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Water stress in indeterminate soybeans : no critical stage in fruit development

Alix PIGEAIRE ([1]), Michel SEBILLOTTE (*) & Robert BLANCHET

I.N.R.A., Station d'Agronomie, Centre de Recherches de Toulouse, B.P. 12, F 31320 Castanet-Tolosan
(*) INA-PG, Chaire d'Agronomie, 16, rue Claude-Bernard, F 75231 Paris Cedex 05.

SUMMARY

The length of the period of maximal sensitivity to water stress in indeterminate soybeans is prolonged compared to other species. In order to determine whether this is due to length of flowering period, or to absence of a critical stage in fruit development, two cultivars (Hodgson and Kingsoy) were subjected to short, severe water stresses at three different times during this period of maximum sensitivity. For both cultivars each water stress resulted in a significant reduction of seed weight per plant, essentially caused by a reduction in pod number. The profiles of pod number and seed number per node on the main stem were similar for each of the three water stresses for each variety, despite these stresses being imposed at different times. Abortions were therefore not related to fruit age, but rather to the position of the organs on the plant. Secondary inflorescences were more affected than principal ones. For the principal inflorescences, the low and the high parts of the stem were more affected than the central one, and distal pods on the raceme more affected than the proximal ones. Theses positions are, generally, the most affected ones over a wide range of conditions.

Additional key words : *Yield components, pod number, seed number.*

RÉSUMÉ

Contrainte hydrique chez le soja de type indéterminé : absence d'un stade critique dans le développement des organes reproducteurs.

Dans le but de déterminer si l'étalement de la période de sensibilité maximale à la sécheresse chez le soja de type indéterminé est dû à l'étalement de la floraison ou à l'absence d'un stade critique dans le développement des organes reproducteurs, des contraintes hydriques fortes et de courte durée (arrêt total de la fourniture en eau pendant 2 à 3 jours) ont été appliquées aux deux variétés Hodgson et Kingsoy à 3 dates différentes au cours de la période de sensibilité maximale. Pour les 2 variétés, chacune des 3 contraintes hydriques a entraîné une réduction significative de la production de graines par plante provenant principalement d'une réduction du nombre de gousses par plante. Pour une même variété, les profils de nombres de gousses et de graines résultant des différentes contraintes appliquées étaient très voisins. L'avortement des organes reproducteurs ne s'est donc pas effectué en fonction de leur âge au moment de la contrainte. La position des organes sur la plante a par contre joué un rôle. L'avortement est plus fort sur les inflorescences latérales que sur les inflorescences centrales. Pour les inflorescences centrales, le bas et le haut de la tige sont plus touchés que la partie médiane, les gousses distales sur le racème plus touchées que les proximales. Ces positions sont celles qui, d'une façon générale, dans des conditions variées ont déjà les plus grandes probabilités d'avortement.

Mots clés additionnels : *Composantes du rendement, nombre de gousses, nombre de graines.*

I. INTRODUCTION

The effects of water stress on yield depend not only on the characteristics of this stress (intensity, duration) but also on the time of occurrence with respect to the development cycle of the plant. Sensitivity to water stress during plant development varies amongst species. Whereas maize has a critical period for yield at the time of female flower differentiation (ROBELIN, 1963), the maximum sensitivity of indeterminate soybean is less pronounced (only 30 % reduction in yield compared to 55 % for maize under identical water stresses) but the period of sensitivity is prolonged (SHAW & LAING, 1966 ; MINGEAU, 1974).

(1) Present adress : I.N.R.A., Station d'Agronomie, 17 rue Sully, F 21034 Dijon Cedex.

The prolongation of the period of maximum sensitivity to water stress for indeterminate soybean may be due to the duration of flowering, or to the absence of a development stage of the pods and seeds particularly sensitive to water stress, or possibly to both these phenomena. Knowing which development stages of the reproductive organs are sensitive to each environmental factor is especially useful when one tries to explain the causes of low yields in a given place. If one knows the flowering dates for the successive nodes of the main stem and the number of pods that they carry, it is possible to link together the abnormal abortions at certain nodes with particular environmental factors. To do this, it is necessary to verify that these factors were actually stressful at the time when the organs that finally aborted were the most sensitive, given their position on the plant and therefore their age. An example of this approach has been given by PIGEAIRE (1986) who observed that yield reduction in soybean was correlated with a period of low temperature at a critical stage of development previously identified by SAITO *et al.* (1970).

