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Effects of Timing of Drought Stress on Leaf Area Development and Canopy Light Interception of Short-duration Pigeonpea

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With one figure and 7 tables

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Abstract

Leaf area index (LAI), fractional canopy light interception (F) and plant mortality at maturity, were determined for nine short-duration pigeonpea (*Cajanus cajan* [L.] Millsp.) genotypes in response to drought during the late-vegetative and flowering (stress 1), the flowering and early podfill (stress 2), or podfill (stress 3) stages. LAI and F were reduced, but plant mortality did not increase under drought. Stress 2 reduced LAI to the greatest extent, consistent with the effects on seed yield. At the end of stress 1, seed yield was closely related to LAI for the different genotypes in stressed but not in unstressed (control) plots. Reductions in LAI due to reproductive growth were as great or greater than those due to water stress. Indeterminate genotypes had smaller but more leaves per plant compared to the determinate genotypes. The importance of these differences to drought resistance was not apparent. Production of leaves with decreasing specific leaf area throughout plant growth may be advantageous, especially when drought is likely to occur during reproductive growth. Values of F during and following water stress gave an indication of genotypic drought resistance, with the most drought-sensitive genotype showing the largest reduction in F under water stress and the slowest rate of recovery following rewatering. For short-duration pigeonpea, where plant mortality is not a factor under water stress, the maintenance of both LAI and F appears to indicate genotypic drought resistance.

Key words: *Cajanus* — pigeonpea — plant mortality — yield relationship

Introduction

Intermittent periods of drought can reduce growth and yield of short-duration pigeonpea (*Cajanus cajan* [L.] Millsp.) sown at the start of the rainy season in India (ICRISAT, 1988, 1989). Seed yield is most affected by drought occurring in the late flowering and early pod development stages. Genotypic differences in drought resistance are associated with the maintenance of dry mass partitioning into leaves during, and dry mass production following, drought periods (Lopez et al., 1996b). Dry matter production depends on canopy light interception and the efficiency of its conversion into dry matter. Both variables can be reduced when pigeonpea is subjected to water stress (Hughes and Keatinge, 1983). Therefore, plant factors which favour the maintenance of canopy light interception under water stress could make an important contribution to drought resistance, if photosynthetic rates are unaffected.

Canopy light interception is a function of the rates of leaf production, expansion and abscission as well as stand density and arrangement. For many grain legumes, leaf area development (leaf production and expansion) is more sensitive to water stress than leaf abscission (Muchow, 1985a). In faba bean (*Vicia faba* L.), the lower leaf area under water stress is largely due to reduced leaf expansion, with relatively minor effects on leaf production and death (Kara Manos, 1978; Farah, 1981). During vegetative growth in soybean (*Glycine max* [L.] Merr.), mild water stress reduces leaf expansion to a greater extent than leaf production with little apparent affect on leaf senescence. Severe water stress, however, reduces leaf area largely by accelerated leaf senescence (Muchow et al., 1986).

In short-duration pigeonpea, leaf abscission is more sensitive to water stress in cultivars of determinate than in those of indeterminate growth habit (Lopez et al., 1996a). More information is required on the maintenance of leaf area and the canopy light interception under water stress in relation to drought resistance. The present study investigated the effects of drought stress on leaf area development, canopy light interception and plant mor-

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tality of short-duration pigeonpea genotypes of varying growth habits (determinate, indeterminate; early, late) and drought responses.

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 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 drop 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 (sub-plot 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 sub-plot consisted of four rows (3.5 m long) on two adjacent ridges.

Leaf area and plant mortality

Three plants were randomly selected and whole shoots removed from control and stressed plots at termination of stress 1 (88 days after sowing; DAS) and stress 2 (102 DAS), and five plants were similarly removed from all plots at the final harvest (133 DAS). On each occasion, the total leaf area (LA) of one plant from each plot was determined by an area meter (Delta T Devices Ltd, Cambridge, England), and the number of leaves counted for all plants sampled. Leaf dry mass (LM) was determined after drying in an oven at 80°C. The specific leaf area (SLA) was calculated as LA/LM, using all leaves from a single plant, and this was used to obtain LA for the remaining plants sampled (LA = LM × SLA). The leaf area index (LAI) was calculated as the product of the average leaf area plant^{-1} and the number of plants m^{-2}, with the latter determined along with plant mortality at final harvest.

