Responses of Soybeans to Water Stress During Germination

II. Water Uptake and Osmotic Potential of Soybeans During Germination

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土壤水分條件에 따른 大豆의 發芽反應에 관한 研究

第2報 發芽期에 있어서 大豆의 水分吸收 및 滲透壓 變異

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ABSTRACT

Laboratory experiements were conducted to evaluate water uptake and osmotic potential of soybean seeds associated with germinability. Bonus, Wayne, Essex and Pickett were selected for this study. Large and small seeds from the four varieties were included in water uptake measurements at 25°C.

There were significant differences in water uptake during germination due to seed size and cultivars at optimum moisture condition, -6 and -15 bars soil moisture. As water stress increased, the water uptake of Pickett and Essex were superior to Bonus and Wayne, and small seeds were superior to large seeds. The seed moisture content at germination was 60.8% on a fresh weight basis under optimum moisture condition. The minimum moisture contents necessary for the germination were 50.2% at -6 bars and 50.9% at -15 bars.

There were significant differences among varieties in seed osmotic potential during germination, although these differences depended on imbibition time. The average osmotic potential ranged from -32.0 bars after 4 hours imbibition to -11.2 bars at the beginning of germination. The correlation coefficient between seedling length and osmotic potential was not significant after any period of imbibition, suggesting that osmotic potential is not directly associated with seedling growth. However, osmotic potential is closely related to water uptake capacity of soybean seed.

INTRODUCTION

Initial step to improvement emergence through breeding is the identification of differential genetic potential for germination under water stress. Additionally, it would be desirable to understand the nature of germinability under water stress. Germination criteria such as water uptake and osmotic potential may be useful indication of drought resistance.

Two major factors have been considered relative to water uptake by seeds. One factor is the internal functions of seeds and the other is the external relationship between the seed and its substrate.[2] The imbibitional phase of germination has been

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described by Ching.[7] Subsequent phases are the metabolic phase and cell division or cell growth phase. Mostly, these phase are essential for rehydration of the seed as the initial step toward germination.

Soil water potential has been found to be an important external factor for germination.[8,12] Collis-George and Hector[8] indicated that matric potential might be an important factor in seed germination. At a given matric potential, rate of water uptake and rate of seed germination were increased by improving the degree of contact between soil and seed.[16] Hunter and Erickson[14] found that soybean failed to germinate at a tension of of more than -6.6 bars. Dasberg[9] found that eight crop species including *Orizopis heliciformis* showed a linear correlation between soil water content and seed water uptake, germination and length of shoot, but not between soil water content and length of root.

Seed structure and compostition have been considered to be important internal factors for seed germination. The rate of water uptake by seed is related to characters such as permeability of the seedcoat and the initial water content of the seed during imbibition.[3] Distribution of moisture throughout the seed is not uniform. Blackblow[3] found that the water content of corn embyros on a dry weight basis was 261% but that of the remainder of the seed was only 50%. Seed size and density(g/cm^3) have been found to be correlated with water uptake and germintion of corn[15], soybean[6,11], and wheat[5]. Edwards and Hartwig[11] reported that a small seeded soybean line showed a higher germination rate and greater development of roots under soil moisture stress than did a large seeded isoline. Harper and Benton[13] have found that large seeds may loose more water because of a large avarporative seed surface. Any gain in efficiency of utilization and transfer of reserve materials to the embyros in small seed resulted in faster growth.[5] In contrast, large soybean seeds take up more water than small seeds. The differences in water uptake are accounted for by differences in cotyledon size since the embyronic axes are identical in weight.[6]

After the initial phase of germiantion, the matric potential of seeds plays a minor role in water uptake of the seed[2]. Shaykewich[8] found that the water potential of rice, wheat, and maize seeds rose from -4000 bars during imbibition to less than -10 bars at the time of visible germination. The rate of decline in germination and seedling growth under water stress has been found to be heritable, varying with crop species and varieties.[10] For example, wheat cultivars differ inherently in their response to water stress. Only those adapted to arid and semiarid conditions become established into uniform and vigorous stand when germinated under moisture stress.[1]

Little information is available on variation among soybean varieties for water uptake, osmotic potential which are functionally related to the capacity for germination. However, based on available literature, it can be reasonably hypothesized that differences in seed osmotic potential and water uptake exist among soybean varieties, and that these differences may be useful in the improvement of the crop.

