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Effects of Timing of Drought Stress on Phenology, Yield and Yield Components of Short-duration Pigeonpea

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With 5 figures and 3 tables

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Abstract

Nine short-duration pigeonpea genotypes were given adequate soil moisture throughout growth or subjected to water stress during the late vegetative and flowering (stress 1), flowering and early pod development (stress 2), or podfill (stress 3) growth stages under field conditions. The stress 1 treatment had no significant effect on the time to flowering. No stress treatment affected maturity or inter-plant flowering synchronization. The interval from a newly opened flower to a mature pod was about 30 days for all genotypes, and was unchanged in plants that were recovering from stress 1 or undergoing stress 2. Seed yield was reduced to the greatest extent by stress 2 (by 37 %) and not significantly affected by stress 3 for all genotypes. No consistent differences were found between determinate and indeterminate genotypes in the ability to maintain seed yield under both stress 1 and stress 2. The harvest index was significantly reduced (22 %) by stress 2 but not by stress 1. However, under each soil moisture treatment, genotypic differences for seed yield were associated largely with differences in total dry matter production (TDM). For all genotypes, the number of pods m^{-2} was the only yield component significantly affected by the water stress treatments. The stability of other yield components should be fully exploited to improve the stability of seed yield under drought conditions (drought resistance). Possible characteristics which may improve the drought resistance of short-duration pigeonpea include the ability to maintain TDM, low flowering synchronization, small pod size with few seeds pod^{-1}, and large 100-seed mass.

Key words: *Cajanus*, drought resistance, pigeonpea, sensitive stage, yield, yield components.

Introduction

Growth and yield of short-duration pigeonpea [*Cajanus cajan* (L.) Millsp.] grown during the rainy season in India is often reduced by intermittent periods of drought stress, and large genotypic differences exist in response to soil moisture availability (ICRISAT, 1988, 1989). Responses of seed yield to drought depend on the growth stage at which drought occurs for many grain legumes (SIONIT and KRAMER, 1977; TURK et al. 1980; ZISKA and HALL, 1983; ACOSTA GALLEGOS and SHIBATA, 1989). Therefore, progress in selection of drought-resistant genotypes (with greater yield stability under drought conditions) may be greatly delayed in situations where the occurrence and duration of drought periods are unpredictable and/or genotypes vary in the rate of phenological development. Establishment of the physiological basis for genotypic differences in drought response can hasten improvements in drought resistance, but this requires a greater understanding of drought effects on parameters essential to yield and mechanisms of drought resistance.

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In many legumes, reductions in seed yield under drought conditions are due largely to reductions in the number of pods m^{-2} (MUCHOW, 1985), and seed yield is more sensitive to drought during the reproductive compared to the vegetative growth stage (SIONIT and KRAMER, 1977; TURK et al. 1980; ACOSTA GALLEGOS and SHIBATA, 1989). More detailed experiments indicate that the period from mid-pod elongation to just before the start of seed enlargement is most critical for seed yield responses to irrigation in soybean (KADHEM et al. 1985a), while the period after flowering is more crucial than that during flowering in *Vicia faba* (GRASHOFF, 1990). Under unpredictable drought conditions, the stability of seed yield will depend on the degree of synchronization and duration of drought susceptible growth stages within genotypes. In short-duration pigeonpea, yields of indeterminate genotypes are relatively more stable under water stress compared to those of the determinate genotypes, but genotypic differences also occur within each group (ICRISAT, 1989), and more information is required to ascertain physiological bases for these differences.

The present study investigates the effects of timing of drought stress on phenology, yield and yield components of nine short-duration pigeonpea genotypes of varying growth habits and drought responses. Drought stress was imposed at different growth stages under field conditions by rain exclusion through automatic rain shelters and controlled irrigation. Subsequent papers will examine growth, abscission, water relations and selected chemical constituents of plant tissues in response to drought.