The aim of the present work was to determine whether the reproductive organs of indeterminate soybeans have a critical development stage with respect to water stress. Two varieties, reputed to react differently to water stress in the field, were subjected to conditions of high water stress over a short period applied at 3 different dates during the socalled phase of maximum sensitivity. The identification of the reproductive organs which aborted following each water stress period has been achieved by comparing the numbers and positions of pods and seeds produced at each node of the treated and control plants.

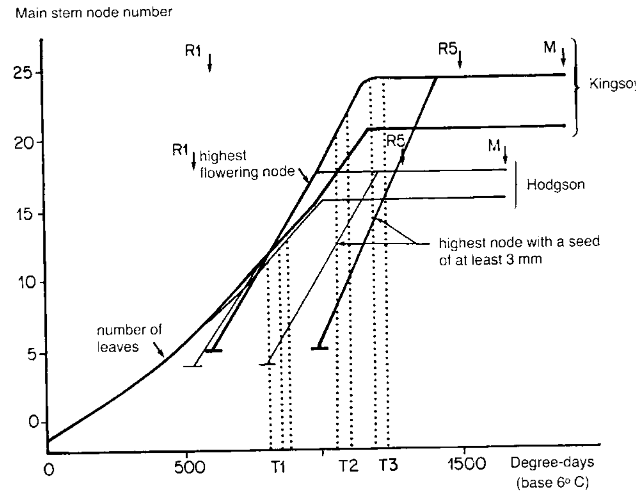

Figure 1

Position of water stress periods in relation to development of main stem for both cultivars Hodgson and Kingsoy. The presentation follows PIGEAIRE *(1984, 1986). Node 1 is for the first trifoliate. R1 = beginning of anthesis, R5 = stage R5 of* FEHR *et al.*'s scale (1971), *corresponding also with the end of the final stage in seed abortion (*PIGEAIRE *et al., 1986), M = maturity.*

Dates d'intervention des contraintes hydriques par rapport au stade de développement de la tige principale pour les 2 variétés Hodgson et Kingsoy. La représentation adoptée est celle de PIGEAIRE *(1984, 1986). Le nœud 1 est celui de la 1re feuille trifoliée. R1 – début floraison ; R5 = stade R5 de l'échelle de* FEHR *et al.* (1971), *ce stade correspond aussi à la fin de franchissement du stade limite d'avortement des graines (*PIGEAIRE *et al., 1986) ; M = maturité.*

II. MATERIALS AND METHODS

The 2 varieties used were Hodgson (maturity group I), reputed to be more sensitive to drought than Kingsoy (maturity group II). They were cultivated in the glasshouse in pots containing 8 kg of soil and 4 plants per pot. The pots were placed in individual basins joined together by plastic pipework. Apart from the period of drought applied, watering was carried out using an automatic solenoid valve which maintained a constant level of water in the basins. The temperature was regulated between 15° and 33 °C to avoid abortion due to excessively high or low temperatures. Excess nitrogen was supplied in mineral form, NH_4NO_3.

The pots of each of the 2 varieties were divided into 4 groups. The first group was the control and to the 3 other groups, one of the three water stress periods, T1, T2 or T3, was applied. These water stresses were applied between the beginning of flowering and the end of pod elongation, before reaching stage R5 as described by FEHR *et al.* (1971). The actual dates of application were slightly different for each variety as their earliness of flowering differs (fig. 1). The interval between the beginning of T1 and T2, then T2 and T3 was 2 weeks and 1 week respectively.