Canopy light interception

Canopy light interception (F) was determined at mid-day by measurements using a quantum sensor (LI-COR Inc., Nebraska, USA) above, and a line quantum sensor (1.0 m long; LI-COR Inc.) below the canopy. Single observation was made in each replication. Measurements of F were made in stressed plots during development and just before termination of the drought treatments, and corresponding measurements were made in control plots on these occasions.

Data analysis

Data were analysed using standard analysis of variance procedure and regression analysis using GENSTAT software. The two earliest flowering genotypes produced a second flush of pods by the time of final harvest and were therefore omitted from the analysis.

Results

Leaf area index (LAI)

Water stress reduced LAI by 25–45 % at the end of stress 1, and by 40–60 % at the end of stress 2 (Table 1). Under stress 1, the LAI was affected most for ICPL 151, and least for the hybrids, ICPH 9 and ICPH 8. Under stress 2, the LAI was most affected for ICPL 87 and least affected for ICPL 151 and ICPH 8. At final harvest, which coincided with the end of stress 3, the LAI was < 1.0 for all genotypes, with very little effect of the soil moisture treatment and high variability among replications (data not shown). There was a significant positive relationship between seed yield in the stress 1 ($r^2 = 0.98$) and stress 2 ($r^2 = 0.63$) treatments whereas no such relationship was apparent between yield and LAI in the respective control treatments (Fig. 1).

Table 1: Effect of water stress on the leaf area index (LAI) of seven short-duration pigeonpea genotypes[1] at the end of stress 1, and stress 2

Genotype	Growth habit[2]	Control	Stress 1	Control	Stress 2
ICPL 85043	I	2.7	1.6	1.3	0.6
ICPL 85037	I	2.8	1.8	1.9	0.9
ICPL 151	D	4.0	3.1	2.4	1.5
ICPH 9	D	4.1	2.9	2.9	1.4
ICPL 85045	I	3.1	2.1	1.9	0.9
ICPL 87	D	4.5	2.9	2.5	0.9
ICPH 8	I	4.9	3.6	3.2	1.9
SE±			0.41 (0.42)[3]	0.29 (0.29)	
CV %			27.0	33.4	

[1] Genotypes are arranged in order of increasing time to flowering
[2] Growth habit: I = Indeterminate, D = Determinate
[3] SE values in parentheses are for comparing means at the same level of treatment