Materials and Methods

Crop establishment

The experiment was conducted in an Alfisol (Udic Rhodustalf) field at ICRISAT Centre, India (17 °N, 78 °E; 500 m elevation), with shelters that closed automatically to prevent rain on an experimental area of 50 × 25 m. The soil had a maximum plant available water holding capacity of 60–100 mm. It was surface tilled incorporating 100 kg ha^{-1} of diammonium phosphate, and ridges spaced at 0.6 m were established. Prior soil analyses and plant growth tests had established that nutrient deficiencies would be unlikely in this soil and that native *Rhizobium* were adequate to ensure optimum nodulation and nitrogen fixation of pigeonpea. Seeds were hand sown on 7 July 1988, with two plant-rows (0.3 m apart) established on both sides of ridges and a spacing of 0.1 m within rows. Agronomic operations were carried out as necessary for adequate protection against pests, diseases and weeds. During the early growth stages, the experimental plots depended entirely on rainfall, and no supplemental irrigations were given. From 52 days after sowing (DAS), the automatic rain shelters were activated to exclude rainfall and differential irrigation treatments commenced.

Experimental design and treatments

The experiment was laid out as a split-plot design with four replications. The four drought stress timing treatments applied in the main plots were: (a) Control – Optimum moisture (maintained near field capacity) throughout the crop growth period; (b) Stress 1 – Water withheld from 52 DAS until about 50 % leaf abscission in genotype ICPL 87 (88 DAS); (c) Stress 2 – Water withheld from 50 % flowering of ICPL 87 (78 DAS) until about 50 % leaf abscission (102 DAS); (d) Stress 3 – Water withheld from mid-podfill of ICPL 87 (110 DAS) until harvest (133 DAS). Main plots were 10.5 × 3.6 m and were separated from each other by a 1.2 m wide border strip planted to ICPL 87. Water was applied by drip irrigation at intervals of 2–4 days depending on surface soil dryness in control plots. A flow meter on the main irrigation line indicated the amount of water applied on each occasion. Drought stress treatments were applied by closing lateral irrigation lines to specified plots.

Nine short-duration pigeonpea genotypes (subplot treatments) with varying growth habit (I = indeterminate, D = determinate), and other (H = hybrid, E = extra-early) characteristics were used in the study: (1) ICPL 87 – D; (2) ICPL 151 – D; (3) ICPL 85010 – D; (4) ICPL 85045 – I; (5) ICPL 85043 – I; (6) ICPH 8 – I, H; (7) ICPH 9 – D, H; (8) ICPL 84023 – D, E; (9) ICPL 85037 – I, E. Each subplot consisted of four rows (3.5 m long) on two adjacent ridges. For determinate genotypes, the shoot apical growing point is terminated by an inflorescence and pod production is more synchronized compared to indeterminate genotypes. Extra-early genotypes can mature in less than 100 days compared to about less than 140 days for the short-duration genotypes.

Phenology, yield and yield components

Weekly observations were made to determine the time to 25 %, 50 % and 75 % flowering, and time to maturity for each subplot. Treatment effects on time for individual pod development were investigated for control, stress 1 and stress 2 treatments by tagging newly opened flowers with woollen threads at 90 DAS, and time to early pod-wall senescence and mature dry pod stages were recorded. Plants

Table 1. Mean (averaged over moisture treatments) time to 25 %, 50 % and 75 % flowering, and to maturity for seven short-duration pigeonpea genotypes grown under different soil moisture conditions

Genotype	Growth habit[1]	Time to flowering (days) 25 %	50 %	75 %	Time to maturity (days)
ICPL 85043	I	63	68	72	109
ICPL 85037	I	64	70	76	115
ICPL 151	D	67	72	78	118
ICPH 9	D	68	74	82	121
ICPL 85045	I	69	77	83	117
ICPL 87	D	70	81	87	123
ICPH 8	I	78	84	88	119
SE		±0.6	±0.8	±0.8	±1.4

[1] I = Indeterminate, D = Determinate

were harvested by cutting them at soil level at 133 DAS. The net plot consisted of the two middle rows (3 m long) for each subplot. Pods were sun-dried for 2 weeks and then oven-dried at 80 °C for 2 days, while the remaining shoot parts were oven-dried at 80 °C to constant mass. Total dry mass and seed yield were determined for each subplot, and 100-pod subsamples were used to obtain the number of seeds pod^{-1} and 100-seed mass.

Data analysis

Data were analysed using standard analysis of variance procedure using GENSTAT software. Two earliest flowering genotypes, ICPL 85010 and ICPL 84023, produced a second flush of pods by the time of final harvest and were therefore omitted from the analysis.