The treatments consisted of simply cutting off the water supply so that the plants existed on the water reserve held in the pot. Water consumption was measured at 0 900, 1 300 and 1 700 each day during the water stress periods (fig. 2). They were determined by weighing each pot, in the 3 water stress treatments, and by measuring the water replaced to raise the level back to normal in the control. To avoid direct evaporation from the pots they were covered with polystyrene balls glued together, while each basin had a plastic cover with a hole fitting snugly around each pot.The dynamics of water consumption differed greatly between treatments due to climatic variations (fig. 2). The more the climatic demand was elevated (treatment T2), the more quickly the difference in transpiration between the treated plants and the control plants was observed. When the transpiration rate of the treated plants fell to about 20 % of the control plants, in the last period measured, the pots were watered to stop the treatment and the automatic watering reinstalled. The duration of the treatments thus varied between 2.5 (T2) and 3.5 days (T1 Kingsoy - the treatment T1 was applied to Kingsoy half a day later than Hodgson which explains its lateness with respect to the latter). Important wilting occurred on all treatments. Some partial leaf necrosis was observed in T2 and T3. During treatment T3 the water consumption of the plants of the variety Hodgson, treated in T1 and T2, was also measured. This had regained 91 and 70 % of the control level respectively.

The development stage of the control plants (fig. 1) was noted throughout their growth cycle as follows: number of leaves, number of the highest flowering node, and number of the highest node with a seed of at least 3 mm (SINCLAIR, 1984; PIGEAIRE, 1986). Node 1 is that with the first trifoliate leaf. Just before and after each treatment, the development stage of each individual stem, for all treated and control plants, was noted in the same manner.

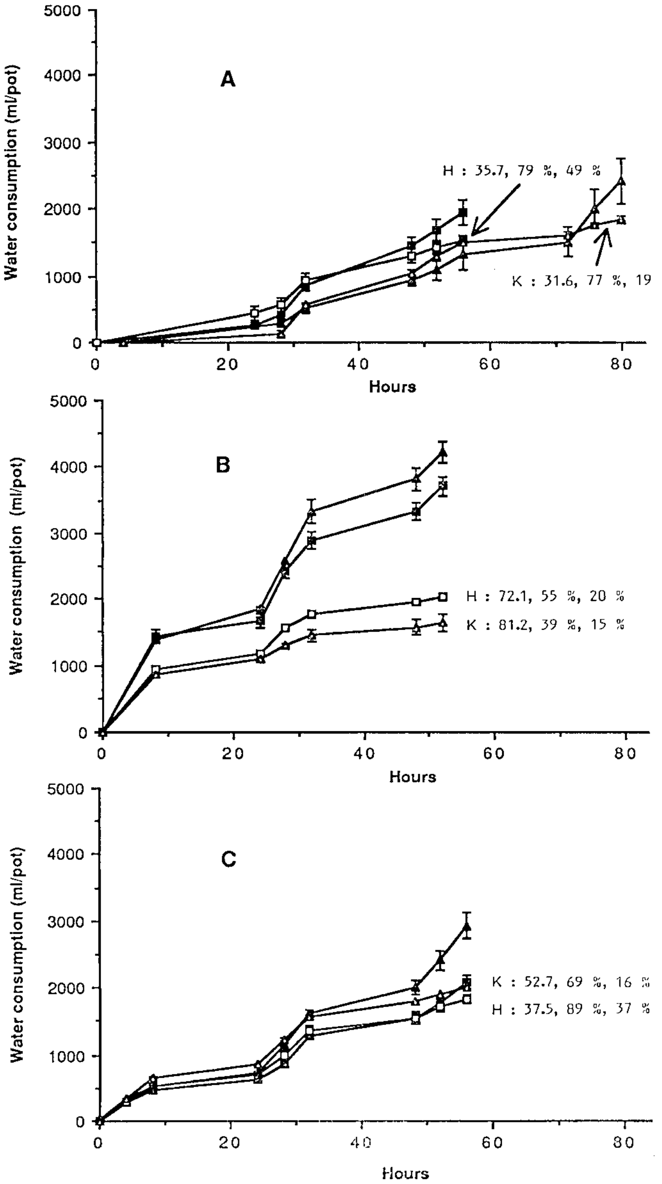

Figure 2

Cumulative water consumption during treatment T1 (A), T2 (B), T3 (C). Measurements were made at 09, 13 and 17 h. Vertical bars are standard errors of the means. The 3 numbers annotated for each variety on each figure represent respectively, the average water transpired by the control plants during the total treatment period in ml/pot/hr, and the water transpired by the treated plants expressed as a percentage of the control, for the total treatment period and then for the last period of measurement. Hodgson (■) control and (□) treated pots. Kingsoy (▲) control and (△) treated pots.

