Responses of Groundnut Genotypes to Drought

1894

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Abstract

Drought-stress effects on groundnuts depend primarily on the stress pattern because genotypic variation is usually of secondary significance. The differential responses of groundnut cultivars to drought are therefore assessed relative to the mean response of all genotypes to drought. Since three major aspects of drought, (i.e., duration, intensity, and timing relative to crop phenophases) may vary independently, the main effects of these components on groundnut are described.

The timing of drought has a large impact on the variation about the mean response. In general, the sensitivity of a genotype to drought increases with yield potential, increasing the closer the drought ends to final harvest.

Genotypic variation in response to drought exists in the water-use ratio (WUR) of genotypes, with some being able to accumulate up to 30% more shoot dry matter than others with the same total transpiration. Variations also exist in the proportion of this dry matter that is used for pod growth.

Large variations in the response of genotypes to midseason droughts are due to recovery differences after the drought is relieved. The physiological reasons for recovery differences are under investigation.

In addition, a three-factor interaction of genotype, gypsum, and drought exists because the gypsum may increase early pod development, thus providing escape effects.

Résumé

Réponses des génotypes d'arachide à la sécheresse : *Les effets du manque d'eau sur l'arachide dépendent principalement de la nature du manque, car les variations dues aux génotypes sont secondaires. La réponse différentielle des cultivars d'arachide à la sécheresse a été évaluée d'après l'effet moyen de tous les génotypes. Puisque trois caractéristiques majeures des sécheresses (durée, intensité, occurrence par rapport aux phénophases) peuvent être indépendantes, les principaux effets de ces composantes sur l'arachide seront décrits.*

La période où la sécheresse survient à un effet important sur la variation de la réponse moyenne. En général, la sensibilité à la sécheresse d'un génotype augmente avec son potentiel de rendement et s'accroît lorsque la sécheresse survient à la récolte.

Des différences de réponse des génotypes existent dans le taux d'utilisation de l'eau, certains étant capables d'accumuler jusqu'à 30% de matières sèches supplémentaires, avec la même transpiration. Des variations sont notées aussi dans la proportion de cette matière sèche utilisée pour la croissance des gousses.

Nous avons observé de fortes variations de la réponse des génotypes aux sécheresses de mi-saison, que

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nous avons attribué à des différences dans la récupération après la fin de la sécheresse. Les raisons physiologiques des différences dans la récupération sont étudiés.

De plus nous avons observé qu'une interaction génotypes-gypse-sécheresse existe, à cause de l'effet du gypse sur la phase initiale du développement des gousses, mettant en jeu un effet de "fuite".

Introduction

Agriculturally significant droughts usually occur when normally expected rains fail. This failure is largely random. Other speakers will discuss methods of determining expected amounts of rain, the probabilities of these amounts occurring, along with the factors that determine how long this water is able to support growth. Lack of rain may cause drought at any or many stage(s) of development (timing), may vary the evapotranspirational demand relative to the water shortage (intensity), and may also vary the duration of drought experienced by the crop.

There is also substantial morphological variation between groundnut genotypes. Plant types range from prostrate runners to upright bunch types. The valencias have only four branches, while the virginia type may have numerous branches. Individual leaflet area may vary 10-fold, while the time to maturity may vary from 80-180 d. The size and nature of the root system may also vary substantially (Ketring 1984). Previous research has major limitations within this field since either only one genotype has been utilized for comprehensive physiological studies (Pallas et al. 1979, Nageswara Rao et al. 1985) or, when several genotypes have been tested, the results were not in sufficient depth to allow a comprehensive understanding of the crop within its environment. For this reason the bulk of the research results presented are those obtained from our research at ICRISAT Center.

General Responses

Of the many investigations of groundnut responses to drought, very few have been able to establish generalized response patterns. The response may vary with the timing of the drought. However, results have not been consistent because of differences in either genotypes or in growing conditions. Billaz and Ochs (1961) found that midseason drought decreased yields more than end-of-season drought, while Pallas et al. (1979) and Nageswara Rao et al. (1985) found that end-of-season drought yields were lower. The latter authors also reported the possibility of higher yields from stress during the preflowering phase.