Results

The total rainfall received between sowing and activation of rain shelters (52 DAS) was 414 mm. In the preceding 5 weeks, the beginning of the rainy season, 146 mm had been received. The total amount of water applied by drip irrigation was 277 mm for control, 229 mm for stress 1, 191 mm for stress 2, and 185 mm for stress 3. Stress 1 coincided with the late vegetative and flowering stages, stress 2 with the flowering and early pod development stages, and stress 3 with the podfill growth stage for most genotypes.

Time to flowering

The times to 25 %, 50 % and 75 % flowering were not significantly affected by stress 1 treatment, and data for all main-plot treatments were pooled for each genotype (Table 1). Among the seven genotypes considered for analysis, ICPL 85043 was the earliest and ICPH 8 the latest to flower, while ICPL 85037 did not behave as an extra-early genotype in the present study. The interval between 25 % and 75 % flowering for determinate genotypes was shortest for ICPL 151 (11 days) and longest for ICPL 87 (17 days), and for indeterminate genotypes was similar for ICPH 8 (10 days) and ICPL 85043 (9 days) (Table 1). The order in which genotypes flowered was maintained for 25 %, 50 % and 75 % flowering (Table 1).

Individual pod development

For flowers tagged at 90 DAS, the time for individual pod development was the same for all genotypes and was not affected by water stress treatments. The duration from a newly opened flower to the early pod wall senescence stage was 27 days (range ± 1 day), and 3–4 days more to the mature dry pod stage in all cases. Ten days after newly opened flowers were tagged, pod length was over 20 mm for all genotypes and was not affected by water stress treatments (data not shown).

Time to maturity

The time to maturity was not significantly affected by any of the water stress treatments, and data for all main-plot treatments were pooled for each genotype (Table 1). Of the seven genotypes considered, ICPL 85043 was the

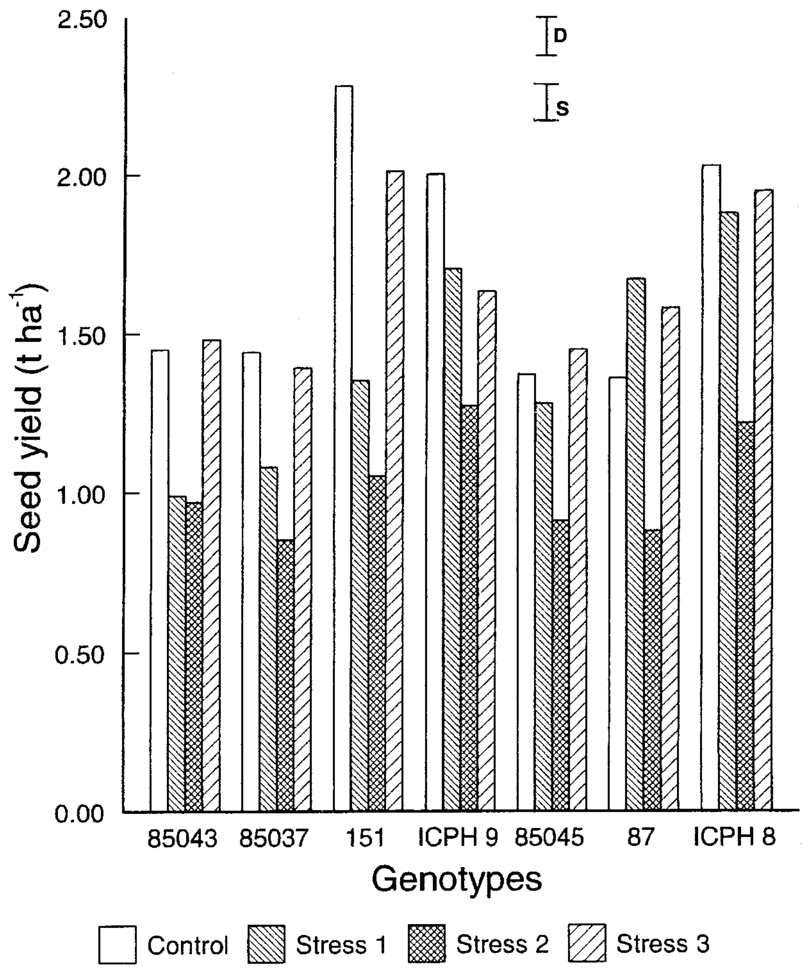

Fig. 1. Effects of drought stress timing on the seed yield of seven short-duration pigeonpea genotypes. Stress 1 was the earliest (52 DAS) and stress 3 the latest (110 DAS) drought treatment applied. Genotypes are arranged from left to right in order of increasing time to 50% flowering. Standard error bars for comparisons at the same (S) or different (D) soil moisture levels are indicated

earliest and ICPL 87 was the latest maturing, and the order in which genotypes matured was different from that in which they flowered. Maturity of the determinate genotypes was slightly more delayed than that of the indeterminate genotypes of comparable flowering times (Table 1).