MATERIALS AND METHODS

Seed and Soil source

Wayne, Bonus, Essex and Pickett were selected for this study. Seeds were collected from plants grown in 1978 at Columbia, Missouri, U.S.A. Seeds were selected for freedom from seedcoat damage. Each variety was seperated into three sizes (large, medium and small) by passing the seeds through sieves with different opening sizes. Two sizes (large and small) were used for testing water uptake. The medium size was used for measurement of osmotic potential.

Seed ensity was measured as the weight of 10 seeds divided by the volume of water which they displaced. The formular $4\pi r^2$ was used to calculate the area of seed surface. The r indicated radius of the sieve openings. The moisture contents of the seeds were measured by oven drying at 95°C for 24 hours. These seed characteristics are shown in Table 1. Seeds were stored in sealed glass bottles at 5°C until testing.

Table 1. Characteristics of seeds selected for study.

Variety	Size	Initial Moisture	Weight	Volume	Density	Surface Area
		%	(g/10 seeds)	(ml/10 seeds)	(g/ml)	(cm^2)
Bonus	Large	0.2	2.40	2.02	1.19	0.64
	Small	8.9	1.86	1.52	1.22	0.39
	Medium	8.9	2.20	1.90	1.16	0.50
Wayne	Large	0.4	2.22	1.85	1.18	0.64
	Small	9.0	1.87	1.51	1.23	0.40
	Medium	9.1	2.00	1.72	1.17	0.50
Essex	Large	9.0	1.50	1.20	1.25	0.28
	Small	8.9	1.29	0.98	1.32	0.20
	Medium	9.0	1.40	1.10	1.27	0.24
Pickett	Large	9.1	1.35	1.09	1.24	0.28
	Small	9.0	1.20	0.90	1.32	0.20
	Medium	9.0	1.30	1.02	1.27	0.24

Water Uptake

Twenty seeds were placed in each of 192 petri dishes lined with 2 layers of 9 cm filter paper (Whatman No. 1) moistened with 10 ml of distilled water. Ten seeds per replication were randomly removed at 1,4,8,12,16,24,48 and 72 hours. In the soil moisture treatments, fifty seeds were placed in plastic containers, each with 500 g of soil adjusted to either -6 or -15 bars soil moisture tension by procedure described in the previous study.[15]. Ten seeds per replication were removed from each container at one day intervals for 5 days. The experiment consisted of a total of 24 plastic containers (2 seed sizes x 4 varieties x 3 replications). The 10 seeds removed were immediately weighed after blotting surface water or soil dust from them. Germination was observed at the time of sampling to determine the seed moisture content necessary for germination. Seed were considered germinated if the radicle extended 0.5cm. Dry weight was measured after oven drying at 95°C for 24 hours. Seed moisture contents were calculated and expressed on a fresh weight basis.

Osmotic potential

Ten seeds (medium size) from each variety were imbibed in a petri dish lined with 2 layers of filter paper moistened with 10ml of distilled water at 25°C. Three seeds per replication were randomly removed from petri dishes after 4, 8, 12, 16, 20, 24, 28 and 48 hours, and placed in a covered test tube after blotting the surface water from the seeds. The test tubes were maintained at -10°C. One of the three seeds was immediately removed from the test tube and immersed in 95% liquid nitrogen for one minute. Seed sap was extruded from the immersed seed with a Model DAH-107 (1½ ton capacity) Dura-Lift (Mid States Distributing Co., St. Paul, Minn.).

One drop of the sap was placed in a sample container and inserted into the sample chamber of a HR-Dew Point Microvoltmeter (Wescors Inc.). The dew point in microvolt was read at 30 minutes intervals until it equillibrated. The remaining two seeds in the test tube were sequentially measured by the above procedure. This experiment was conducted with 12 replications, each replication consisting of three seeds. Osmotic potential of the seeds was read from a standard curve developed with mannitol solutions (Figure 1.).