Consommations d'eau cumulées pendant les contraintes T1 (A), T2 (B), T3 (C). Mesures effectuées à 9, 13 et 17 h. Les barres verticales indiquent les écarts-type. Les 3 chiffres reportés pour chaque variété sur chaque figure représentent respectivement la consommation d'eau moyenne des plantes témoin pendant la période de contrainte en ml/pot/h, et la consommation d'eau des plantes traitées exprimées en % du témoin, pour la totalité de la période de contrainte, puis pour la dernière période de mesure. Hodgson, pots témoin (■) et traités (□), Kingsoy, pots témoin (▲) et traités (△).

For the variety Kingsoy, only one sampling was made at harvest. For the variety Hodgson several samplings were made before and after each treatment, with both the control and treated plants. Some supplementary samples from the controls were taken afterwards to describe the end of the growth curves for the different organs ; and from treatment T1 to describe the after effect of the treatment on the gain in dry matter. Using 2 pots each time, each sample consisted of the six most homogenous plants considering the development stage of the main stem at the treatment period. The position of the pods present at each node (central inflorescence, lateral inflorescence, left or right, position on the raceme) was determined by counting the scars of abcissed organs aided by a stereo microscope. The dry matter determinations were made by separating the plant into leaves and shoots, pods, and seeds.

III. RESULTS

A. Consequences of water stress on seed production and dry matter accumulation

In spite of the date of application, all water stress treatments resulted in a highly significant reduction ($P = 0.01$) in seed production and total dry matter per plant (table 1). For variety Hodgson the smaller reduction in seed dry matter was due exclusively to a decrease in the number of pods produced. For variety Kingsoy it was also due to a decrease in the number of seeds per pod, and for the T3 treatment, a decrease in average seed weight (table 1). The harvest index for this last treatment was also significantly lower than that of the control.

The comparison of daily gains in dry matter between treated and control plants for the variety Hodgson are presented in table 2. During the stress period, the treatments caused, for the vegetative parts of the plants, either a reduction in dry matter gain (T1), or even, a loss of dry matter (T2 and T3). This difference between treatments is probably due to the fact that the water stress T1 was applied at the moment when the vegetative parts were still growing vigorously, while the other water stresses, T2 and especially T3, were preceded by a slowing of vegetative growth. The loss of leaves, that took place following the water stress period, was not compensated by subsequent gains in dry matter. The fruit always showed positive gains in dry matter. Water stress T1 had repercussions on the accumulation of dry matter following on from the treatment period itself. The senescence of vegetative parts was earlier than the control. The dry matter gains of the fruit also remained smaller, a consequence of a lower number of growing pods following some abortions.

B. Identity of aborted reproductive organs

Under the experimental conditions, the main stem was responsible for the greatest proportion of the plant's production, from 83 to 90 % in each case. This proportion did not differ significantly between treated and control plants (table 1). The water stresses applied therefore affected the main stem and the branches with the same intensity. As a small number of reproductive organs were present on the branches, the identification of aborted organs was carried out using the main stem.

1. *Age of reproductive organs at the time of application of water stress*

The development stages of treated plants, noted just before and after each stress period, are presented in

TABLE 1

Treatment effects on the production of seeds and total dry matter per plant at the time of harvest. MS = main stem. For each cultivar, means in the same column followed by the same letter are not significantly different (P = 0.01, Duncan's test).

Effets des traitements sur la production de graines et de matière sèche totale par plante à la récolte. MS = tige principale. Pour chaque variété, les moyennes d'une même colonne suivies d'une même lettre ne sont pas significativement différentes au seuil 1 % (test de Duncan).

