BIOLOGIA PLANTARUM (PRAHA)

23 (6) : 434–441, 1981

Drought Tolerance Processes in Soybeans

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Abstract. Fifteen soybean cultivars were evaluated in two water supply conditions, inducing or not a drought stress. Main canopy traits were measured several times during the reproductive period and, at maturity date, the yield components were estimated. Using principal components analysis, the main physiological functions involved in soybean drought tolerance are described: leaf cells enlargement and assimilates transport. These processes could be a good basis on which to define new selection criteria for soybean drought tolerance.

Additional index words: Glycine max (L.) MERRILL, cultivars.

The extension of soybean cultivation in the south of Europe is limited by climatic conditions and, above all, by drought appearing each year during summer, at a time which is a critical period for water supply of soybeans, the grain and pod filling stages (MINGEAU 1975, BLANCHET *et al.* 1977). So, grain yields may decrease drastically by action of this drought, more especially as used cultivars originate from the north part of the United States, a country where rainfall is very common in summer. Then, we may consider that the American cultivars are unadapted to the special climatic conditions of the south of Europe.

As irrigation is very often impossible, one of our most important breeding objectives is drought tolerance. This is a long term work, which needs first an understanding of the drought tolerance mechanisms in soybeans; in order to have in hand a breeding test, simple and common, used for determination of the best parental lines and for screening among the unfixed material.

Water relations in soybeans have already formed the subject of numerous papers (BEARDSELL and MITCHELL 1973, SIONIT and KRAMER 1977, BLANCHET and GELFI 1978, REICOSKY and DEATON 1979) but the cultivar aspect has rarely been taken into account. MEDERSKI and JEFFERS (1973) tested several soybean cultivars in drought conditions but they measured only the seed yield. SAMMONS *et al.* (1979) observed different physiological and morphological parameters on several cultivars but they did not study the relation with seed yield drought susceptibility. In case of a cultivated crop, drought tolerance must be understood in terms of production and not

Received March 10, 1981; accepted April 27, 1981

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in term of survival. So, concerning soybeans, we can say that a cultivar will be more drought tolerant as its grain yield will be less affected by a drought stress. The goal of the work presented in this paper is to search for relations between drought tolerance appreciated in terms of seed production and physiological or morphological parameters measured on several occasions during the reproductive period.

MATERIAL AND METHODS

Fifteen indeterminate cultivars of *Glycine max* (L.) MERRILL of several maturity groups and origins (Table 1) were cultivated in the field in drought boxes (1 $m^2 \times 0.6$ m depth) and kept since flowering time until maturity, under two water supply levels (A and B) based on the consumption of a well watered check cultivar:

Treatment A = 80% of the consumption of check (80% were chosen rather than 100% to avoid an early lodging);
treatment B = 40% of the consumption of the check.

By treatment B a severe drought stress was induced.

Since flowering time until maturity five plants were harvested every two weeks in each cultivar and each water treatment. At maturity, thirty plants were harvested in each box. The following parameters were measured (variable, parameter, abbreviation):

During vegetation period

1 = Leaves Dry matter Weight per plant = LDW
2 = Leaf Area Index = LAI
3 = Specific Leaf Weight = SLW
4 = Number of Leaves per plant = NL
5 = Mean Leaf Surface = MLS
6 = Total Petiole Length per plant = TPL
7 = Petiole Dry matter Weight per plant = PDW
8 = Specific Petiole Weight = SPW
9 = Mean Petiole Length = MPL
10 = Leaf Water Content = LWC
11 = Petiole Water Content = PWC
12 = Stem Water Content = SWC

At maturity

13 = Vegetative part Dry Weight = VDW
14 = Seeds Number per plant = SN
15 = Pods Number per plant = PN
16 = Seeds Number per Pod = SNP
17 = Hundred Seeds dry Weight = HSW
18 = Nodes Number = NN
19 = Seeds Dry Weight per plant = SDW

As we have said in the Introduction we have chosen to appreciate the drought tolerance in terms of seed production. Several formulas are possible for a Drought Tolerance Index (DTI). We used the simplest one:

$$\mathrm{DTI} = \frac{\mathrm{SDW\ in\ treatment\ B}}{\mathrm{SDW\ in\ treatment\ A}} \times 100 .$$

Of course, we checked that in our experiment this index is independent of earliness and productivity (*i.e.* SDW in treatment A) of cultivars: the correlation coefficient between SDW in A and DTI is + 0.06.