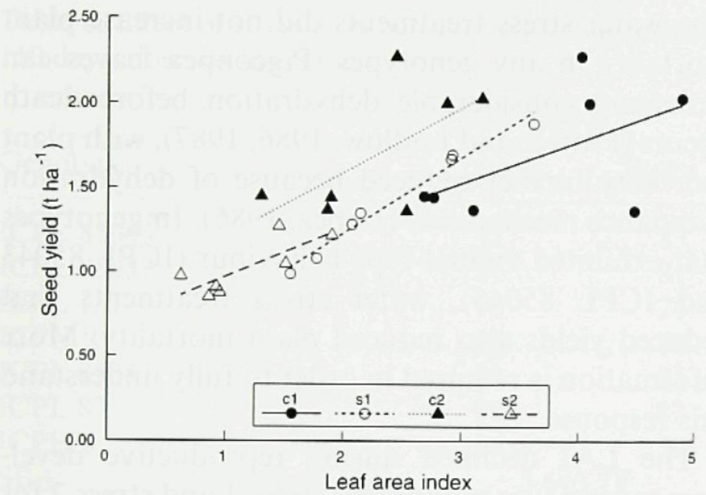

Fig. 1: Effect of water stress on the relationship between seed yield and leaf area index (LAI) of seven short-duration pigeonpea genotypes at the end of stress 1 (c1, s1) and stress 2 (c2, s2) for control (c1, c2) and stressed (s1, s2) plots. Linear regression equations are:-
$y = 0.79 + 0.31 \times$ for c1 ($r^2 = 0.31$); $y = 0.33 + 0.45 \times$ for s1 ($r^2 = 0.98$);
$y = 0.83 + 0.38 \times$ for c2 ($r^2 = 0.42$); $y = 0.68 + 0.29 \times$ for s2 ($r^2 = 0.63$).

Table 2: Specific leaf area (cm^2 g^{-1}) for seven short-duration pigeonpea genotypes[1] at the end of each drought stress treatment[2]

	Soil moisture treatment		
Genotype	Stress 1	Stress 2	Stress 3[3]
ICPL 85043	230.9	175.4	141.3
ICPL 85037	227.0	172.2	132.7
ICPL 151	244.1	210.4	174.8
ICPH 9	235.8	189.2	138.3
ICPL 85045	238.7	189.3	158.4
ICPL 87	221.3	170.2	134.7
ICPH 8	242.78	193.0	154.6
SE±	±6.13	±6.60	±3.47

[1] Genotypes are arranged in order of increasing time to flowering; their growing habits are as indicated in Table 1
[2] Data for control and stressed treatments were pooled for each genotype, since treatment effects were non-significant
[3] At the end of stress 3, pooled data for all soil moisture treatments are given

Leaf characteristics

The specific leaf area (SLA; cm^2 g^{-1}) in the stress treatments was not significantly less than the control at comparable times and therefore means of stress and control treatments are presented (Table 2). Specific leaf area was highest for genotype ICPL 151 and lowest for ICPL 87 or ICPL 85037. Specific leaf area declined from stress 1 to stress 2 for all genotypes, with ICPH 9 showing the greatest and ICPL 151 the least decline.

Water stress reduced leaf number plant^{-1} by 15–35 % under stress 1 and by 20–45 % under stress 2, with the earliest flowering affected most under stress 1 and least under stress 2 (Table 3). Leaf size (cm^2 leaf^{-1}) tended to decline under water stress for most genotypes. The reduction was significant only for ICPL 87 at the end of stress 1, and for ICPH 9 and ICPL 87 at the end of stress 2 (Table 4).

Canopy light interception

During the development of stress 1 (at 71 and 86 DAS), water stress significantly reduced canopy light interception (F) for all genotypes, with ICPL 151 most affected (Table 5). Two weeks after stress 1 was relieved (101 DAS), differences in the F between control and stressed treatments remained significant

Table 3: Effect of water stress on leaf number plant^{-1} of seven short-duration pigeonpea genotypes[1] at the end of stress 2

Genotype	Control	Stress 1	Control	Stress 2
ICPL 85043	64	46	39	26
ICPL 85037	59	44	48	30
ICPL 151	41	27	30	24
ICPH 9	43	30	31	17
ICPL 85045	76	58	59	41
ICPL 87	43	34	27	15
ICPH 8	81	68	79	48
SE±	5.6 (4.7)[2]		4.6 (4.6)	
CV %	18.6		25.1	

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

[2] SE values in parentheses are for comparing means at the same level of treatment

Table 4: Effect of water stress on average leaf size (cm^2 leaf^{-1}) of seven short-duration pigeonpea genotypes[1] at the end of stress 1 and stress 2

Genotype	Control	Stress 1	Control	Stress 2
ICPL 85043	14.7	10.7	9.9	6.8
ICPL 85037	15.4	13.5	12.7	9.6
ICPL 151	31.1	27.1	30.1	25.6
ICPH 9	31.0	29.8	35.0	25.9
ICPL 85045	15.7	12.4	10.5	9.4
ICPL 87	36.2	29.4	22.8	26.0
ICPH 8	20.0	18.1	14.8	15.5
SE±	1.38 (1.34)[2]		2.06 (2.06)	
CV %	12.3		21.8	

