elevation) to examine the functional relationships listed in the introduction for a range of pigeonpea cultivars (Table 1).

In the first study, radiation interception, biomass accumulation and partitioning of biomass to above-ground organs of diverse cultivars were measured. On 3 July 1990, nine pigeonpea cultivars from

Table 1
Phenology of the cultivars used in the 1990–1991 and 1991–1992 studies

Cultivar	Growth duration class	1990–1991		1991–1992	
		Days to first flower	Days to maturity	Days to first flower	Days to maturity
ICPL 83015	Extra-short	58	95		
ICPL 84023	Extra-short	54	95		
ICPL 85037	Extra-short	62	111		
ICPL 87	Short	66	116		
ICPL 88026	Short	68	114		
UPAS 120	Short	64	114		
ICPL 8357	Medium	110	168	109	171
ICP 1-6	Medium	106	176	108	171
ICPL 87119	Medium	112	177	112	171

three maturity groups were sown in a split-plot experiment with three replicates. Extra-short (100–110 days to maturity) [ICPL 84015 DT, ICPL 84023 DT, ICPL 85037 NDT] and short-duration (120–140 days) (ICPL 87 DT, ICPL 88026 DT, UPAS 120 NDT) cultivars were sown at a density of 33 plants m^{-2} while medium-duration cultivars (ICPL 87119 NDT, ICP 1-6 NDT, ICPL 8357 NDT) were sown at 6.67 plants m^{-2} . While these plant densities are normal agronomic practice for the various maturity groups, it is not possible to test for significance between groups in physiological parameters due to the confounding of duration with density and possible effects on k , RUE and biomass partitioning. Hence in this experiment it was only possible to statistically compare extra-short and short-duration groups, and qualitatively compare these two groups with the medium-duration group. Main plots were water supply regimes of irrigation and dryland conditions. Irrigated plots were watered at regular intervals to prevent water stress. Only data from irrigated plots are used here. Cultivars with similar maturity duration formed sub-plots, which measured 9 m \times 6 m. The soil was a vertisol (very fine, clayey, montmorillonitic, calcareous, hyperthermic typic pellustert by USDA classification).

In the second study, radiation interception, biomass accumulation and partitioning of biomass to above-ground organs of three medium-duration cultivars were measured. On 22 June 1991, six pigeonpea cultivars were sown in a split-plot experiment with three replicates, including three cultivars common to the 1990/1991 experiment: ICPL 87119, ICP 1-6, ICPL 8357. Plants were sown at 6.67 plants m^{-2} . Main plots were water supply regimes of irrigation and dryland conditions. Irrigated plots were watered at regular intervals to prevent water stress. Only data from irrigated plots of the three cultivars common to 1990/1991 are analysed here. Sub-plots measured 9 m \times 6 m. The soil type was an alfisol (a clayey skeletal, mixed *iso*-hyperthermic, udic rhodustalf).

In both studies, a basal application of di-ammonium phosphate (18% N, 20% P) at 100 kg ha^{-1} was applied. Seeds were treated with thiram and metalaxyl before sowing to control soil-borne fungal diseases. Sowing was done in shallow furrows on both sides of 60 cm ridges. Two seeds per hill were sown and plants were thinned to one per hill at 20 days after sowing (DAS) to provide the target plant population density.

Plots were weeded manually at regular intervals in the early growth stages till the canopy closed. Insecticides (endosulfan or methomyl) were used at frequent intervals, starting from the time of flowering, to control insect pest damage, especially that caused by *Helicoverpa armigera* and *Maruca testulalis*. Irrigation was applied every 3–5 days depending on the dryness of the soil surface at a rate equal to pan evaporation.

2.2. Measurements

Meteorological data including maximum and minimum air temperature, and incident radiation were recorded daily. Every 7–14 days, leaf area index (LAI) and biomass were determined by sampling three plants in each sub-plot. Total biomass and grain yield were determined at maturity by harvesting 3.6 m^2 . On each sampling occasion, plants were separated into leaves, stems, pods, and flowers and then dried at 70°C for 48 h to determine dry weight. To determine grain yield, pods were dried in sunlight before threshing and drying. Leaf area of harvested plants was determined by using an automatic leaf area meter (Delta-T Devices, Cambridge, UK). In the second (1991/1992) study, in order to calculate total biomass production including senesced leaves, fallen leaves were collected from a permanently marked quadrat area in each sub-plot and dried at 70°C to determine dry weight. Leaves were collected at a greater frequency than biomass samplings were taken, so as to avoid decomposition losses.

Canopy photosynthetically active radiation interception was measured at midday at different growth stages with a line quantum sensor and a quantum sensor (LI-COR, Inc., Lincoln, NE). Two measurements were made per plot, one with inter-row placement and other with intra-row placement. The line quantum sensor was placed below the canopy to measure transmitted light, while the quantum sensor was situated above the canopy to measure incoming radiation. The output of both sensors was recorded simultaneously and fractional interception (f) calculated.