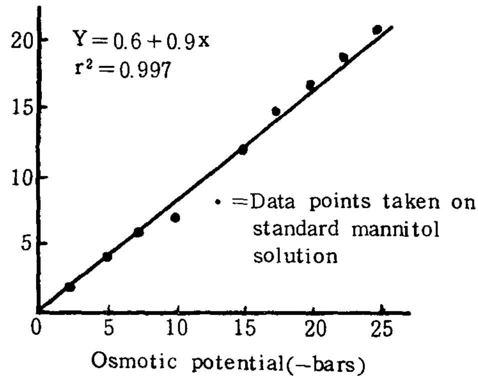

Fig. 1. Standard curve for osmotic potential developed with mannitol solutions.

Statistical Analysis

All data were subjected to analysis of variance. The 5% level of probability was applied to compare treatment means. For those comparisons where F-test was significant, an LSD was calculated. Equations for osmotic potential of soybean varieties as a function of imbibition were established using non linear squares methods. The equation form was $-\Psi_0 = a + b_1/T + b_2/T^2 + \ldots\ldots + bi/T^i$ in which $-\Psi_0$ = predicted osmotic potential value, a = intercept, b = regression coefficient and T = imbibition time. Correlation coefficients between osmotic potential at each imbibition time and seedling length grown in petri dish for three days were calculated.

RESULTS AND DISCUSSION

1. Water Uptake

The effects of variety, time and size on water uptake were highly significant at each moisture

Table 2. Water uptake (%) by two seed sizes of four soybean varieties imbibed under optimum moisture condition.

Variety	Size	Imbibition (hours) 1	4	8	12	16	24	48	72	Average
Bonus	Mean	27.0	46.8	55.9	57.5	58.9	59.7	59.7	62.1	53.4
	Small	24.6	45.6	55.6	57.5	59.4	59.9	60.0	63.0	53.2
	Large	29.3*	47.9	56.1	57.4	58.4	59.5	59.3	61.1	53.6
Wayne	Mean	25.9	47.4	54.5	58.7	59.6	59.5	59.8	61.5	53.3
	Small	25.3	47.7	53.7	58.7	60.3	60.2	60.4	62.7*	53.6
	Large	26.5	47.1	55.2	58.7	58.8	58.8	59.1	60.3	53.1
Essex	Mean	30.9	51.7	57.3	59.0	59.3	60.3	61.5	67.5	55.9
	Small	31.9	54.1*	58.1	58.9	59.8	60.3	61.8	67.8	56.6
	Large	29.8	49.3	56.5	59.0	58.8	60.3	61.1	67.1	55.2
Pickett	Mean	35.9	56.7	60.9	64.0	62.9	61.9	62.2	65.1	58.7
	Small	35.6	57.5	62.8*	66.9*	64.2*	62.7	62.6	66.3*	59.8
	Large	36.2	55.9	58.9	61.0	61.5	61.0	61.7	63.8	57.5
Average	Small	29.3	51.2	57.5	60.5	60.9	60.8	61.2	64.9	55.8
	Large	30.5	50.0	56.7	59.0	59.3	59.9	60.3	63.2	54.9
	Mean	29.9	50.7	57.2	59.8	60.1	60.4	60.8	64.1	55.5

*Significant at 5% level between sizes at given variety and time.

——Note germination

LSD .05 = 0.5 for variety, 0.3 for size, 0.7 for time, 1.4 for variety x time, 0.7 for variety x size, 1.0 for time x size, and 2.2 for variety x time x size.

level. All interractions were significant under optimum moisture condition and -6 bars except the interaction of time x size at -6 bars (Table 2 and 3). At -15 bars, none of interactions were not significant (Table 4). The interaction of variety x time x size indicates that the differences between seed sizes are due to differences in responses of variety with increase in imbibition time. The differences in water uptake between seed sizes were not consistent with time and variety at the optimum moisture condition, but in general, the differences bacame more pronounced with increase in time (Table 2). At -6 bars, the small seeds of Essex showed higher water uptake at all imbibition times than did the large seeds. From the second day onward, the small seeds of Pickett and Bonus showed greater moisture uptake than did large seeds (Table 3).

Table 3. Water uptake (%) by two seed sizes of four soybean varieties planted at -6 bars soil moisture.