Seed yield

In the control treatment, seed yield was just over 2.0 t ha^{-1} for ICPL 151, ICPH 9 and ICPH 8, and about 1.4 t ha^{-1} for the other genotypes (Fig. 1). Stress 1 tended to reduce seed yield to a greater extent for earlier flowering compared to later flowering genotypes. Stress 2 reduced seed yield to the greatest extent compared to the other water stress treatments for all genotypes, with ICPL 151 seemingly most affected (Fig. 1). Seed yield was not significantly affected by stress 3 for all genotypes. The interaction between genotype and stress timing was not significant for yield.

Total dry matter and harvest index

For the control treatment, total dry matter production (TDM) was highest for genotypes showing the highest seed yield; it was 7.1 t ha^{-1}

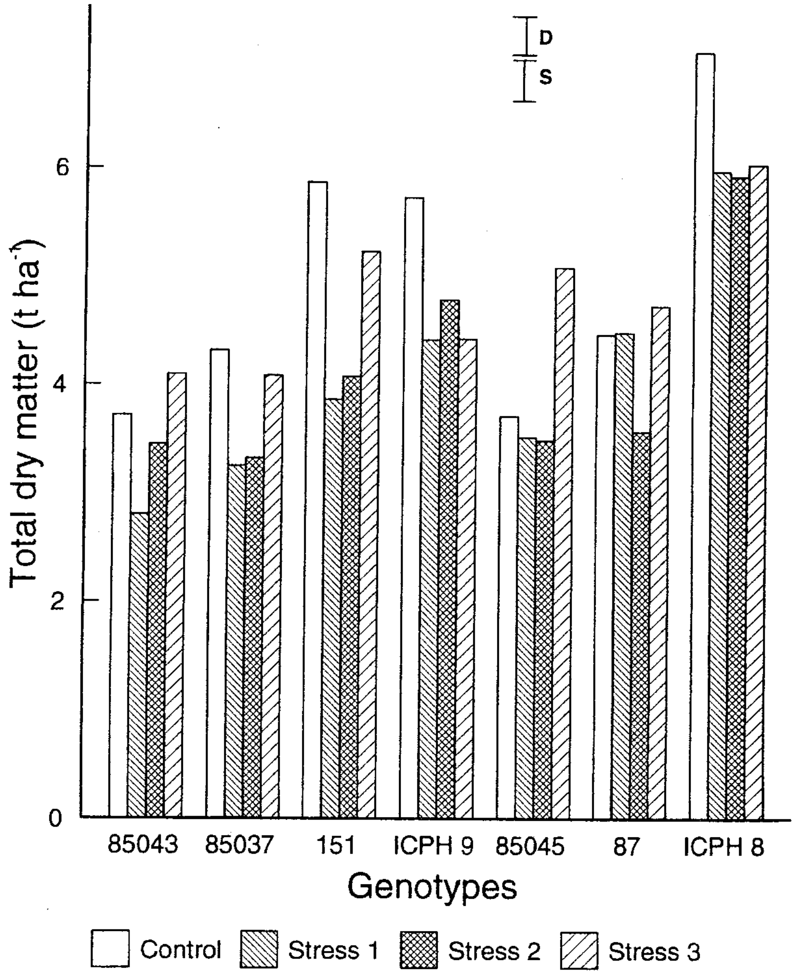

Fig. 2. Effects of drought stress timing on the total dry matter production of seven short-duration pigeonpea genotypes. Relative time to 50 % flowering of genotypes and timing of stress treatments, and error bars are as indicated for Fig. 1

for ICPH 8 and close to 6.0 t ha^{-1} for both ICPL 151 and ICPH 9 (Fig. 2). Generally, TDM was reduced by water stress, with stress 3 having the least effect. TDM appeared to be most affected by stress 2 for the later flowering genotypes, and by stress 1 for earlier flowering genotypes (Fig. 2). The harvest index (HI) was not adversely affected by stress 1 or stress 3 but was greatly reduced by stress 2 (Table 2).