2.3. Data analysis

Canopy radiation extinction coefficients (k) were determined with least-square regression by calculating

the slope of the relationship between $\ln(1 - f)$ and LAI. Values of f for each day after sowing were interpolated between actual measurements using fitted polynomial curves. Cumulative intercepted radiation was calculated by multiplying the daily incoming solar radiation by f for each day after sowing. RUE was calculated as the slope of the regression of accumulated biomass on cumulative intercepted radiation. The regression was fitted using a step-wise regression procedure where, starting at crop maturity, data were dropped from the regression until no further improvement was gained in the proportion of variance accounted for by the regression. Biomass excluding fallen leaves was used so that RUE estimates could be compared between the two seasons.

Partitioning of biomass between leaf and stem from emergence to the onset of flowering was determined by regressing leaf biomass against stem biomass, with the slope of the relation being the partitioning coefficient. The rate of increase in harvest index

during pod-filling was determined by regressing harvest index against days after onset of flowering. The regression was also fitted using a step-wise regression procedure where, starting at crop maturity and at the first sampling during pod-filling, data were dropped from the regression until no further improvement was gained in the proportion of variance accounted for by the regression. In the 1991/1992 study it was possible to calculate harvest index either excluding or including the weight of fallen leaves.

3. Results

3.1. Radiation interception

Fitted relationships between f and LAI, to determine k , were reasonable, with R^2 -values between 0.83 and 0.94 (Fig. 1 and Table 2). Goodness of fit tended to be less for the extra-short duration cultivars because fewer data were taken in the shorter-season cultivars.

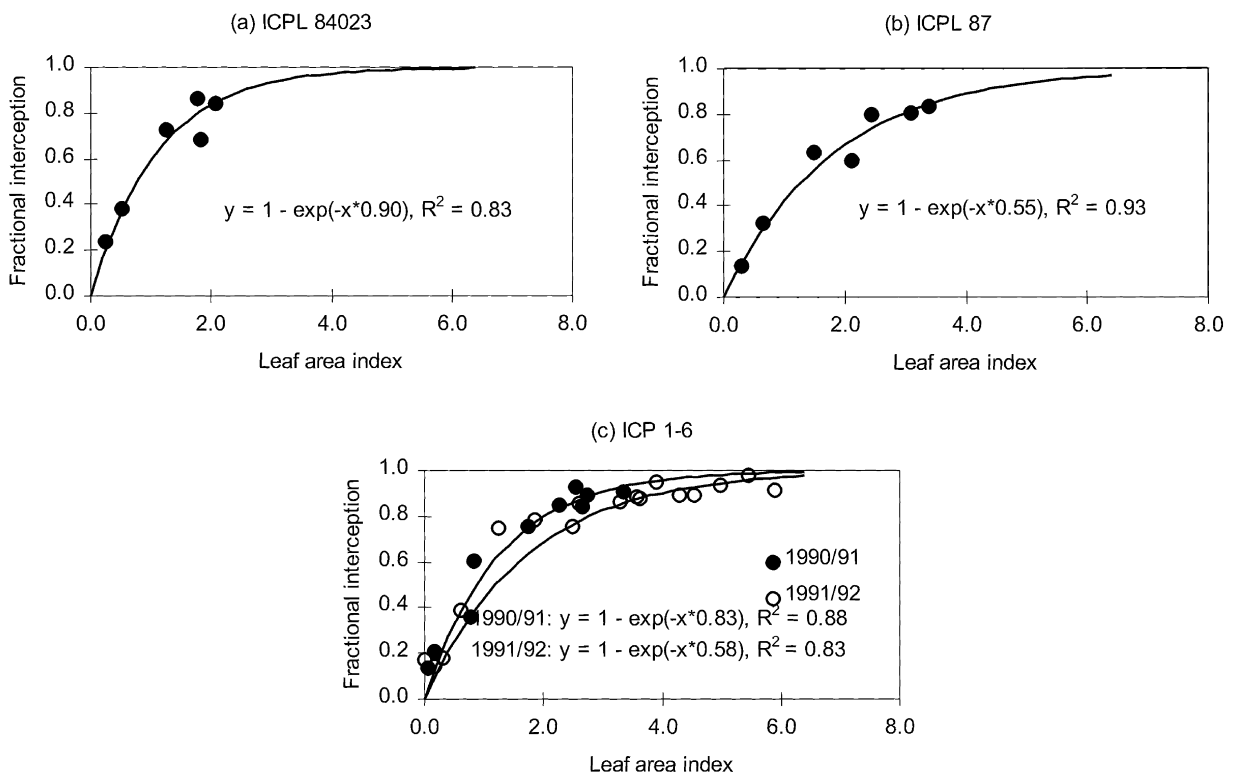


Fig. 1. Relationship between fractional radiation interception and leaf area index. Equations of the fitted relationships were fitted using least-squares regression. The value of the exponent in the fitted regression is the radiation extinction coefficient. Regression coefficients of other cultivars in the studies are given in Table 2.