Since there are innumerable combinations of the timing, intensity, and duration of drought, and these apparently elicit different responses from different genotypes, generalizations are necessary to describe both the droughts and the variations of genotypic response. In our drought screening we have examined some 800 genotypes, exposing them to three combinations of timing and duration (patterns) of drought, and to six or eight intensities of drought within each pattern. Our drought patterns ha[illegible]en designed to simulate commonly occurring droughts of the SAT (end-of-season, midseason, and long-term drought). In these drought patterns the pod yields generally decreased in a linear fashion as the intensity of drought increased.

Since this method involved screening of genotypes in only three selected 'typical' droughts, a further experiment examined the performance of a selected number of genotypes across a wider range of droughts. Twenty-two genotypes (of similar maturity) identified in the drought-screening process as either resistant, average, or susceptible to drought were used. The genotypes were then subjected to 12 different drought patterns (Fig. 1), which varied both the duration and the timing of single and multiple drought phases relative to phenological development. By using the line-source (LS) technique (Hanks et al. 1976), the drought intensity was varied progressively from a nonstressed control plot (nearest to the sprinkler line) to a plot that received no wat[illegible]r the duration of the drought. Irrigation was ma[illegible]d so that the control plot did not show wilting symptoms at midday.

When the drought intensity was expressed as the irrigation deficit relative to the Class A pan evaporation during the drought period, the nonstressed control treatments had deficits which ranged from 20-40%. This deficit level, despite the nonstressed condition maintained by irrigation, is due to incomplete canopy and to water-utilization pattern of the plants from the soil profile, which was fully charged at the start of the stress periods. For comparison

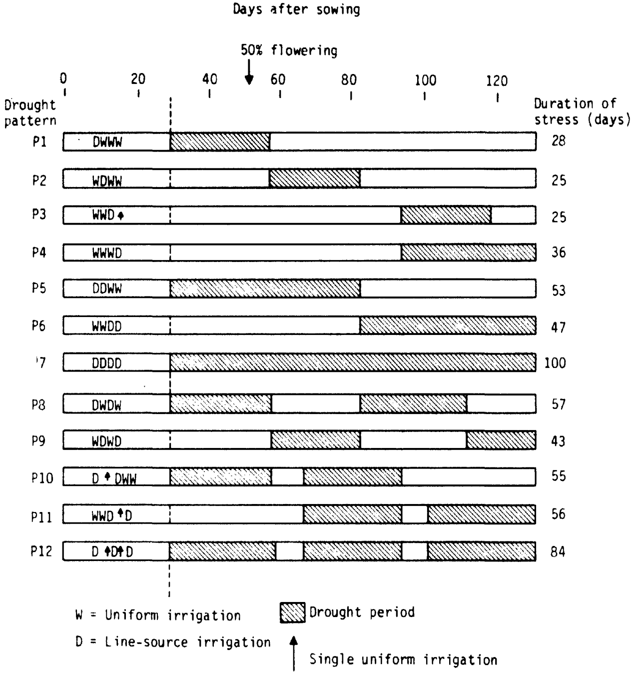

Figure 1. Timing and duration of single and multiple droughts.

purposes, yield potential achieved in nonstress control plots are estimated at 30% water deficit (Y_{30}). The pod yield decreased in most patterns in a linear fashion from yields in nonstressed conditions. Sensitivity to drought has been estimated using linear regression as the average yield loss per unit of water deficit ("b" slope or term of the regression). Only in the very long-term stresses was there a curvilinear response of pod yield to increasing drought intensity (Fig. 2).