TDM relationship with seed yield

Under the control, stress 1 and stress 3 treatments, there was a strong linear relationship between seed yield and TDM regardless of the genotype and soil moisture regime (Fig. 3). Under stress 2, seed yield became less sensitive to increasing TDM. A closer-fitting relationship between seed yield and TDM was observed under stress 1 and stress 2, compared to that under either control or stress 3 (Fig. 3).

Yield components

The 100-seed mass and the number of seeds pod^{-1} were not significantly affected by the water stress treatments. Therefore, data for all main-plot treatments were pooled for each genotype (Table 3). Among the seven genotypes considered, the 100-seed mass and the number of

Table 2. The effect of drought stress timing on the harvest index (%) of seven short-duration pigeonpea genotypes[1]

Genotype	Control	Stress 1	Stress 2	Stress 3
	Soil moisture treatment			
ICPL 85043	39	36	28	36
ICPL 85037	33	33	26	34
ICPL 151	39	35	25	38
ICPH 9	35	38	26	37
ICPL 85045	37	36	26	30
ICPL 87	31	37	25	33
ICPH 8	28	32	21	32
SE		±1.8[2]		

[1] Genotypes are arranged in order of increasing time to flowering; their growing habits are as indicated in Table 1

[2] For comparing means at the same soil moisture level, SE = 1.7

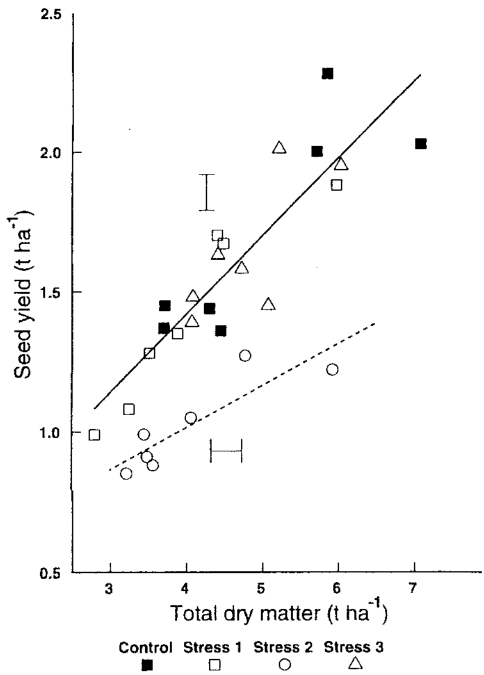

Fig. 3. Relationship between seed yield and total dry matter production for seven short-duration pigeonpea genotypes subjected to different drought stress timing treatments as for Fig. 1. The regression line is $y = 0.3 + 0.28x$; $R^2 = 0.79$ for control, stress 1, and stress 3, and $y = 0.4 + 0.15x$; $R^2 = 0.77$ for stress 2. Both regressions are significant at the 1% probability level. Standard errors for x- and y-values are indicated

seeds pod^{-1} were greatest for ICPL 151 and least for ICPL 85043.

For the control treatment, genotypes ICPH 8, ICPH 9 and ICPL 85043 produced the greatest number of pods m^{-2} (Fig. 4). Pod production was reduced to the greatest extent by stress 2, with no significant effects observed for stress 3. For each genotype, there was a close linear relationship between seed yield and pod number regardless of the soil moisture regime (Fig. 5). This relationship was the same for all genotypes except ICPL 151 and ICPL 85043.

Discussion

Water stress at different growth stages did not significantly affect phenology but had varying effects on seed yield, total dry matter (TDM) and yield components of the short-duration pigeonpea genotypes considered. Although stress 1 received more water than either stress 2 or stress 3, the duration of stress was for a much longer period. Stress 2 and stress 3 received similar amounts of water, but completely different genotypic responses resulted.