Variety	Size	Planting (days)					Average
		1	2	m3	4	5	
Bonus	Mean	37.3	47.5	52.5	55.2	56.9	49.9
	Small	37.1	48.1	54.4*	56.7*	59.5*	51.1
	Large	37.4	46.8	50.6	53.8	54.3	48.6
Wayne	Mean	36.7	47.0	52.5	56.2	56.7	49.8
	Small	37.5	48.6*	52.5	56.4	56.1	50.2
	Large	36.2	45.4	52.5	55.9	57.2	49.4
Essex	Mean	43.3	51.0	57.2	59.6	65.0	55.2
	Small	46.6*	53.6*	59.7*	62.2*	66.9*	57.8
	Large	40.1	48.4	54.7	56.9	63.1	52.6
Pickett	Mean	46.5	55.2	61.4	61.1	70.0	58.8
	Small	46.4	57.5*	64.9*	62.9*	72.4*	60.8
	Large	46.5	52.8	57.8	59.3	67.5	56.8
Average	Small	41.9	52.0	57.9	59.5	63.7	55.0
	Large	40.1	48.4	53.9	56.5	60.5	51.9
	Mean	41.0	50.2	55.9	58.0	62.1	53.5

*Significant at 5% level between sizes at given variety and time.

___Note germination.

LSD .05 = 3.3 for variety, 1.4 for time, 1.0 for size, 1.2 for vareity x size, 2.5 for variety x time, and 2.7 for variety x time x size.

Ashraf and Abu-shakra[1] found varietal differences in water uptake, and that a reduction in water uptake under moisture stress appeared to be a major factor affecting rate of germination of wheat. Pickett had a higher water uptake content at the three moisture conditions than did other varieties except that differences between pickett and Essex were not significant at -15 bars (Table 3). The water uptake content of Essex was superior to Bonus and Wayne at all moisture conditions. There were no significant differences between Bonus and Wayne at any of the moisture levels (Table 2, 3, and 4).

As water stress increased, the effect of seed size on water uptake increased. There were no significant differences between seed sizes of Bonus and Wayne at the optimum moisture condition (Table 2). Water uptake by small seeds of Bonus, Essex and Pickett was significantly higher at -6 bars than water uptake by large seeds (Table 3).

Table 4. Water uptake (%) by two seed sizes of four soybean varieties planted at -15 bars soil moisture.

Variety	Size	Planting (days) 1	2	3	4	5	Average
Bonus	Mean	29.1	38.7	40.6	44.7	47.9	40.2
	Small	30.8	40.8	42.8	45.9	49.3	41.9
	Large	27.4	36.5	38.3	43.4	46.4	38.4
Wayne	Mean	32.4	36.5	42.8	45.0	48.4	41.0
	Small	34.2	37.9	43.3	46.5	49.6	42.3
	Large	30.6	35.0	42.3	43.5	47.1	39.7
Essex	Mean	34.4	41.4	48.3	49.6	52.3	45.2
	Small	36.2	42.0	50.3	51.0	53.1	46.5
	Large	32.5	40.8	46.2	48.1	51.5	43.8
Pickett	Mean	35.8	42.7	47.4	52.6	55.1	46.8
	Small	35.8	41.8	48.6	53.6	55.6	47.1
	Large	35.8	43.6	46.2	51.6	54.5	46.4
Average	Small	34.3	40.6	46.3	49.3	51.9	44.5
	Large	31.6	39.0	43.3	46.7	49.9	42.1
	Mean	33.0	39.8	44.8	48.0	50.9	43.3

____Note germination.

LSD .05 = 2.5 for variety, 1.8 for time, and 0.7 for size.

For corn[16], wheat[5], and soybean[11], various researchers have reported that small seeds show a higher germination rate under water stress than do large seeds. Bermner *et al*[5] suggest that any great efficiency in small seeds in utilization and transfer of reserve materials to embyros resulted in faster growth. Large seeds may loose more water because of a large evaporative seed surface.[13] In contrast, large seeds require more water than do small seeds. The differences in water uptake is accounted for by the differences in cotyledon size since the embyronic axes are indentical in weight.[6] In this study, the relative faster water uptake contents by small seeds of Essex and Pickett may have resulted as a consequence of less seed volume, higher seed density and smaller seed surface area. These characteristics may be related to better germination under stress.