When analyzing the mean response of these *fastigiata* genotypes, we found that depending on whether or not the early phase in crops' life (until shortly after the first flowers had been produced) had been stressed, the response to any subsequent droughts was modified (Fig. 3). Besides this, the timing of the drought had little effect on the mean response of all the genotypes to drought. Ninety percent of the yield variations were accounted for by the intensity (I) of drought, and the cumulative duration of stress(es)

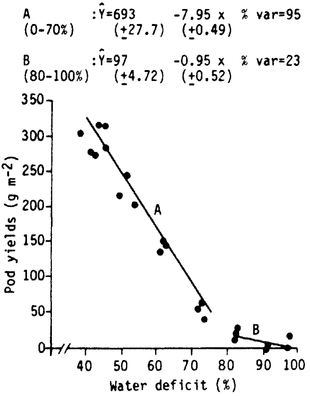

Figure 2. The effect of drought intensity on pod yields in a long-duration drought (P7).

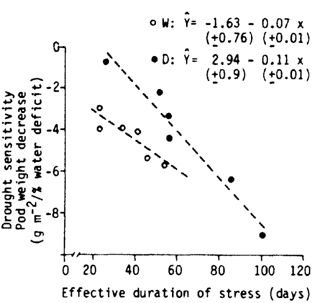

Figure 3. Effect of irrigation or drought during the preflowering stage on the sensitivity of groundnuts (mean of 22 cultivars) to droughts of different durations.

(D). Depending on whether or not the early phase was stressed, the predicted yield (Y) was indicated by one of the following two equations:

Equation 1 (early stress)

$\hat{Y}$ = 306 + 1.52 I + 3.087 D − 0.085 I × D.
SE: (±29.4) (±0.433) (±0.476) (±0.0069)
Variance accounted for = 87%

Equation 2 (no early stress)

$\hat{Y}$ = 370 + 1.33 I + 3.676 D − 0.076 I × D
SE: (±23.6) (±0.33) (±0.625) (±0.008)
Variance accounted for = 93%

Genotype Yield Responses

To examine the relative performances of these genotypes in all these drought combinations is a formidable task. To simplify the process, the yields from nonstressed conditions and the relative yields when the irrigation deficit was 70% (Y_{70}) are discussed. (Relative yield is based on the regression-estimated yield in these conditions converted to a percentage of the mean yield, which is also provided). In the droughts, the mean Y_{70} varied significantly between the patterns of drought, which is why relative yields (Tables 1 and 2) allow an easier evaluation of varietal performance across drought patterns.

It is apparent that the lines tested could be classified into three groups: those with below-average yields in all types of drought, those either resistant or sensitive to specific drought patterns, or those resistant to all droughts.

However, it is not useful to compare the relative performance of genotypes at a 70% irrigation deficit and examine drought responses without considering yield in nonstressed conditions (Y_{30}). A genotype may perform poorly in both a drought and a nonstressed condition. For instance, yield of genotype JL 24 was 18% below average at 30% deficit and at 70% deficit in five other patterns. The Senegalese genotype EC 109271 (55-437) yielded 10.7% [illegible]e average in nonstressed conditions, only 2% above average in pattern 1, but 25% above average in pattern 2, 20% in pattern 3, and 87% in pattern 4.

TMV 2, that yielded 12.7% above average in nonstressed conditions, was 20% above average in drought pattern 1, 10% above average in drought pattern 2, and 3% above average in drought pattern 3.

Another feature of these results was that the genotypes with high yields in the nonstressed conditions were sensitive to many of the drought patterns. This

Table 1. Changes in pod yields (as a percentage of the mean of 22 genotypes) in nonstressed conditions (30% water deficit) and stressed conditions (70% water deficit) in different drought patterns.