To describe the behaviour of each of the fifteen cultivars we used a Principal Components Analysis (PCA) based on the variables listed in Table 3. These variables are the ratios $\frac{\text{value in treatment B}}{\text{value in treatment A}} \times 100$ of the parameters

TABLE 1
Drought Tolerance Index (DTI)

Cultivar		Maturity group	Origin	DTI
Kagon	(KA)	I	U.S.A.	57.7
Giessen 456-64	(GI)	0	Germany	56.1
Amsoy 71	(AM)	II	U.S.A.	53.8
F 68-199	(FF)	0	Romania	52.1
Kirovogradskaya	(KI)	I	U.S.S.R.	51.7
Wolfsthaler	(WO)	I	Germany	51.3
Harman	(HA)	II	U.S.A.	48.6
IASI 10	(IA)	II	Romania	45.9
Szurkebarat	(SZ)	0	Hungary	44.3
SRF 100	(SR)	I	U.S.A.	43.2
Wysokonoska	(WY)	00	Poland	41.3
Grant	(GR)	0	U.S.A.	40.9
Nepolegayushchaya II	(NE)	III	U.S.S.R.	40.2
Hodgson	(HO)	I	U.S.A.	39.6
A – 100	(A0)	II	U.S.A.	39.2

measured at harvest time and during the vegetation period: in this last case we used the mean of three successive measurements made between the R_2 and R_4 stages, as defined by FEHR and CAVINESS (1977). So, the variables used in this analysis square with the drought stress effect on the observed parameters.

It seems useless to describe the principles of PCA which have been well presented by several authors (LEFEBVRE 1980). We applied this analysis separately on the canopy parameters and on the yield components.

RESULTS AND DISCUSSION

1) Drought Tolerance Index (DTI)

The DTI values for each cultivar appear in Table 1. The most tolerant cultivar in our experiment seems to be Kagon and the most sensible one, A-100. We can also notice that Amsoy 71 is more tolerant than Hodgson; that agrees with observations made in fields over several years. To test the statistical validity of the differences between cultivars, the following method was used: 30 plants were harvested in the two water treatments, 30 ratios SDW_B/SDW_A were calculated, at random, for each cultivar. Then a variance analysis was made and the cultivar effect was tested by an F test. This operation was replicated ten times with always randomized ratios

TABLE 2
F Values for DTI Variance Analysis

Replication	1	2	3	4	5	6	7	8	9	10
F value	1.80	2.56	2.02	1.91	2.31	2.74	2.00	2.52	2.00	2.26

$F_{(14,435)} = 1.72$ at 5% level

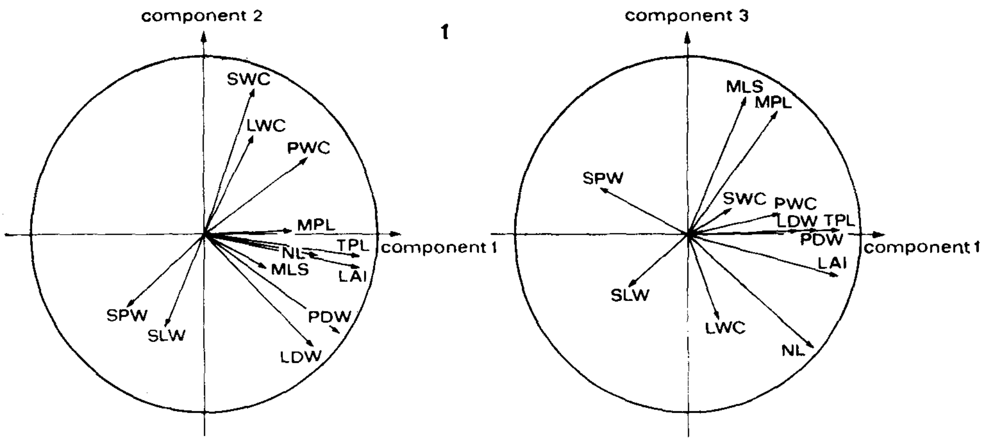
SDW_B/SDW_A. Each time, the F test was significant (Table 2) at the 5% level. Therefore this experiment gives a clear indication of a genetic variability for soybean drought tolerance.