Table 2

Fitted values (\pm standard error) of the radiation extinction coefficient (k) and RUE in the 1990–1991 and 1991–1992 studies^a

Cultivar	Growth duration class	1990–1991		1991–1992	
		k	RUE	k	RUE
ICPL 83015	Extra-short	0.60 \pm 0.05 (0.85)	0.89 \pm 0.07 (0.97)		
ICPL 84023	Extra-short	0.90 \pm 0.08 (0.83)	0.58 \pm 0.02 (0.99)		
ICPL 85037	Extra-short	0.67 \pm 0.03 (0.96)	0.77 \pm 0.04 (0.97)		
ICPL 87	Short	0.55 \pm 0.03 (0.93)	0.81 \pm 0.05 (0.97)		
ICPL 88026	Short	0.66 \pm 0.03 (0.94)	0.94 \pm 0.05 (0.97)		
UPAS 120	Short	0.84 \pm 0.05 (0.93)	0.79 \pm 0.11 (0.93)		
ICPL 8357	Medium	0.78 \pm 0.05 (0.85)	0.56 \pm 0.02 (0.98)	0.71 \pm 0.03 (0.93)	0.70 \pm 0.04 (0.96)
ICP 1-6	Medium	0.83 \pm 0.04 (0.88)	0.75 \pm 0.03 (0.98)	0.58 \pm 0.03 (0.83)	0.77 \pm 0.03 (0.99)
ICPL 87119	Medium	0.83 \pm 0.05 (0.88)	0.62 \pm 0.02 (0.97)	0.55 \pm 0.03 (0.85)	0.76 \pm 0.03 (0.97)

^a R^2 -values are given in brackets.

In addition, only one of the six extra-short or short cultivars achieved values of f greater than 0.9, while all medium-duration cultivars achieved values of f greater than 0.9. This estimate of k -values for the short and extra-short groups is probably less reliable than those from the medium-duration group.

Variation in the value of the radiation extinction coefficient (k) was as high among cultivars of the same growth duration, as it was across growth-duration groups. There was no difference for k between the extra-short and short-duration groups in 1990/1991 and the mean of these two groups was within the standard error of the group mean for the medium-duration group: the mean for the three groups was 0.72 for extra-short, 0.68 for short and 0.81 (1990/1991) and 0.61 (1991/1992) for medium-duration groups. The lack of response of k to growth-duration occurred despite the maximum LAI varying from 2 to 3 for extra-short, 2.5 to 3.5 for short, and 3.5 to 6 for medium-duration. Interestingly, there was an effect of season on the value of k for two out of the three medium-duration cultivars ($P < 0.01$), with higher k -values in 1990/1991, associated with greater fractional interception at LAI values between 1 and 3. It is difficult to draw a strict comparison between seasons, as the 1991/1992 crops had LAI values over 4 and the 1990/1991 crop did not.

3.2. Radiation use efficiency

Relations between biomass and cumulative intercepted radiation (Fig. 2 and Table 2), gave R^2 -values between 0.93 and 0.97. All cultivars except UPAS 120

maintained a constant RUE until late in pod-filling. In those cases where RUE slowed before maturity, this was also associated with a cessation of pod biomass accumulation. Within a growth-duration group, the mean RUE was 0.75 g MJ⁻¹ for extra-short, 0.85 g MJ⁻¹ for short, and 0.74 g MJ⁻¹ for medium-duration cultivars (1991/1992). The mean RUE for the extra-short duration group was biased downwards by ICPL 84023, which had an RUE of 0.58 g MJ⁻¹, considerably lower than the other eight cultivars. If the RUE for this cultivar is excluded, then the mean RUE increases to 0.83 g MJ⁻¹, which is comparable to the other two maturity groups.

RUE was lower for two of the medium maturity cultivars in the 1990/1991 season. RUE was 18% lower for ICPL 87119 and 20% lower for ICPL 8357, and not significantly different between seasons in ICP 1-6. Lower biomass production in the 1990/1991 season was due to both lower RUE and less radiation intercepted over the growing season.