Cultivar	Relative mean pod yield at 30% deficit	Relative mean pod yields at 70% deficit in drought patterns P_1 to P_6					
		P_1	P_2	P_3	P_4	P_5	P_6
CGC 4063	-9.0	-18.4	-4.1	-13.4	-15.2	-12.1	5.5
J 11 × Robut 33-1	8.5	15.8	4.1	1.8	8.7	14.6	21.5
ICGS 24	11.2	3.3	8.6	7.9	5.9	5.3	-1.2
ICGS 36	-10.0	-5.0	-14.0	-4.1	-0.6	-6.6	-11.0
ICGS 11	4.2	-3.9	-0.7	-8.8	-5.4	-11.1	17.7
ICGS 35	-4.9	-33.3	-3.2	-6.6	-21.3	12.1	-1.3
ICGS 21	-4.5	10.7	-11.1	1.4	-18.6	-7.3	3.9
X41 × 1 B × Goldin 1	11.9	10.3	7.2	5.0	4.1	10.1	1.5
Manfredi × X 14-4 B 19 B	-1.6	3.5	3.5	1.3	-10.3	-8.4	11.1
TMV 2	13.6	7.6	14.7	25.3	12.9	16.4	12.4
Faizapur 1-5-2	-21.9	-7.3	-33.8	-10.7	-4.3	-19.3	-11.3
J 11	-6.4	-4.7	-14.0	-9.8	-4.8	-7.7	-9.5
NC Ac 17090	8.2	5.9	7.3	8.7	-1.4	4.7	2.2
NC [illegible] 17142	9.2	7.9	1.6	15.3	0.7	15.4	7.3
Ga[illegible]puri	24.1	20.4	25.7	19.0	9.5	21.4	24.2
EC 76444	-0.3	-0.5	-9.6	1.1	-2.4	14.0	-16.4
EC 109271(55-437)	10.7	2.3	24.7	19.8	87.5	17.9	-4.6
EC 21024	13.3	4.9	-2.2	-8.8	-6.6	22.6	-16.2
Manfredi 107	12.4	-10.8	5.8	-18.1	-18.5	-9.8	-26.5
Krapovicas Str 16	-11.8	0.2	-1.2	0.7	-4.5	11.6	5.9
NC Ac 16129	12.7	19.8	10.3	3.3	16.7	9.6	5.0
JL 24	-18.3	-28.9	-19.7	-30.3	-31.9	-25.0	-19.9
Mean Pod wt (g m^{-2})	403.8	367.8	320.1	189.1	195.7	242.9	175.8

prompted us to examine the genotypes for a relationship between yield in nonstressed conditions and drought sensitivity. For some drought patterns the nonstressed yield was very closely related to drought sensitivity, while in others these two components were not closely related. When the interval between the release of drought and final harvest was large (i.e., early droughts), yield sensitivity generally was not well correlated to yield potential, but when stress occurred during the grain-filling phase, the correlation was good. The association between the time when drought ended and the correlation coefficient between genotype sensitivity to drought and yield potential is presented in Figure 4.

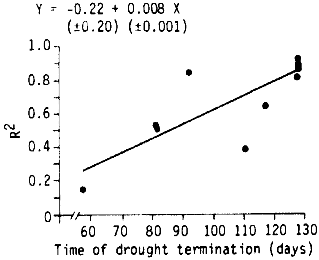

Figure 4. Effect of when drought ends on the amount of variation in drought sensitivity that is accounted for by the yield potential of genotypes. The Y axis is the regression coefficient for the relationship between sensitivity to drought and yield potential.

Physiological Differences between Genotypes

In addition to these agronomic studies, a more detailed examination was made of the basic physiological responses of four contrasting genotypes in a limited range of drought conditions. This was a joint research project with the University of Nottingham, funded by the British Overseas Development Administration (ODA) and ICRISAT.

By comprehensive measurement of the crop environment, the sources of yield variation between genotypes were examined in detail. Water-extraction patterns and total water use, radiation-interception patterns, and the growth and reproductive responses to the imposed droughts have been described (D. Harris, and R. Matthews, University of Nottingham, personal communication, 1985).

Although there was evidence for rooting variations in these four genotypes in an Alfisol, the total water transpired did not differ (Table 3). However, there were differences in the efficiency of water use from different soil horizons. NC Ac 17090 was able to use water in the surface horizons faster than the other cultivars, suggesting an advantage for this genotype when rainfall is likely to be confined to small showers that only wet the upper horizons. Robut 33-1 extracted water earlier from deeper horizons (Fig. 5), an ability which might be important where the soil depth does not limit root growth and the amount of available water.