2) Cultivar Behaviour in Drought Conditions

The Principal Components Analysis, used as reported in Material and Methods gives the following results:

a) Canopy parameters

Components 1, 2 and 3 take into account 77.2% of the total variability. Fig. 1 describes the relations between all variables: the weight or surface reduction of the canopy (as affected by drought stress) seems to be independent of the water content decrease and of the specific leaf or petiole



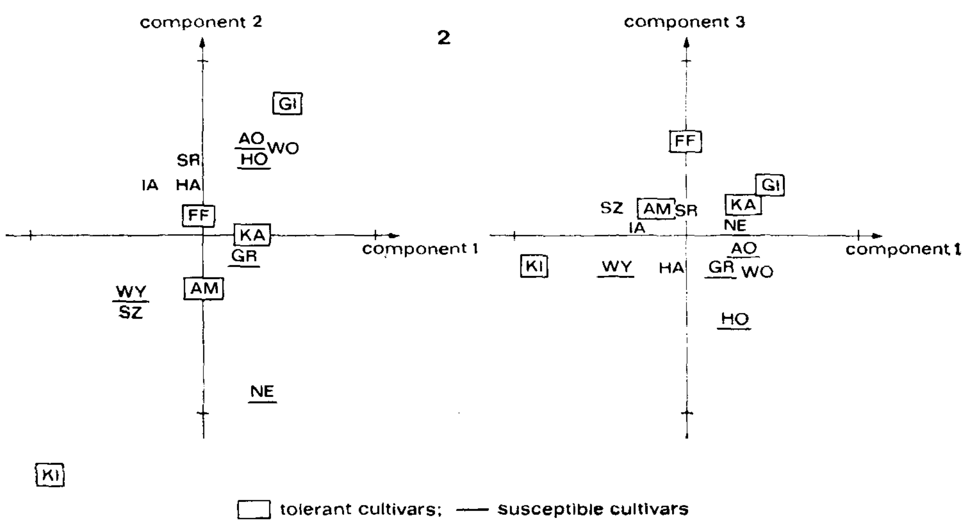
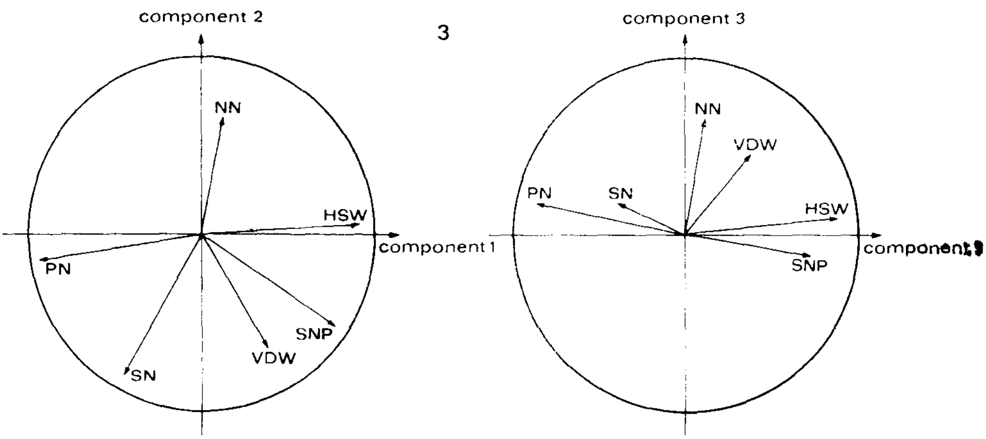
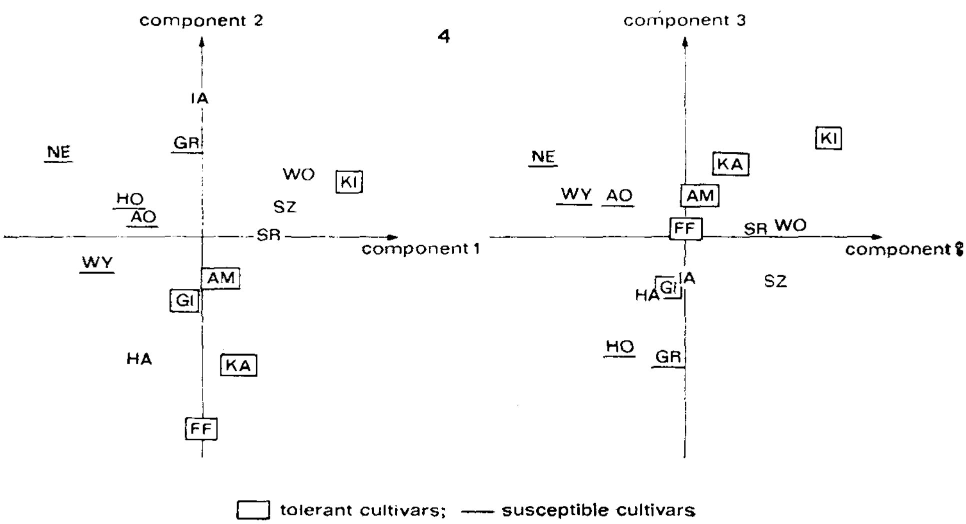