Cultivar	Treatment	Seed dry weight		Total dry matter (g)	Harvest index	Pod number	Seed number /pod	Seed number	Weight /seed (mg)
		Total (g)	% from MS						
Hodgson	Control	27.52a	83a	53.46a	0.51 a	73.9a	2.08a	154a	180a
	T1	20.04b	86a	41.51b	0.48 a	54.5b	2.01a	110b	182a
	T2	15.46b	85a	31.55b	0.49 a	44.9b	2.01a	90b	169a
	T3	17.88b	83a	34.18b	0.52 a	49.7b	1.92a	95b	187a
Kingsoy	Control	39.22a	85a	76.16a	0.52 a	78.4a	2.30a	180a	218a
	T1	22.74b	83a	48.11b	0.47ab	51.8b	1.93b	100b	228a
	T2	20.63b	89a	43.77b	0.47ab	49.3b	1.99b	98b	209a
	T3	15.72b	90a	40.29b	0.39 b	44.3b	1.97b	88b	177b

TABLE 2

Changes in dry weight ($mg.d^{-1}$) for the main stem during (T1, T2, T3) and after stress (T1) — cv. Hodgson.

Gains journaliers de matière sèche ($mg.j^{-1}$) de la tige principale pendant la contrainte (T1, T2, T3), et après la contrainte (T1) — cv. Hodgson.

			Dry matter gain ($mg.d^{-1}$) for the main stem		
			Total	Stems + leaves	Fruit
During the treatment	T1	Control	721	512	209
		Treated	531	332	199
	T2	Control	503	172	331
		Treated	− 81	− 231	150
	T3	Control	988	302	686
		Treated	− 86	− 505	419
After the treatment ([1])	T1	Control	746	237	509
		Treated	367	− 31	398

([1]) From the end of the treatment to the date, in the controls, corresponding to the maximum dry matter accumulation in the vegetative plant parts, which was 71 days or 1 294 degree-days (base 6 °C) after emergence.

TABLE 3

Stages of development of the treated plants just before and after the treatment.

Stades de développement des plantes traitées juste avant et après la contrainte.

		Number of leaves		Highest			
				Flowering node		Node with a seed of at least 3 mm	
		Before	After	Before	After	Before	After
Hodgson	T1	10.8 ± 0.5	12.1 ± 0.6	12.0 ± 0.4	14.2 ± 0.6	([2])	
	T2	16.0 ± 1.0	16.3 ± 1.1	18.0 ± 1.3	18.4 ± 1.2	11.3 ± 1.0	14.3 ± 0.8
	T3	([1])		([1])		17.1 ± 0.9	17.6 ± 0.8
Kingsoy	T1	11.2 ± 0.5	12.1 ± 0.5	11.2 ± 0.8	13.0 ± 0.9	([2])	
	T2	16.6 ± 0.6	17.2 ± 0.9	19.0 ± 1.1	20.8 ± 1.6	Not measured	
	T3	20.8 ± 0.4	22.1 ± 0.4	24.5 ± 0.8	24.5 ± 0.8	12.5 ± 0.8	13.5 ± 0.8

([1]) No further leaves expanding and flowering terminated.
([2]) Stage not yet reached.

table 3. The standard deviations are small, resulting in coefficients of variation of between 5 to 7 %. In these conditions, the age of the reproductive organs at the time of water stress application can be considered as dependent only on the node number and the type of inflorescence which carry them. The lateral inflores-

cences began, on average, to flower at the same time as the central inflorescences situated 3 nodes higher.

Figures 3 and 4 present respectively the numbers of pods and seeds per pod, on the central and lateral inflorescences of each node of the main stem. The profiles of pod numbers were more irregular than the profiles of seed numbers/pod.

For the same variety, the profiles resulting from the different water stress treatments had nearly the same forms (fig. 3 and 4), which means that the aborted reproductive organs were the same whatever the date of application of the water stresses. Moreover, between central and lateral inflorescences, there was not a 3-node difference in the position of the aborted organs (fig. 3 and 4). Thus abortion did not depend on the age of the reproductive organs at the moment water stress was applied.