The amount of dry matter accumulated by a crop is closely related to the amount of water transpired (WUR). For groundnuts, 1.7-1.9 g of shoot material are accumulated per kg of water transpired (Kassam et al. 1975, Nageswara Rao et al. 1985). However, the WUR of these genotypes varied significantly, with the drought-susceptible line EC 76446(292) accumulating 30% less shoot dry matter than the other genotypes, although the same amount of water was used. These differences in water-use efficiency (WUE) were associated with other responses to water-status, including effective-radiation load shedding by leaf folding during severe stress.

However, the largest differences between these genotypes were the effects of drought on their reproductive growth. TMV 2, that produced the [illegible]

Table 2. Changes in pod yields (as a percentage of the mean of 22 genotypes) in nonstressed conditions (30% water deficit) and stressed conditions (70% water deficit) in different drought patterns.

Cultivar	Relative mean pod yield at 30% deficit	Relative mean pod yields at 70% deficit in drought patterns P_7 to P_{12}					
		P_7	P_8	P_9	P_{10}	P_{11}	P_{12}
CGC 4063	-9.0	-9.7	-10.1	-12.2	-4.7	-19.0	-11.8
J 11 × Robut 33-1	8.5	-4.4	-3.5	12.1	24.8	14.1	17.8
ICGS 24	11.2	-6.5	12.0	2.5	19.1	7.2	13.1
ICGS 36	-10.0	1.4	-8.0	-11.4	-21.1	-8.2	0.2
ICGS 11	4.2	24.9	12.7	10.3	-0.6	-7.9	-0.1
ICGS 35	-4.9	-20.6	-2.3	-10.7	-6.9	-0.9	-15.4
ICGS 21	-4.5	-11.3	-17.4	5.1	-0.2	-15.8	-1.4
X41 × 1 B × Goldin 1	11.9	0.9	17.8	15.3	6.5	8.4	15.5
Manfredi × X 14-4 B 19 B	-1.6	3.4	0.0	3.4	3.4	-6.2	9.1
TMV 2	13.6	-1.1	-23.2	-9.6	-38.7	-9.7	-9.2
Faizapur 1-5-2	-21.9	21.0	24.7	27.2	0.7	23.3	[illegible]
J 11	-6.4	2.4	-21.4	-2.1	-15.5	-8.6	-1.7
NC Ac 17090	8.2	0.1	3.3	4.2	10.6	-5.0	0.5
NC Ac 17142	9.2	-2.6	16.9	2.7	2.1	12.8	10.6
Gangapuri	24.1	24.9	38.2	30.5	31.3	20.2	16.6
EC 76444	-0.3	10.5	-10.4	-11.1	-6.4	1.1	-0.0
EC 109271(55-437)	10.7	11.7	8.5	4.2	16.0	12.6	1.4
EC 21024	13.3	8.0	-7.2	-15.5	3.0	-6.8	-15.5
Manfredi 107	12.4	-16.6	-6.5	-25.9	-16.3	-0.0	-24.6
Krapovicas Str 16	-11.8	5.7	-5.8	-15.3	-7.5	-5.3	-2.6
NC Ac 16129	12.7	0.1	26.1	14.0	14.3	11.7	24.5
JL 24	-18.3	-26.1	-19.1	-17.6	-12.3	-19.6	-23.8
Mean Pod wt (g m^{-2})	**403.8**	**120.6**	**203.5**	**209.3**	213.9	199.2	161.9

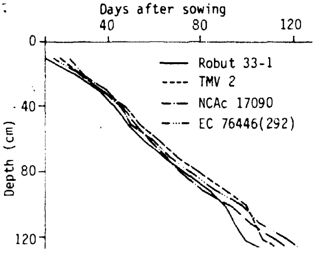

Figure 5. Water-extraction depth changes over time of four genotypes subjected to drought.

pod yield in the drought, had a harvest index 84% greater than that of EC 76446(292), the most-susceptible genotype (Table 3).