Fig. 1. Principal Components Analysis on canopy parameters — variables representation.
Fig. 2. Principal Components Analysis on canopy parameters — cultivars representation.

weight increase. Water contents and specific weights are negatively correlated. Mean Leaf Surface and Mean Petiole Length reactions to drought are positively correlated and seem to be also independent of the Leaf Area Index decrease.

These observations show that the reactions to drought can be very different between cultivars. This is well illustrated by Fig. 2 where cultivars are projected in plans defined by components 1—2 and 1—3. In this figure the five most tolerant cultivars are encircled and the five less tolerant ones are underlined. It appears that there is no relation between canopy size decrease and drought tolerance level. On the other hand, it seems that the partition between tolerant and susceptible cultivars is good enough accroding to component 3 which represents especially the Mean Leaf Surface and





☐ tolerant cultivars; —— susceptible cultivars

Fig. 3. Principal Components Analysis on yield parameters — variables representation.
Fig. 4. Principal Components Analysis on yield parameters — cultivars representation.

TABLE 3
Variables Used in Principal Components Analysis = (value in treatment B/value in treatment A) × 100

Variables	KA	GI	AM	FF	KI	WO	HA	IA	SZ	SR	WY	GR	NE	HO	AO
1 : LDW	84.4	79.1	86.2	70.1	73.9	81.2	70.2	64.4	71.3	64.1	69.2	85.7	100.2	70.3	78.2
2 : LAI	77.3	76.4	73.1	57.9	54.4	69.5	64.9	58.4	59.8	65.1	64.4	77.0	83.6	80.6	71.5
3 : SLW	112.4	105.6	117.2	101.0	130.4	120.3	109.0	111.0	122.6	99.7	118.1	114.3	120.6	105.0	109.5
4 : NL	78.8	85.2	78.6	76.0	79.1	85.8	80.3	72.6	65.4	71.5	82.9	93.2	91.0	98.1	86.5
5 : MLS	97.4	87.4	93.7	90.7	73.2	80.1	81.0	81.1	93.1	86.4	73.7	82.1	92.2	78.8	86.5
6 : TPL	77.4	82.8	68.0	88.8	61.6	78.4	63.4	62.4	55.5	66.8	74.0	86.7	93.5	85.0	73.5
7 : PDW	85.7	81.0	84.6	76.4	70.3	76.1	71.6	65.5	72.0	71.3	82.3	87.8	103.0	79.8	77.5
8 : SPW	103.3	102.4	128.4	102.9	117.5	100.0	88.7	97.8	136.8	101.2	102.9	105.6	92.9	100.0	108.0
9 : MPL	100.6	96.9	87.3	118.9	78.6	91.7	79.8	86.7	87.9	95.4	90.3	94.3	102.8	87.6	85.2
10 : LWC	96.4	95.0	94.9	91.8	91.0	99.0	97.2	95.9	95.3	96.7	94.3	96.5	93.4	100.2	97.1
11 : PWC	96.5	97.1	93.9	94.8	91.4	97.5	94.9	95.1	93.8	94.6	90.9	95.0	95.1	94.7	97.7
12 : SWC	95.3	98.9	95.5	96.7	91.7	96.5	96.0	96.2	94.3	96.8	95.7	95.2	93.0	96.2	96.8
13 : VDW	69.0	62.2	65.6	70.8	69.0	63.7	67.4	57.5	66.4	68.4	64.2	57.0	60.3	56.7	65.5
14 : SN	64.1	60.5	58.7	62.6	48.9	50.6	58.4	49.3	47.4	50.0	60.9	50.0	55.1	55.2	55.2
15 : PN	59.0	62.9	62.7	64.6	51.1	53.2	67.1	57.9	51.7	56.4	73.0	56.7	76.7	63.5	66.5
16 : SNP	97.9	94.0	93.0	96.2	96.4	95.5	86.6	84.2	91.3	89.1	82.8	87.8	71.7	88.0	79.7
17 : HSW	89.7	92.9	91.6	84.0	105.7	101.7	83.3	94.6	93.4	101.2	68.0	80.3	73.7	70.8	71.5
18 : NN	91.0	85.3	91.5	81.8	98.8	94.3	79.1	93.3	87.0	88.3	90.5	87.2	97.7	86.0	92.0