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

[2] SE values in parentheses are for comparing means at the same level of treatment

only for genotypes ICPL 85043 and ICPL 151, and one week later only for ICPL 151. During the development of stress 2, water stress reduced the F for all genotypes, with the exception of ICPL 85043 and ICPL 85037 at 93 DAS, and ICPL 85037 at 101 DAS (Table 6). One week after the relief of stress 2 (at 110 DAS), water stress induced differences in the F persisted for all genotypes, with ICPL 85037 remaining relatively unaffected. Stress 2 affected the F of ICPL 151 to the greatest extent compared to the other genotypes, and ICPL 151 showed the least recovery one week after water stress was relieved. For most genotypes, the F continued to decrease in the stress treatments after the relief of stress 2, with the decline being greatest for ICPL 151.

Plant mortality

With adequate soil moisture throughout growth, plant mortality was lowest for the latest flowering genotypes, ICPL 87 and ICPH 8, and was significantly higher for the earlier flowering indeterminate genotypes (Table 7). The water stress treatments did not increase plant mortality. Plant mortality was actually reduced when ICPL 85043 and ICPL 85045 were subjected to stress 1 and/or stress 2. For all genotypes at the time of harvest, all dead plants had fully mature dry pods.

Discussion

The water stress treatments did not increase plant mortality in any genotypes. Pigeonpea leaves can withstand considerable dehydration before death occurs (Flower and Ludlow, 1986, 1987), with plant mortality further reduced because of dehydration avoidance mechanisms (Lopez, 1986). In genotypes that exhibited annual-type behaviour (ICPL 85043 and ICPL 85045), water stress treatments that reduced yields also reduced plant mortality. More information is required in order to fully understand this response.

The LAI declined during reproductive development and was reduced by stress 1 and stress 2 for all genotypes. Water stress induced reductions in growth and yield of several grain legumes are associated with reductions in LAI (Pandey et al., 1984; Muchow, 1985a; Acosta Gallegos and Shibata, 1989). Genotypic differences in drought resistance were reflected in the ability to maintain LAI particularly under stress 1. The decline in LAI due to reproductive development was greater than that due to stress 2 for all genotypes, and drought resistance can possibly be improved by reducing this growth stage effect, perhaps as exemplified by ICPH 9.

In pigeonpea, yield is related to the length of time spent at LAIs at which F is large (Hughes et al., 1991). The reduction in LAI of the control treatment between 88 and 102 DAS was primarily due to leaf abscission (Lopez et al., 1996b), and was as large as the reduction due to water stress at the end of stress 1. Abscising leaves might contribute to yield by meeting the mineral N requirements of the developing seeds through remobilization (Kumar Rao and Dart, 1987). A lack of correlation between leaf area and yield in the control may be because the remaining leaf area is still above critical LAI for these

Table 5: Effect of stress 1 on the fractional canopy light interception of seven short-duration pigeonpea genotypes[1] at 71, 88, 101 and 110 days after sowing (DAS)

Genotype	71 DAS		86 DAS		101 DAS		110 DAS	
	Control	Stress 1	Control	Stress 1	Control	Stress 1	Control	Stress 1
ICPL 85043	89	69	92	79	89	73	76	66
ICPL 85037	60	84	90	76	85	83	77	77
ICPL 151	94	66	96	77	96	77	88	68
ICPH 9	93	80	95	85	91	90	84	81
ICPL 85045	86	74	95	87	81	77	71	69
ICPL 87	91	71	95	84	94	86	83	75
ICPH 8	97	75	96	86	88	83	83	74
SE±	4.9 (4.5)[2]		2.2 (2.1)		4.2 (4.0)		5.0 (4.7)	
CV %	11.3		4.8		9.9		13.3	

[1] Genotypes are arranged in order of increasing time in flowering; their growth habits are as indicated in Table 1
[2] SE values in parentheses are for comparing means at the same level of treatment