The reasons for differences in the drought sensitivity of reproductive growth are yet to be established, but it is apparent that superior yields under drought conditions may be based on two separate mechanisms: resistance and recovery. The initiation of pods by these four genotypes during a drying cycle and following the release of stress is presented in Figure 6. TMV 2 apparently achieved higher yield by producing pods despite the drought, while Robut 33-1 demonstrated a superior recovery response to the release of stress. The relative advantages of these two strategies will depend on the growth duration possible following the stress release.

The basis for these different responses of the reproductive initiation processes to drought is not fully understood, but very subtle differences in drought timing in relation to phenological development may result in substantial yield differences. The importance of small differences in pod initiation is best demonstrated by the interaction of drought with gypsum applied at flowering.

Table 3. Contribution of total water used, water-use ratio, and harvest index to cultivar yield differences, using EC 76446(292) as a reference, under water-deficit conditions, ICRISAT Center, 1983.

Cultivar	Total water use (%)	Water-use ratio (%)	Harvest index (%)
TMV 2	98	111	181
Robut 33-1	101	125	156
NC Ac 17090	101	118	125
EC 76446(292)	100	100	100

Gypsum applied at flowering increased the yield of genotypes subsequently subjected to drought, but there was no obvious response if there was no drought since the soils at ICRISAT Center have adequate available amounts of Ca (±600 ppm) (Rajendrudu and Williams, 1986a). In well-watered conditions the application of gypsum produced small (not statistically significant) but consistent (across three genotypes) increases in pods initiated within the first 2 weeks of pod setting. In a drought treatment the same gypsum application significantly increased pod initiation (Fig. 7) which generally increased yields until the drought stress was relieved by irrigation, (Rajendrudu and Williams, 1986b).

Conclusions

The responses of groundnut genotypes to drought have been shown to be influenced by the timing of drought relative to phenological development and by the yield potential in nonstressed conditions. The major sources of variation observed between genotypes have been associated with the reproductive physiology; where the ability to initiate fruit despite drought, or to recover rapidly after drought provides opportunities for the genotypes to better adapt to long-term drought probabilities. Genotypic varia-

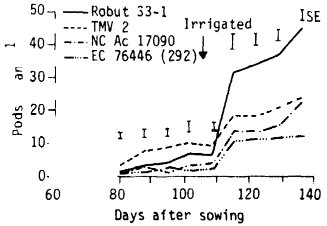

Figure 6. Number of pods developed over time by four groundnut genotypes during drought stress and after irrigation, ICRISAT Center, postrainy season 1982/83.

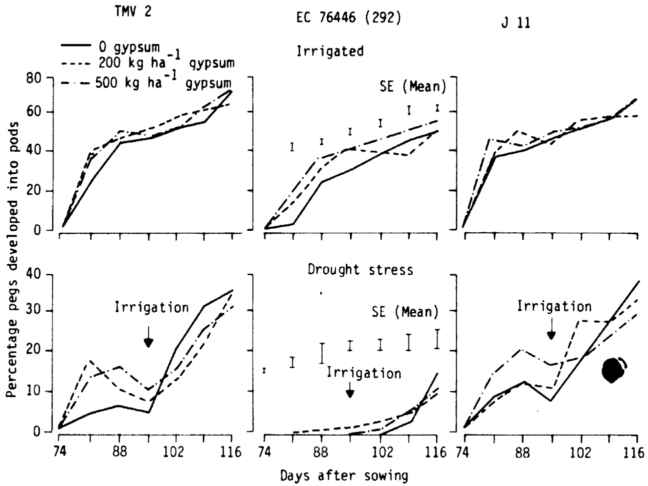

Figure 7. Changes with time in the percentage of subterranean pegs developed into pods for groundnut cultivars grown in wet (T1) and dry (T4) conditions after gypsum applications at early flowering, ICRISAT Center, postrainy season 1981/82. (Source: Rajendrudu and Williams 1986b.).

tions in the profile-water use patterns and in WUE were observed. There is scope for effective use of this information in crop improvement to select genotypes better adapted to different agroclimatological conditions.

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