For pigeonpea and other grain legumes, long periods of water stress during early vegetative growth have little effect on the time to flowering, but shorten the duration of flowering and pod-filling, resulting in a reduction in the time to

Table 3. Mean (averaged over moisture treatments) 100-seed mass and number of seeds pod^{-1} for seven short-duration pigeonpea genotypes[1] grown under different soil moisture conditions

Genotype	100-seed mass (g)	Number of seeds pod^{-1}
ICPL 85043	6.81	3.3
ICPL 85037	7.65	3.3
ICPL 151	9.79	3.9
ICPH 9	7.67	3.6
ICPL 85045	7.83	3.4
ICPL 87	8.35	3.6
ICPH 8	7.16	3.7
SE	±0.117	±0.05

[1] Genotypes are arranged in order of increasing time to flowering, their growth habits are as indicated in Table 1

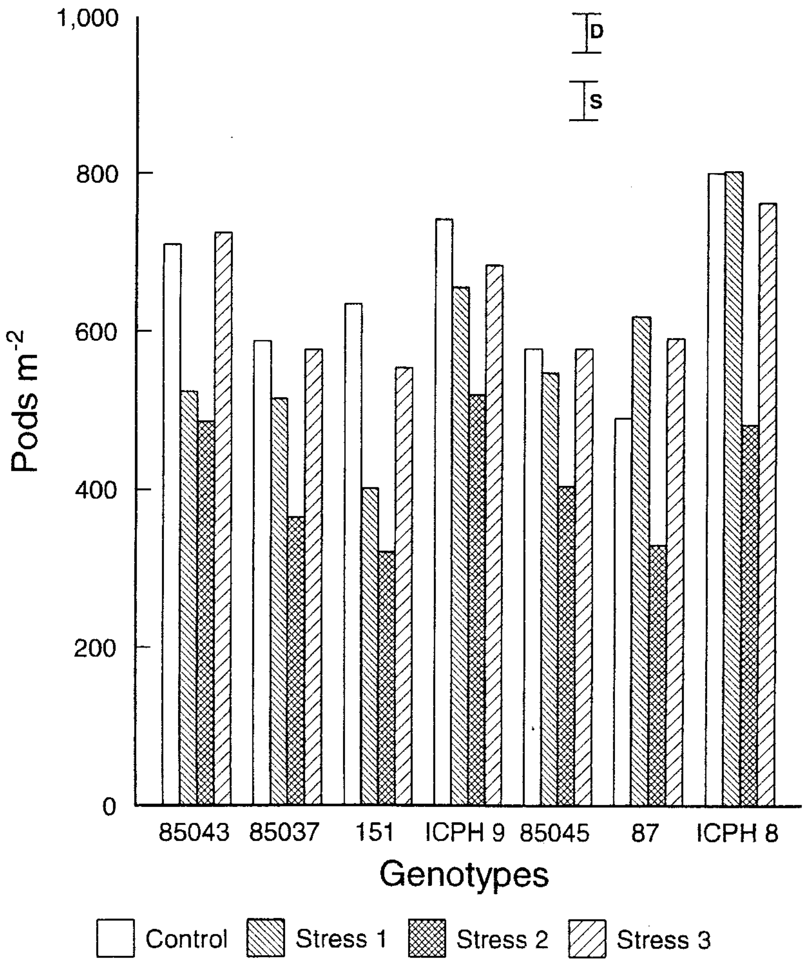

Fig. 4. Effects of drought stress timing on the number of pods m^{-2} of seven short-duration pigeonpea genotypes. Relative time to 50 % flowering of genotypes and timing of stress treatments, and error bars are as indicated for Fig. 1

maturity (MUCHOW, 1985). Terminal water stress beginning from flowering reduces the time to maturity for two short-duration pigeonpea genotypes (ICPL 87 and ICPL 151; LOPEZ et al. 1994), which were also included in the present study. Thus, a more prolonged or severe water stress period than the one in the present study can reduce the duration of reproductive growth in these genotypes. In soybean, there is conservation of seed growth rate during water stress, although the duration of seed fill can be reduced (MECKEL et al. 1984; WESTGATE et al. 1989). No variation in time for individual pod development was observed

High synchronization of reproductive development may lead to low yield stability under drought conditions, and the possibility that drought can occur when all plants are in a particular sensitive growth stage. The duration from 25 % to 75 % flowering gives an indication of inter-plant synchronization of flowering, and intra-plant synchronization of flowering will generally be lower for indeterminate compared to determinate genotypes. Inter-plant synchronization of flowering was greater for the drought susceptible ICPL 151 compared to the tolerant ICPL 87, while for indeterminate genotypes was similar for the drought susceptible ICPL 85043