3.3. Partitioning between stem and leaf before flowering

There were strong linear relationships between leaf and stem biomass for samplings between emergence and flowering, implying a constant rate of partitioning between leaf and stem (Fig. 3). Regression fits gave R^2 -values between 0.98 and 0.99 and partitioning coefficients between stem and leaf were similar for the extra-short and short growth duration groups at 1.03 and 1.14, and these two values were within the standard error of the mean for the medium-duration

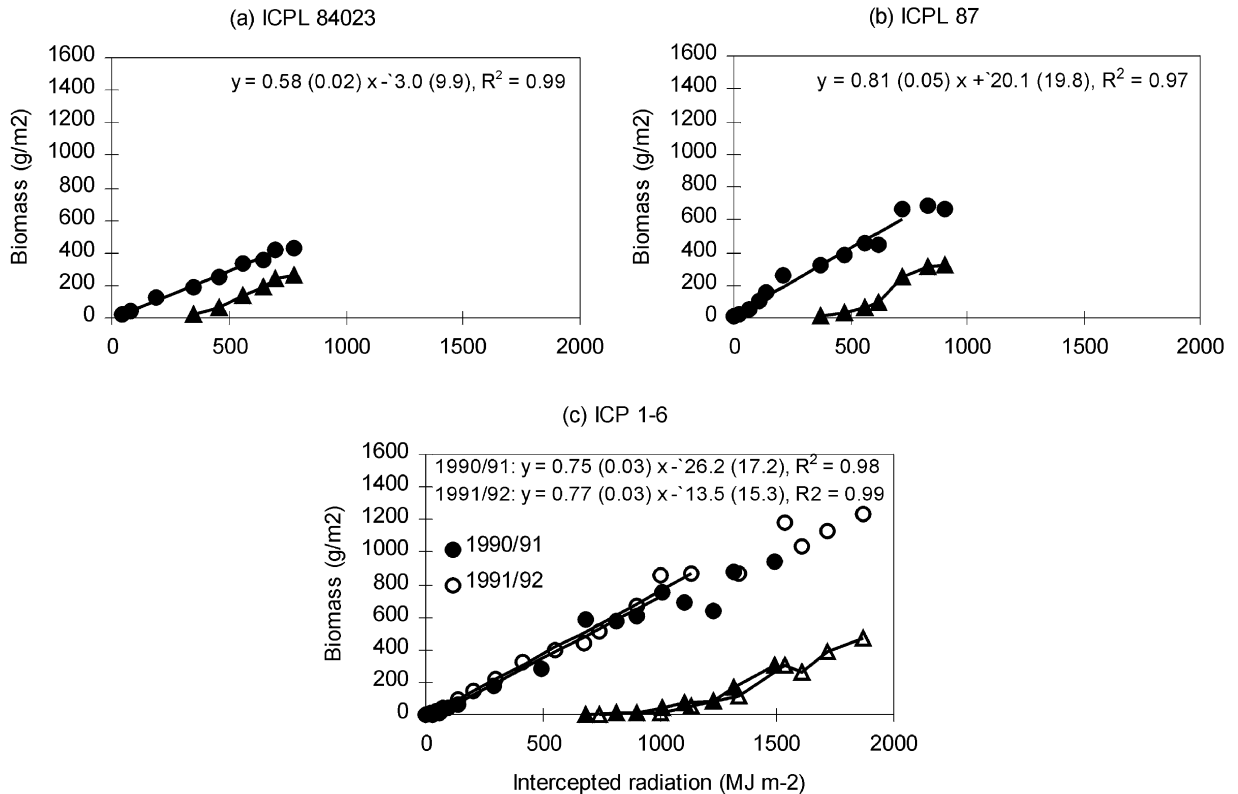


Fig. 2. Relationship between above-ground biomass (circles) and pod biomass (triangles) biomass and cumulative intercepted solar radiation. Equations of the fitted relationships between above-ground biomass and intercepted radiation were fitted using least-squares regression, with standard errors of coefficients in brackets. The value of the slope in the fitted regression is the RUE. Regression coefficients of other cultivars in the studies are given in Table 2.

cultivar group (1.08 and 1.13). In contrast to the extinction coefficient and RUE, there was no effect of season on partitioning to leaf in the medium-duration cultivar group.

3.4. Rate of increase in harvest index during pod-filling

In the 1990/1991 experiment, harvest index was calculated as pod biomass divided by net above-ground biomass (i.e. exclusive of fallen leaves). There was variation among cultivars in the pattern of increase in HI (Fig. 4). For example, ICPL 84023 showed a sigmoidal increase in HI, while HI increase in ICPL 85037 was more concave with time after first flower. Regressions of HI against thermal time, rather than calendar time, neither improve linear fits nor reduce the differences among cultivars (data not

shown). Bindi et al. (1999), in an analysis of seed-filling in wheat, soybean, sunflower and pea, found that HI increase was not constant for the entire seed growth period. However, a linear increase in HI was found to be statistically appropriate when HI was increasing from 10 to 90% of its maximum value. Consequently, we fitted linear regressions to HI against days after first flowering. These regressions accounted for 95–96% of the variance across the three growth-duration groups (Fig. 4 and Table 3). There were no significant differences in regression fits among cultivars of a given growth-duration group, so cultivars were pooled and a common regression line fitted to each growth duration group. Slope of the regression relationship, the rate of linear increase in HI, was 0.14, 0.13 and 0.07 per day for extra-short, short and medium-duration cultivars, and there was a significant difference in the slope between the two