Active seedling elongation may have marked following 48 hours imbibition under the optimum moisture condition (Table 2). The basic period for germination was 48 hours at 25°C without any limiting moisture factors. On the everage, the seed moisture content at germination was 60.8% on a fresh weight basis under optimum moisture condition (Table 2). Hunter and Erickson[14] suggested a critical or minimum seed moisture content for germination : 50.0%. This value is a relative higher amount compared to other crop such as corn, sugar beet and rice.[14] Essex and Pickett obtained the necessary seed moisture contents for germination at -6 bars in 2 days compared to 3 days for Bonus and Wayne (Table 3). At -15 bars, Essex and Pickett required 5 and 4 days, respectively to obtain the minimum moisture for germination, but Bonus and Wayne did not obtain enough moisture to germination in 5 days (Table 4).

Small seeds of the four varieties tested obtained the necessary average moisture for germination in 2 days after planting at -6 bars and 5 days after planting at -15 bars. The large seeds required 3 days for obtaining the necessary moisture at -6 bars and did not obtain it 5 days after planting at -15 bars soil moisture tension (Table 3 and 4). These results suggest that small seeds take up water faster than do large seeds. Essex and Pickett obtained more water for germination under water stress. Germination at 25°C occurs when seed moisture contents were above 50% on the fresh weight basis. This value is same as the findings of Hunter and Erickson[14] and Bowen and Hummel.[4]

2. **Osmotic Potential**

The mean averaged across the varieties estimates the average effect of changing imbibition time on osmotic potential of soybean seeds. There were large and significant difference in osmotic potential with imbibition time. However, the average osmotic potentials were not different between 28 and 48 hours imbibition (Table 5). The average values ranged from -32.0 bars at the time of the first measurement (4 hours) to -11.2 bars at the beginning of germination (48 hours). The average osmotic potentials were -19.4 for Bonus, -18.3 for Wayne, -15.1 for Essex and -13.2 bars for Pickett (Table 5).

The variety x time interaction indicetes differences in magnitude of variety response to the increase in imbibition time. The mean osmotic potential of pickett tended to be higher then those of the other varieties at all imbition times. There were no significant differences in the mean osmotic potentials of Bonus, Wayne and Essex at 24, 28 and 48 hours imbibition, but Essex showed significantly higher value at other imbibition times than did Bonus and Wayne (Table 5).

Table 5. Mean osmotic potential of four soybean varieties at different imbibition times.

Variety	Imbibition (hours)								Average Variety
	4	8	12	16	20	24	28	48	
	Osmotic potential (-bars)								
Bonus	38.9	24.7	21.6	16.9	15.4	13.6	12.3	11.8	19.4
Wayne	36.9	21.6	20.5	15.9	14.3	13.2	12.1	11.7	1 18.3
Essex	25.0	17.4	15.2	13.8	13.3	12.3	12.0	11.6	15.1
Pickett	27.1	14.8	12.5	10.7	10.2	10.0	10.1	9.8	13.2
Average time	32.0	19.6	17.5	14.3	13.3	12.3	11.6	11.2	16.5

LSD .05 = 0.3 for average variety.
0.4 for average time.
0.9 for interaction of variety x time.

Equations describing changing osmotic potential of the four varieties as a function of imbibition time were developed by nonlinear squares analysis. The equations are plotted in Figure 2. Osmotic potential increased rapidly (became less negative) between 4 and 8 hours imbibition, and estimates ranged from -11.0 bars for Bonus to -9.5 bars for Pickett at beginning of germination. The rapid increase in osmotic potential at early imbibition may result from osmotic activity of storage materials. After this rapid increase phase, the increase of osmotic potential may result from an increase of water uptake capacity due to difference in seed size. Thus, the small seeded variety Essex and Pickett showed higher osmotic potential than did the large seeded variety Bonus and Wayne. A possible explanation for the differences in osmotic potential among the varieties is that the seeds of Essex and Pickett may be more powerful osmotic substrates than are Bonus and Wayne. After the initial imbibition phase and hydration of cell walls and cell contents of seeds, the matric potential plays a minor role in attracting water into cells of seeds.