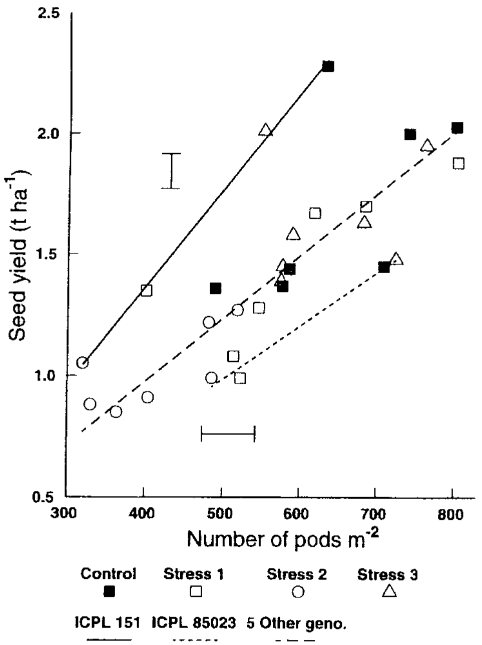

Fig. 5. Relationship between seed yield and the number of pods m^{-2} for seven short-duration pigeonpea genotypes subjected to different drought stress timing treatments as for Fig. 1. The regression line is $y = -0.25 + 0.0041x$; $R^2 = 0.99$ for ICPL 151, $y = -0.18 + 0.0023x$; $R^2 = 0.99$ for ICPL 85043, and $y = -0.06 + 0.0026x$; $R^2 = 0.93$ for the other genotypes. All the regressions are significant at the 1% probability level. Standard errors for x- and y-values are indicated

and the tolerant ICPH 8. In short-duration pigeonpea, a greater yield stability under water stress was associated with the indeterminate compared to the determinate growth habit (ICRISAT, 1989). For improved drought tolerance, lower inter-plant synchronization of flowering may be required for determinate compared to indeterminate genotypes.

Seed yield was more affected by stress 2 than by stress 1, indicating greater resistance to water stress of vegetative compared to reproductive growth stage. The tendency for stress 1 to reduce seed yield more than for the earlier compared to the later flowering genotypes, and the non-significant effects of stress 3 suggest that seed yield was less affected by water stress applied during the late compared to the early reproductive growth stage. Thus, a relatively drought sensitive stage may occur within the late flowering and early pod developmental stages. In other grain legumes, seed yield is relatively insensitive to water stress applied during vegetative growth (TURK et al. 1980; ACOSTA GALLEGOS and SHIBATA, 1989; SPECHT et al. 1989; STIRLING et al. 1989), and in soybean, the period during pod elongation is most sensitive (KORTE et al. 1983; KADHEM et al. 1985a). The similarity in the responses of ICPH 8 and ICPH 9 indicates that drought resistance can be equally high for determinate and indeterminate genotypes. However, the greater drought resistance of these hybrids can be attributed to their high initial growth rates, of both shoots and roots (C. JOHANSEN and Y. S. CHAUHAN, unpubl. data).

Genotypic differences in seed yield under each soil moisture treatment were due largely to differences in TDM, with HI relatively unchanged by stress 1 and stress 3 but greatly reduced by stress 2. The HI can be decreased by drought at the time of flowering and increased when drought occurs at earlier growth stages (PASSIOURA, 1983, 1986; LAWN, 1989). For some grain legumes, both TDM and HI increase linearly with decreasing levels of moisture stress (PANDEY et al. 1984a,b), while in chickpea, increases in seed yield with irrigation during reproductive growth are largely through increases in TDM (SAXENA et al. 1990). There were no consistent differences in the HI between determinate and indeterminate genotypes under all soil moisture treatments, indicating no special advantage of the determinate growth habit for partitioning of shoot dry matter into seed yield under drought conditions. The lack of competing sinks in the semi-determinate compared to indeterminate soybean may allow a more favourable response to water stress imposed during reproductive growth (NEYSHABOURI and HATFIELD, 1986).