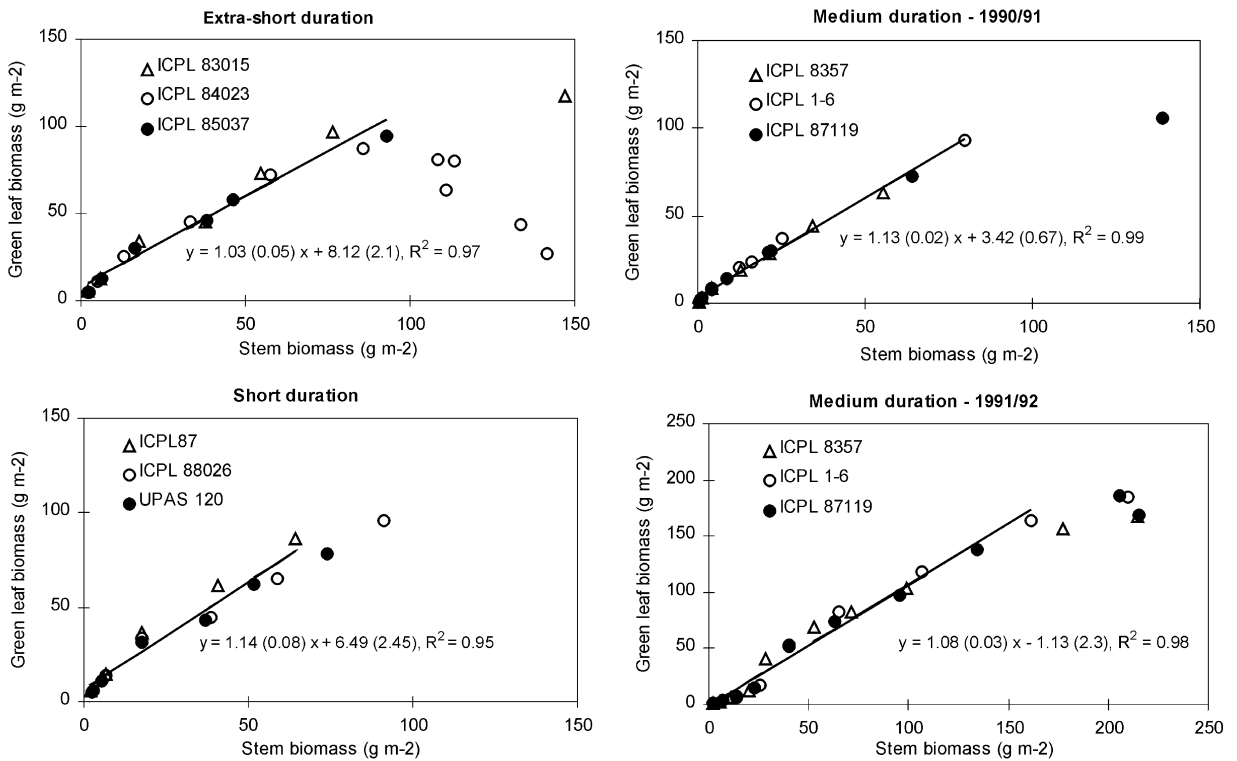


Fig. 3. Relationship between green leaf biomass and stem biomass for the extra-short, short and medium-duration cultivar groups in 1990/1991 and the medium-duration cultivar group in 1991/1992. Data points until early flowering are shown. Equations of the fitted relationships for samplings between emergence and flowering were fitted using least-squares regression, with standard errors of coefficients in brackets. The value of the slope in the fitted regression is the partitioning coefficient between leaf and stem prior to flowering.

earlier maturing groups, and these were different to that in the medium group. The intercept of the relationship with the x -axis (days after the onset of flowering) provides an estimate of the effective start to the linear phase of HI increase. In the extra-short group, this intercept was near zero, while in the two other groups it was around 2–3 days. There were not enough sampling points late in pod-filling to confidently fit a

plateau final harvest index, however, by visual inspection of Fig. 4 it appears to be ca. 0.60, 0.55 and 0.30 for the extra-short, short and medium-duration groups, respectively. Hence, the later maturing groups had both a lower rate of increase in harvest index and consequently a lower final harvest index at maturity because duration of pod-filling was similar across duration groups (Fig. 4).

Table 3

Fitted coefficients (\pm standard error) of the relationship between harvest index and days after first flowering for the medium-duration cultivars grown in the 1991/1992 sowing at ICRISAT^a

Cultivar	Net biomass			Gross biomass		
	Slope	Intercept	R^2	Slope	Intercept	R^2
ICPL 8357	0.0072 \pm 0.0004	-0.032 \pm 0.013	0.99	0.0064 \pm 0.0003	-0.091 \pm 0.023	0.99
ICP 1-6	0.0065 \pm 0.0005	-0.103 \pm 0.025	0.97	0.0059 \pm 0.0005	-0.027 \pm 0.0009	0.97
ICPL 87119	0.0060 \pm 0.0003	-0.061 \pm 0.016	0.99	0.0053 \pm 0.0003	-0.054 \pm 0.014	0.99

^a Regressions are conducted where biomass is exclusive (net biomass) or inclusive (gross biomass) of fallen leaves.