Table 6: Effect of stress 2 on percent light interception of seven short-duration pigeonpea genotypes[1] at 93, 101 and 110 days after sowing (DAS)

Genotype	93 DAS		101 DAS		110 DAS	
	Control	Stress 2	Control	Stress 2	Control	Stress 2
ICPL 85043	91	83	89	64	76	56
ICPL 85037	86	81	85	77	77	64
ICPL 151	95	74	96	65	88	40
ICPH 9	94	80	91	72	84	55
ICPL 85045	88	75	81	64	71	52
ICPL 87	96	82	94	71	83	63
ICPH 8	94	79	88	67	83	64
SE±	3.6 (3.7)[2]		4.2 (4.0)		5.0 (4.7)	
CV %	9.1		9.9		13.3	

[1] Genotypes are arranged in order of increasing time to flowering; their growth habits are as indicated in Table 1
[2] SE values in parentheses are for comparing means at the same level of treatment

Table 7: Effect of drought stress timing on plant mortality (%) of seven short-duration pigeonpea genotypes[1]

Genotype	Soil moisture treatment			
	Control	Stress 1	Stress 2	Stress 3
ICPL 85043	27 (30)[2]	23 (29)	8 (16)	23 (28)
ICPL 85037	9 (17)	9 (17)	6 (12)	7 (13)
ICPL 151	6 (10)	7 (13)	2 (5)	2 (9)
ICPH 9	4 (9)	6 (11)	1 (5)	1 (4)
ICPL 85045	31 (33)	17 (23)	11 (18)	28 (32)
ICPL 87	1 (2)	2 (6)	2 (8)	1 (5)
ICPH 8	1 (2)	1 (4)	2 (6)	2 (5)
SE		(±3.1)		

[1] Genotypes are arranged in order of increasing time to flowering; their growing habits are as indicated in Table 1
[2] Angular transformed values are given in parentheses

pigeonpea genotypes. By contrast, in the stress treatments remaining leaf area index may have declined below the critical LAI. The low incidence of pod abscission (Lopez et al., 1996b), and high stability of seeds pod^{-1} and 100-seed mass (Lopez et al., 1996a) suggest that sufficient leaf area is retained to complete the maturation of expanded pods under both stressed and control conditions. The specific leaf area (SLA) declined from the end of stress 1 to the time of final harvest, but was not significantly affected by the water stress treatments. A reduction in the SLA is generally observed for grain legumes under water stress (Turk and Hall, 1980; Pandey et al., 1984; Muchow, 1985a), possibly indicating thicker leaves which aids in leaf water conservation because of the lower surface/volume ratio. Genotype ICPL 151 maintained the highest SLA during reproductive development, while the SLA for ICPH

9 showed the greatest decline. Compared to other grain legumes, the juvenile plant growth rate of pigeonpea is relatively slow (Brakke and Gardner, 1987), and a high SLA during early growth may allow a more rapid canopy development, since more leaf area is produced per unit investment in leaf dry mass. As crop development proceeds, production of leaves with increasingly lower SLA may allow a more favourable response to drought at later growth stages.

Leaf size was greater and the number of leaves plant^{-1} smaller for determinate compared to indeterminate genotypes, and both parameters tended to decline during reproductive development or under water stress. Reduction in the average leaf size during development occurs because later produced leaves are smaller while the older leaves that abscise are larger. Since leaf abscission increases under water stress (Lopez et al., 1996a), a more uniform leaf size during crop development will minimize reductions in LAI due to smaller average leaf size. Leaf size was significantly reduced by both stress 1 and stress 2 for the late flowering, determinate genotype, ICPL 87, but not for indeterminate genotypes of comparable flowering times. For the traditionally indeterminate faba bean, reduced leaf expansion is largely responsible for LAI reduction under water stress (Karamanos, 1978; Farah, 1981). Although leaf loss is less sensitive to water deficits compared to leaf area development for several grain legumes (Muchow, 1985a), reduced F under severe water stress is largely due to accelerated leaf senescence (Muchow et al., 1986). For the maintenance of LAI under water stress, the comparative advantage of having a large number of small leaves or a small number of large leaves is not indicated by the present data.