Mean Petiole Length decreases. Therefore, it appears that the cellular growth phenomena which are well represented by these two parameters are less affected by a drought stress in the drought tolerant than in the drought susceptible cultivars. The conclusions of this analysis agree with results of SAMMONS *et al.* (1978) who pointed out the effect of drought stress for the leaf growth rate.

b) Yield components

Variables included in this analysis are variables 13 to 18. Components 1, 2 and 3 take into account 89% of the total variation. Therefore, the representations given by these three components are very fair.

Fig. 3. describes the relations between variables; pods number decrease by effect of the drought stress, seems to be negatively correlated with the hundred seeds dry weight, and seeds number per pod decreases. On the other hand, these two last parameters are positively correlated. Usually there is a negative correlation between hundred seeds dry weight and seeds number per pod: if we find that the evolution of these two parameters by a drought effect is positively related it seems to indicate that it is dependent on the same physiological process. The negative correlation with the pods number decrease shows off the balance phenomenon between the two main yield components: the pods number per plant and the pods content. Therefore, confronted with a drought stress, some cultivars present a large pods number decrease and the content of these pods is not very affected whereas other cultivars present the opposite behaviour.

This is well demonstrated by Fig. 4 where cultivars are projected in plants defined by components 1, 2 and 3. We can see that behaviours of cv. Nepolegayushchaya, cv. Kirovogradskaya and cv. 68-199 are very different. In plan 1—2, there is a fair separation between the tolerant and susceptible cultivars. By comparison with Fig. 3 it appears that this separation is made according to the following variables: Pods number, seeds number per pod, one hundred seeds dry weight and vegetative parts dry weight. It seems that the drought tolerant cultivars may be characterized by a larger decrease of pods number per plant and a smaller decrease of the vegetative parts dry weight, the seeds number per pod and the hundred seeds dry weight.

By this Principal Components Analysis made on the canopy and seed yield characters, two physiological processes appear to be connected with drought tolerance: the leaf and petiole cellular growth rate and the assimilates transport to the seeds.

Concerning the leaf and petiole growth rate, our experiment confirms the results presented by several authors (BUNCE 1978, SIVAKUMAR and SHAW 1978, SAMMONS *et al.* 1979) who also estimated that the leaf growth rate is related to the drought tolerance level.

The part of the assimilates transport is revealed by the yield components behaviour under effect of a drought stress. The studies done by the Agronomic Research Station of Toulouse (1978) show that indeed the hundred seeds dry weight and the seeds number per pod in soybeans are closely related with the quality of the transport processes. As the tolerant cultivars when confronted with a drought stress, show up a smaller decrease of these two parameters, it means that, even in drought conditions, these cultivars remain able to transport the products of photosynthesis. This effect of a drought stress on assimilates transport had also been demonstrated by SILVIUS *et al.* (1977) by way of labelled CO_2. But, in a breeding purpose it is interesting to find that it is in relation with the genetic drought tolerance variability. Nevertheless, it is impossible to say with our own results if the high level of assimilates transport is a cause or and effect of drought tolerance.

Now this experiment allows us to begin the second step of our work in a breeding purpose: the search for morphological parameters, simple and easy to measure, without plant destruction, and well related with the two physiological processes shown before. Such parameters should be good selection criteria for drought tolerance.

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