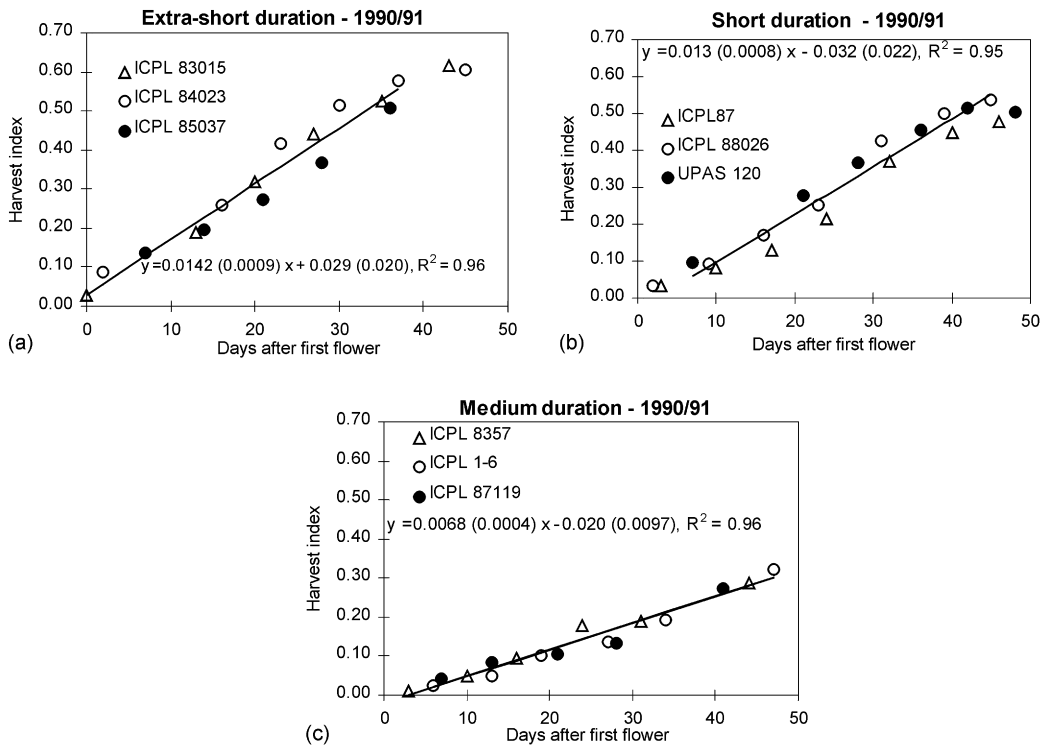


Fig. 4. Relationship between days after first flower and harvest index for the extra-short, short and medium-duration cultivar groups in 1990/1991. All data points from first flower to maturity are shown. Equations of the fitted relationships for samplings lying on the linear phase were fitted using least-squares regression, with standard errors of coefficients in brackets. The value of the slope in the fitted regression is the rate of increase in harvest index. Regression coefficients for the cultivars in the 1991/1992 study are given in Table 3.

In the 1991/1992 experiment, fallen leaves were collected frequently during the season, so this provided an opportunity to assess harvest index increase accounting for leaf loss during pod-filling. Coefficients of linear regressions of harvest index increase for each of the three medium-duration cultivars studied in 1991/1992 and are given in Table 3. In one case harvest index was calculated as in 1990/1991, i.e. pod biomass divided by net biomass. The resulting slopes of 0.072 per day for ICPL 8357, 0.065 per day for ICP 1-6 and 0.060 for ICPL 87119, are similar to the value of 0.06 per day fitted to the same three pooled cultivars in the previous season. Effective start to pod-filling (4–15 days) was later and maximum harvest index (ca. 0.35) was higher than the 1990/1991 values. By adding the weight of fallen leaves to the biomass denominator in the harvest index calculation (Table 3), harvest index increase was reduced to 0.064, 0.059 and 0.053 per day, an average reduction of 11%.

4. Discussion

4.1. Radiation interception

The value of the radiation extinction coefficient did not vary systematically across duration groups, indeed there was just as much variation among cultivars of one group as there was across groups. An overall cultivar mean for k for the nine cultivars in the 1990/1991 study comes to 0.74, which translates to an LAI of ca. 4 for 95% interception. This value is similar to 0.76 measured by Muchow (1985a), but higher than those measured in other studies using similar methodology, plant population density and row spacing. For instance, Nam et al. (1998) measured k -values between 0.41 and 0.65 under irrigation for six extra-short duration cultivars at ICRISAT. Squire (1990, p. 74) calculated a k value of 0.52 from the studies of Natarajan and Willey (1980) and Sivakumar

and Virmani (1980). Other estimates (e.g., Rowden et al., 1981) are difficult to compare because of the different methods used to measure light interception.