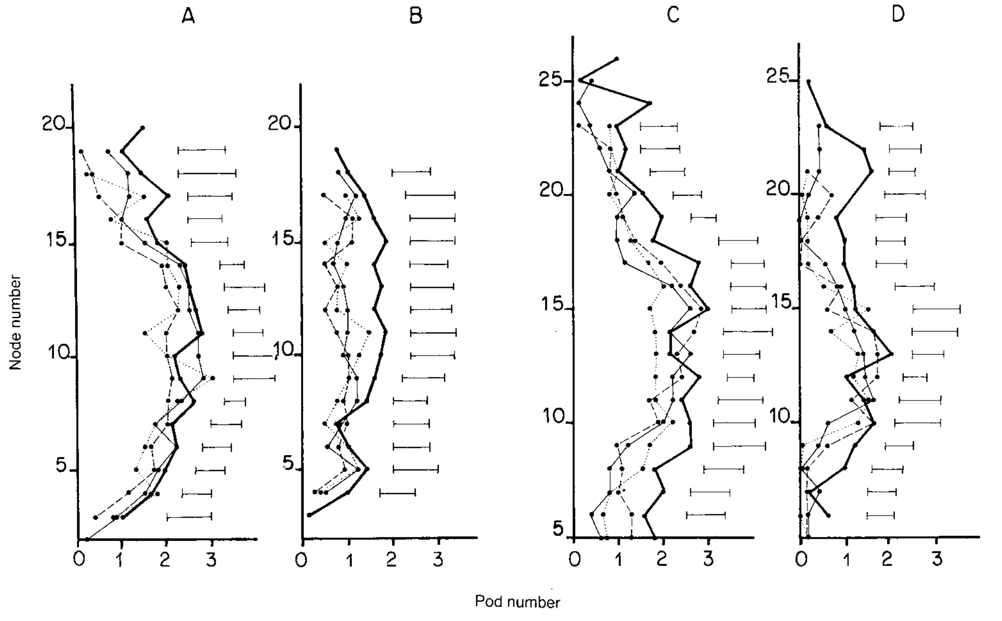

Figure 3

Pod numbers per node on the main stem. A and B, cv. Hodgson, central (A) and lateral (B) inflorescences. C and D, cv. Kingsoy, central (C) and lateral (D) inflorescences. (———) control, (———) T1, (----) T2, (----) T3. Horizontal bars indicate the lsd (P = 0.05).

Profils des nombres de gousses par nœud sur les tiges principales. A et B, cv. Hodgson, inflorescences centrales (A) et latérales (B). C et D, cv. Kingsoy, inflorescences centrales (C) et latérales (D). (———) Témoin, (———) T1, (----) T2, (----) T3. Les barres horizontales indiquent les ppds (P = 0.05).

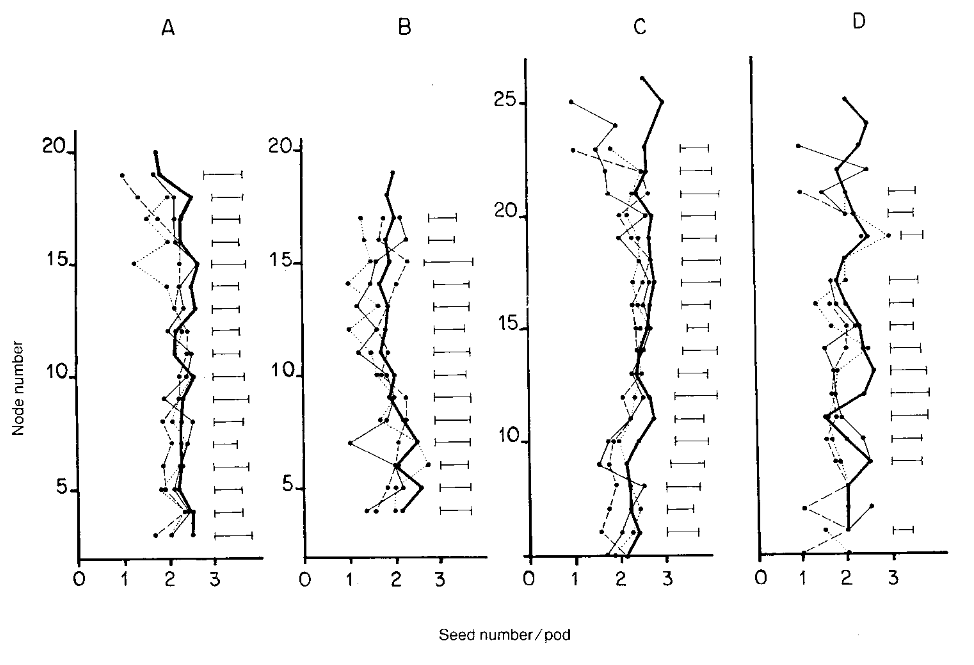

Figure 4

Idem figure 3. Seed numbers per pod.