Differences in seed yield due to soil moisture treatments were due almost entirely to differences in the number of pods m^{-2} with non-significant changes in the number of seeds pod^{-1} and 100-seed mass. Although the number of pods m^{-2} is the most sensitive among yield components to water stress in many grain legumes, significant changes in the other yield components are also observed (PANDEY et al. 1984a; MUCHOW, 1985; ACOSTA GALLEGOS and SHIBATA, 1989). In pigeonpea, the number of seeds pod^{-1} appears to be the most stable yield component under water stress (KEATINGE and HUGHES, 1981). When two short-duration pigeonpea genotypes are subjected to terminal water stress and partial removal of flowers and pods, the number of seeds pod^{-1} is relatively unchanged compared to changes in the number of pods m^{-2} and 100-seed mass (LOPEZ et al. 1994). In soybean, 100-seed mass is more stable under water stress for determinate compared to indeterminate genotypes (KADHEM et al. 1985b), however, no such differences were observed for short-duration pigeonpea in the present study.

The sensitivity of seed yield to changes in the pods m^{-2} under water stress increases with increasing seed mass pod^{-1} (seeds pod^{-1} × mass seed^{-1}), and was greatest for the high yielding genotype ICPL 151. For improvement in the stability of pods m^{-2}, the high stability of the other yield components should be more fully exploited. Production of large pod walls with many seeds pod^{-1} may exacerbate intra-plant competition for available plant factors at the time of pod set, which can possibly limit seed yield of short-duration pigeonpea under water stress conditions (LOPEZ et al. 1994). Many small pods with fewer but larger seeds may help transfer some of the intra-plant competition among reproductive units to later growth stages because of the lower initial requirements of each expanding pod. However, possible problems due to correlations between seed size and pods plant^{-1}, as occurs in medium-duration pigeonpea (Y. S. CHAUHAN and C. JOHANSEN unpublished data), may have to be overcome.

Zusammenfassung

Einflüsse des Einwirkungszeitpunkts von Dürrestreß auf die Phänologie, den Ertrag und die Ertragskomponenten von frühreifen Taubenerbsen

9 frühreife Taubenerbsengenotypen wurden in einer Kontrolle angemessen mit Bodenfeuchtigkeit während des gesamten Wachstums sowie unter Wasserstreßbedingungen während der späten vegetativen und Blühphase (Streß 1), der Blüte und der frühen Hülsenentwicklung (Streß 2) und der Hülsenfüllphase (Streß 3) unter Feldbedingungen angezogen. Die Streßbehandlung 1 hatte keine signifikante Auswirkung auf den Zeitpunkt der Blüte. Die Streßbehandlung beeinflußte nicht die Reife oder die Synchronisation der Blüte innerhalb des Pflanzenbestandes. Das Zeitintervall zwischen den jeweils sich öffnenden Blüten und reifen Hülsen betrug bei allen Genotypen 30 Tage und änderte sich auch bei Pflanzen, die sich nach den Streßbedingungen 1 oder 2 erholten, nicht. Bei allen Genotypen war der Samenertrag am stärksten bei Streßbedingung 2 (um 37 %) aber nicht signifikant unter Streßbedingungen 3 beeinträchtigt. Es wurden keine konsistenten Unterschiede determinierter und indeterminierter Genotypen hinsichtlich der Fähigkeit zur Aufrechterhaltung des Samenertrages unter Streßbedingungen 1 und 2 gefunden. Der Ernteindex war signifikant unter Streßbedingungen 2 (22 %) reduziert, aber nicht unter Streßbedingungen 1. Bei jeder Bodenwasserbehandlung waren die genotypischen Unterschiede hinsichtlich des Samenertrages assoziiert mit Unterschieden in der Gesamttrockenmasseproduktion (TDM). Bei allen Genotypen war die Anzahl der Hülsen/m^2 die einzige Ertragskomponente, die durch Wasserstreßbehandlungen signifikant beeinträchtigt war. Die Stabilität der anderen Ertragskomponenten sollte ausgesutzt werden, um die Stabilität des Samenertrages unter Dürrebedingungen (Dürreresistenz) zu verbessern. Eigenschaften, die Dürreresistenz von frühreifen Taubenerbsen zu verbessern, könnten die Fähigkeit sein, TDM zu erhalten sowie eine niedrige Blütensynchronisation, geringer Hülsengröße mit wenigen Samen/Hülse und einer hohen 100 Samenmasse aufzuweisen.

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