In the current study, k was derived using measures of PAR interception. The value of k depends on whether f is measured in terms of total solar radiation, in the wavelength range 0.4–3.0 μm , or photosynthetically active radiation, in the range 0.4–0.7 μm , because PAR is intercepted more effectively than radiation from the total shortwave band (Marshall and Willey, 1983). Many crop models use k -values calculated on a solar radiation basis, so some conversion between the current measured values and ones based on interception of solar radiation is desirable. Squire (1990, p. 74) gives an empirical relation to convert a value of k made on a PAR basis to one based on solar radiation. Using this conversion, the mean k value for the current study is reduced from 0.74 to 0.53.

The k value in the 1990/1991 study was higher than in 1991/1992. It is possible that some stress (perhaps waterlogging — see below for further discussion) in 1990/1991 increased k by reducing LAI and inflating the contribution of the stems to radiation interception at LAI values between 1 and 3. Sheldrake and Narayanan (1979) showed that during vegetative growth stem area can comprise an extra ca. 30% area in addition to that of the leaves.

4.2. Radiation use efficiency

RUE remained constant until late in pod-filling, demonstrating that pigeonpea is able to maintain high canopy photosynthetic activity almost until maturity. There was no evidence that RUE varied across duration groups, despite season length varying from 100 (extra-short duration) to 115 (short-duration) to 160 days (medium-duration). The overall cultivar mean (excluding ICPL 84023 and the medium-duration cultivars in 1990/1991) was 0.8 g MJ^{-1} . The low RUE of ICPL 84023 may be intrinsic and not just a function of the conditions in this study. Nam et al. (1998) found that this cultivar had the lowest RUE out of six extra-short duration cultivars under irrigated conditions at ICRISAT. It is possible that the lower RUE obtained for the medium-duration cultivars in 1990/1991 was due to waterlogging on the vertisol soil type, which is known to induce waterlogging stresses

in pigeonpea crops at ICRISAT, particularly under irrigation (Chauhan, 1987). The crop received 200 mm rainfall between 36 and 50 DAS and 100 mm between 90 and 99 DAS. The second period of rainfall coincided with the late vegetative period in the medium cultivars when the potential for biomass accumulation was at its greatest, but the extra-short and short-duration cultivars were either mature or almost mature by this time. This may explain why there was no apparent reduction in RUE in the extra-short and short-duration groups, but a 20% reduction in RUE of the medium group. In 1990/1991 RUE was 18% lower for ICPL 87119 and 20% lower for ICPL 8357, and not significantly different between seasons in ICP 1-6. This may be because of cultivar variation in tolerance of waterlogging stresses, which is known to exist (Chauhan, 1987). Excluding data after 90 DAS in 1990/1991 from the linear regression did increase the fitted value of the RUE in ICPL 87119 and ICPL 8357 by about 10% (data not shown).

The value of RUE found in this study is slightly lower than values found by others. Hughes and Keatinge (1983) regressed biomass produced by a range of treatments differing in stand density and cultivar against cumulative radiation intercepted. However, they did not directly measure f but estimated it from LAI and an assumed k . RUE values obtained were 1.04 g MJ^{-1} for biomass at flowering and 1.23 g MJ^{-1} for maximum biomass. Sivakumar and Virmani (1980) measured an RUE of 1.06 g MJ^{-1} (when converted from their quanta of PAR basis), close to the value obtained in the present study. Muchow (1985b) measured a value of 1.1 g MJ^{-1} from emergence to maturity for cv. Royes under irrigated conditions. The RUE derived in the current study is also slightly lower than the generally accepted maximum RUE values for other tropical grain legumes soybean, peanut, mungbean and cowpea of 0.9–1.0 g MJ^{-1} (Muchow et al., 1993b; Sinclair and Muchow, 1999). It is possible that the RUE from this study is an under-estimate because of an over-estimate in the measure of intercepted radiation. In the current study, radiation interception was measured on a PAR basis, whereas intercepted radiation was accumulated through the season using solar radiation, and not PAR. This will result in an over-estimate of intercepted radiation and an under-estimate of RUE because PAR is intercepted more effectively than solar radiation (see discussion above).

An unbiased estimate of RUE from this study may be closer to 0.9 g MJ^{-1} and hence consistent with other studies of pigeonpea RUE and RUE values for other tropical grain legumes.