Idem figure 3. Nombre de graines par gousse.

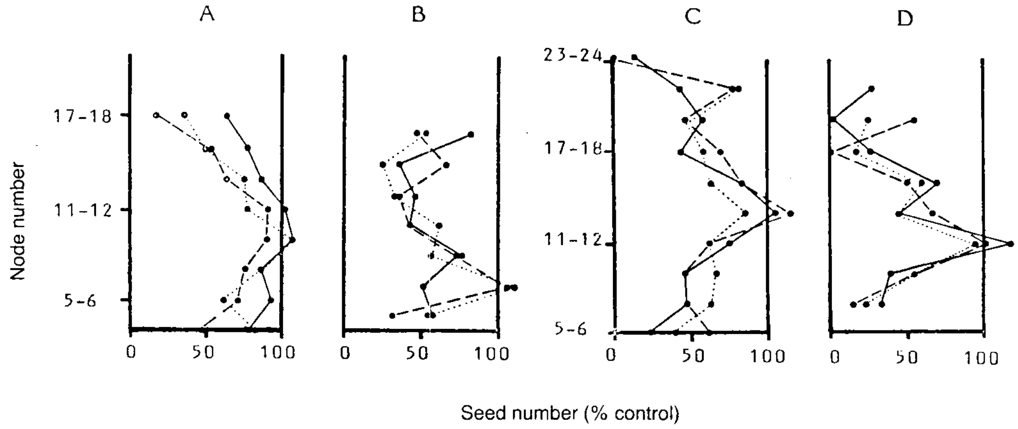

Figure 5

Seed numbers per group of two nodes as percentages of the controls. Codes of treatments and figures are the same as in figure 3.

Profils des nombres de graines par groupe de 2 nœuds, en valeurs relatives par rapport au témoin. Codes des traitements et des figures identiques à ceux de la figure 3.

2. *Position of reproductive organs on the stem*

The position of aborted reproductive organs can be examined in a global fashion (i.e., abortion of pods and seeds per pod together) with the aid of figure 5 showing the numbers of seeds per node for the treated plants relative to the controls. For easy comprehension the nodes were grouped in twos. Generally, the lateral inflorescences (B and D, fig. 5) were more affected than the central inflorescences (A and C, fig. 5). The central inflorescences for both varieties, and the lateral inflorescences for Kingsoy, tended to be more affected at the base and shoot tip rather than the middle part of the stem, whereas the lateral inflorescences for Hodgson showed more of an affect on the entire stem. High relative values for one group of nodes for each variety were due more to a lower than normal number of pods for the control plants, than to a particularly high number for the treated plants (fig. 3). Within the central inflorescences, the distal pods on the raceme were more affected. The relative numbers of seeds decreased systematically from pod position 1 on the raceme to pod position 3 or more (table 4).

IV. DISCUSSION

The effects of water stress observed in this trial agree with the results generally obtained for indeterminate soybean. The three water stresses applied at different dates, but always during the period of maximum sensitivity to drought, all had important effects on plant production (SHAW & LAING, 1966 ; MINGEAU, 1974). The yield component most affected was number of pods per plant (PUECH *et al.*, 1974 ; BLANCHET *et al.*, 1977).

The varietal effect was the inverse of that which is generally described in the field. Variety Kingsoy was more affected than variety Hodgson, which is reputed to be particularly sensitive to drought (VIDAL *et al.*, 1981). During this trial, the intensity of water stress suffered by variety Kingsoy was always greater if one considers the drop in water consumption observed for the treated plants (fig. 2). Apart from the period T1 which commenced later for Kingsoy, the water consumption of control plants was generally greater for Kingsoy than Hodgson, reflecting probably the difference in leaf area index between the two varieties. Consequently, the transpiration of the treated plants was greater for the variety Kingsoy. One observes that for Kingsoy the

TABLE 4

Total seed numbers of the central inflorescences of the main stem according to the position of the pod on the raceme, (as percentages of the controls). Values for the controls are given in parenthesis.