The canopy light interception (F) declined after 101 DAS and was reduced by water stress for most genotypes. For ICPL 151, F was reduced to the greatest extent and recovery following rewatering was slowest in response to both stress 1 and stress 2, compared to the other genotypes. Reduction in F can result from leaf and flower drop (Lopez et al. in prep. b) as well as from leaflet paraheliotropy which increases under water stress (Meyer and Walker, 1981; Oosterhuis et al., 1985). During recovery from water stress the resumption of vegetative and/or reproductive growth and leaflet diaheliotropy possibly delayed the age-related decline in F observed to a larger extent in control plants. The results indicate a more desirable response to water stress in ICPH 9 compared to ICPL 151 among the determinate, and in ICPL 85037 compared to ICPL 85043 among the indeterminate genotypes. The response of F to water stress represents the combined responses of plant mortality, leaf orientation, vegetative and reproductive growth and abscission. Therefore, F may be the ideal variable which integrates most of the important effects of water stress on plant factors influencing seed yield, and is a potential tool in field drought tolerance screening. However, there must be effective control of other environmental factors, particularly pests and diseases, which may also affect F. For short-duration pigeonpea, plant mortality appears to be less sensitive to water stress compared to leaf area at the end of a water stress period during late vegetative and early reproductive growth.

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Zusammenfassung

Einflüsse des Einwirkungszeitpunktes von Dürrestreß auf die Blattflächenentwicklung und die Lichtinterzeption des Bestandes bei frühreifen Taubenerbsen

Der Blattflächenindex (LAI), die Anteile der Lichtinterzeption des Bestandes (F) und die Absterberate der Pflanzen zur Reife wurden für 9 frühreife Taubenerbsen (*Cajanus cajan* (L.) Millsp.) -Genotypen in ihrer Reaktion auf Dürre während der späten vegetativen und Blühphase (Streß 1), der Blüte und der frühen Hülsenfüllphase (Streß 2) und der Hülsenfüllphase (Streß 3) untersucht. LAI und F wurden reduziert; die Pflanzensterblichkeitsrate nahm aber unter Dürrebedigungen nicht zu. Unter Streßbehandlung 2 war LAI am stärksten zusammen mit den Einflüssen auf den Samenertrag reduziert. Am Ende der Streßbehandlung 1 war der Samenertrag straff korreliert mit der LAI der unterschiedlichen Genotypen unter Streßbedingungen, nicht aber in der Kontrolle ohne Streßbedingungen. Die Reduktionen in LAI als Folge des reproduktiven Wachstums waren so groß oder größer als diejenigen der Folge von Wasserstreßbedingungen. Indeterminierte Genotypen hatten kleinere aber dafür mehr Blätter je Pflanze im Vergleich zu den determinierten Genotypen. Die Bedeutung dieser Unterschiede hinsichtlich der Dürreresistenz war nicht erkennbar. Die Produktion von Blättern mit einer abnehmenden spezifischen Blattfläche während des Pflanzenwachstums kann vorteilhaft sein, insbesondere wenn die Wahrscheinlichkeit besteht, daß Dürre während der

reproduktiven Phase auftritt. Die Werte für F während und nach Wasserstreßbedingungen geben einen Hinweis auf die genotypische Dürreresistenz, wobei die Genotypen mit der am stärksten ausgeprägten Dürreempfindlichkeit die stärkste Reduktion von F unter Wasserstreßbedingungen und die geringste Rate der Erholung nach der erneuten Bewässerung zeigten. Für frühreife Taubenerbsen, bei denen die Pflanzenabsterberate kein Faktor unter Wasserstreßbedingungen ist, scheinen das Aufrechterhalten der LAI und F auf eine genotypisch bedingte Dürreresistenz hinzuweisen.

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