4.3. Partitioning between stem and leaf before flowering

The regression relationships between leaf and stem biomass from emergence until flowering showed no effect of cultivar duration on the partitioning between leaf and stem before reproductive growth. Partitioning coefficients varied between 1.03 and 1.14 and are similar to values measured in the tropical grain legumes cowpea, soybean and mungbean (Littleton et al., 1979; Summerfield et al., 1978; Muchow et al., 1993a).

4.4. Rate of increase in harvest index during pod-filling

This study shows that the rate of grain-filling in pigeonpea could be approximated by a linear increase in HI, reported previously for a number of other crops including the grain legumes soybean (Spaeth and Sinclair, 1985), peanut (Hammer et al., 1996; Bennett et al., 1993) and pea (Bindi et al., 1999). There were clear differences among duration groups in the rate of increase and final value of harvest index. The 1990/1991 study showed that the rate of increase in harvest index was less for longer duration, with the value being 0.14, 0.13, 0.07 per day for extra-short, short and medium-duration cultivars, and final harvest index being 0.60, 0.55 and 0.32, respectively. There is little evidence showing an association between growth duration and HI increase in other species. Bennett et al. (1993) found in peanut that three modern cultivars had a similar harvest index increase of 0.006 per day, while an older, later-maturing cultivar had an increase of 0.004 per day. The lower rate of HI increase for later maturing cultivars is associated with their propensity to produce more vegetative growth during pod-filling and also their greater degree of perennality than earlier maturing cultivars (Lawn and Troedson, 1990).

Conventionally, harvest index is calculated as grain weight divided by biomass. In pigeonpea considerable biomass may be lost in fallen leaves before harvest

thus biasing upwards the true estimate of harvest index. Simulation models use harvest index based on grain weight and include senesced leaves, hence there is a need to derive values for use in models from common field measurements. This study shows that fallen leaf accounts for an 11% adjustment. Sheldrake and Narayanan (1979) also showed that the inclusion of fallen leaf can have a significant impact on the calculation of harvest index. In their study, the mean harvest index of medium-duration cultivars was 0.24 excluding fallen material and 0.17 taking fallen material into account.

While long-duration cultivars (140–160 days to flowering) were not included in this study, published values of final HI show that these cultivars follow the trend of declining final HI, and therefore presumably a slower rate of HI increase, with longer maturity group. Kumar Rao and Dart (1987) report HI values for five long-duration cultivars of 0.07–0.14. Lawn and Troedson (1990) show a negative correlation between final HI and time to maturity across a range of studies in India and Australia, and demonstrate that the higher final HI with earlier maturing cultivars is due to the increased proportion of the reproductive phase relative to the vegetative phase.

The association between a low rate of HI increase and propensity for vegetative growth during pod-filling can be used to simulate the continuation of leaf and stem growth concurrently with pod-filling (commonly termed indeterminate growth), by using concepts based upon the supply and demand for assimilate by the grain. The demand for assimilate for grain yield accumulation is defined by the linear increase with time of the harvest index. The ability to meet the grain yield demand is determined by the rate of biomass accumulation and the retranslocation of dry matter that had accumulated in the leaves and stems before the start of pod-filling. If assimilate supply is in excess of grain growth requirements, the excess is used for new leaf and stem growth. Hence this approach would simulate the extent of leaf and stem growth during grain-filling dependant upon the “excess” assimilate available, once the requirements for grain and pod wall growth have been satisfied. In this way, crops, which have a low demand for assimilate for reproductive growth, such as medium and long-duration types (through a low rate of increase in harvest index), will tend to have continued leaf and

stem growth during grain-fill. This approach has promise in solving the problem of Hammer et al. (1996), who noted difficulty in simulating high LAI values in peanut due to unexplained variation in the timing of end of leaf growth.

4.5. Associations between determinants of biomass production across cultivars

Inspection of values for k , RUE and partitioning of biomass to leaf across cultivars reveal some interesting associations. Firstly, there is a negative correlation ($r = -0.69$, $P < 0.05$) between k and RUE using the nine values for the cultivars in the first season. Fig. 3 shows that ICPL 83015 and ICPL 87 have relatively high partitioning to green leaf biomass. Table 2 shows that these two cultivars have the lowest values of k within their respective maturity groups, and they also have relatively high values of RUE. This is in contrast to the Nam et al. (1998) study of six extra-short cultivars who found no significant relation between k and RUE.

5. Conclusions

This study has highlighted important similarities and differences among the main pigeonpea growth duration groups. The radiation extinction coefficient and RUE were consistent across groups, with mean values of 0.53 and ca. 0.9 g MJ^{-1} , respectively. Partitioning between leaf and stem prior to flowering was also consistent across groups. On the other hand, the rate of linear increase in harvest and final harvest index varied across groups, with lower rates of partitioning to grain and final harvest index with the later maturing groups. The consistency of these parameters, that quantify the key processes of radiation interception, biomass accumulation and partitioning, simplifies the task of simulating pigeonpea growth and yield across diverse cultivar groups.

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