Nombre total de graines des inflorescences centrales de la tige principale selon le rang des gousses sur le racème. Valeurs relatives par rapport au témoin. Entre parenthèses, valeurs absolues pour le témoin.

		Pod position on the raceme			
		1	2	3	Σ (> 3)
Hodgson	Control	100 (33.1)	100 (28.9)	100 (16.1)	100 (3.6)
	T1	99	85	73	0
	T2	81	64	36	7
	T3	87	73	37	0
Kingsoy	Control	100 (46.2)	100 (37.2)	100 (19.8)	100 (3.0)
	T1	68	57	35	13
	T2	66	63	50	47
	T3	70	48	46	33

reduction of total seed weight was due not only to a decrease in the number of pods but also in the number of seeds per pod, whereas for Hodgson it was due only to a reduction in the number of pods. This suggests that water stress provokes firstly abortion of flowers and pods and then abortion of seeds. These results are not contradictory with the varietal differences in drought resistance observed in the field (SPECHT *et al.*, 1986), where the role of root colonization of the soil comes into play (PLANCHON, 1984), a factor which cannot express itself in a pot.

The harvest indices were constant when only the component number of pods was affected. They were statistically different from the control, only when the seed weight had been affected (Kingsoy T3). It seems that soybean can counterbalance to a certain point the negative effects of photosynthesis (table 2) by internal redistribution of nutritive elements in favour of the seeds. For example, if one considers daily seed growth rate after the end of the drought period for treatment T1 and the control, one observes respectively, 3.62 and 3.31 mg day^{-1} (from table 1 value, divided by treatment length, and post treatment periods), which are very similar ; by comparison the leaves continuously lost dry matter with T1. There was also perhaps a partial degradation of the root system which inhibited the treated plants from regaining the transpiration rate of the control. During period T3, the transpiration rate of T1 was 90 % that of the control and that of T2 was 70 % ; which indicates an after effect of the treatments of at least one week. This after effect is also visible on the total growth rate of the main stem after water stress T1 (table 2). The loss of seed weight observed uniquely with T3 Kingsoy could therefore be due to an after-effect of treatment T3. This treatment was the last and it was more severe for Kingsoy than for Hodgson (fig. 2, tabl. 1).

Under water stress conditions, the probability of different organs aborting depends on their position on the plant. The organ positions most affected by water stress are in fact those already most affected by abortion on plants well supplied with water. Generally the lateral inflorescences are smaller, produce smaller seeds and less of them than the central inflorescences (SPAETH & SINCLAIR, 1984 ; SPOLLEN *et al.*, 1986). The probability of abortion is greater for pods in a higher position than a lower position on the raceme (HUFF & DYBING, 1980 ; BRUN & BETTS, 1984). Generally speaking the profiles of the numbers of pods, or seeds, per node show higher values for the middle part of the stem, regardless of whether the treatments were irrigated or not (CARLSON *et al.*, 1982 ; HERBERT & LITCHFIELD, 1982).

The explanation of the fact that abortions took place preferentially at the base and the extremity of the stem, under water stress, probably lies in the way in which water stress affects the plant ; as it is in those parts of the stem that wilting is first observed to occur. The onset of abortion may happen from different causes, such as : a direct effect of drought resulting in a lethal change in water potential or water content within the organ concerned ; indirect effects, such as a reduction in the production of assimilates, or a lowering of the transpiration rate which causes a reduction in xylem flow transporting the cytokinins necessary for the development of the young fruit (CARLSON *et al.*, 1987). Whatever is the cause of abortion, in the absence of a stage of development particularly sensitive to water stress, it seems logical that the aborted organs correspond to the positions on the plant that are most quickly and severely affected by water stress. The reasons for differences in behaviour under water stress between different parts of the stem remain to be clarified.

Whatever the variety, a stage of development particularly sensitive to water stress for the reproductive organs has not been observed as was the case for the influence of low temperature (SAITO *et al.*, 1970). When water stress is induced, organs of all ages abort, from the pre-floral stage until the final stage in seed abortion (PIGEAIRE *et al.*, 1986). This diversity in the age of aborted organs has already been observed by PUECH *et al.* (1977) in various experimental conditions. This results in a long period of maximum sensitivity to drought, which lasts until all reproductive organs have passed the final stage in seed abortion.

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