Bewley and Black[2] indicate that some of matrices such as protein and carbonydrates are later hydrolyzed to lower weight molecules. Thus, osmotically active substrates which effect the water

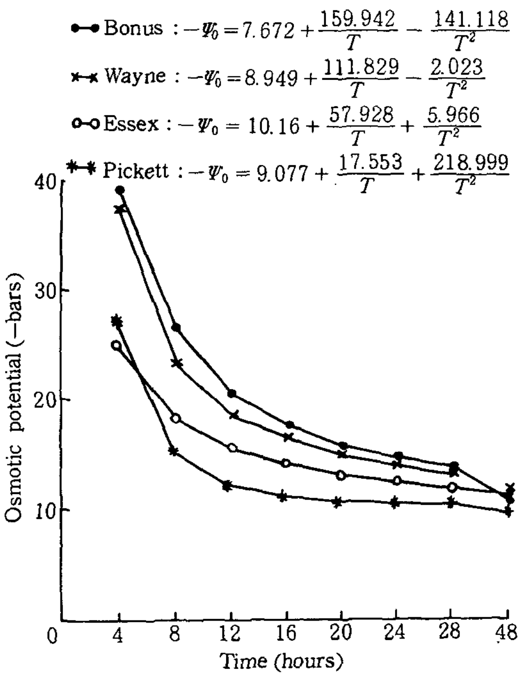

Fig. 2. Osmotic potential of soybean seeds during imbibition.

potential of both the whole seed and embyronic axes increase.

The increase in water uptake at the beginning of germination is initially associated with a decrease in water potential due to changes related to germination, and then by a decrease in osmotic potential due to post-germination reserve hydrolysis.[2] The water potential of a mature, dry seeds is very much lower than that of the surrounding substrate. So water moves in the direction of decreasing water potential. Aš seeds start to take up water, they exert a large swelling pressure. Rape, Wheat and Corn seeds showed -4000 bars of pressure during the initial imbibition phase.[18] This pressure was reduced to elss than -10 bars at beginning of germination. In the present study, it is expected that initial osmotic values of dry seeds were very low (Figure 2).

Correlation coefficients between osmotic potential of soybeans at each of the imbibition times and seedling length measured in petri dishes were not significant (Table 6). This suggests that the osmotic potentials of soybean are not directly associated with seedling elongation. However, the correlation coefficients between seed moisture content and osmotic potential were highly significant (r=.98). Thus, osmotic potentials are related to water uptake. Pickett and Essex had higher water uptake contents than did Bonus and Wayne. This is closely related to the osmotic data presented. It may be possible to use osmotic potential of soybean seeds as a criterion for estimating water uptake capacity under water stress.

Table 6. Correlation coefficients between seedlig length and osmotic potential of soybeans at different imbibition times.

Variety	Imbibition (hours)							
	4	8	12	16	20	24	28	48
	Correlation coefficient							
Bonus	-0.19	0.01	-0.28	-0.16	0.15	-0.33	-0.04	-0.30
Wayne	0.52	-0.10	-0.15	0.11	0.39	0.17	0.09	-0.06
Essex	0.16	-0.46	-0.27	-0.23	0.25	0.35	0.17	0.06
Pickett	0.05	0.55	0.45	0.19	0.43	0.19	0.30	-0.13

Seedling length summing hypocotyl and root measured 3 days after planting in petri dish.

摘 要

本 試驗은 大豆 種子의 水分吸收 및 滲透圧이 發芽에 미치는 影響을 究明코저 遂行되었다. Essex, Pickett, Bonus와 Wayne 4個品種이 供試되었고, 이들 品種들의 種子를 各各 小粒 및 大粒으로 分類하여 水分吸收를 測定하였다. 그 結果를 要約하면 다음과 같다.

1. 모든 水分條件에서 大豆 種子의 水分吸收 能力은 種子의 크기 및 品種間의 有意的인 差를 보였다.

Essex와 Pickett은 Bonus와 Wayne에 비해, 同一品種內에서 小粒은 大粒에 비해 水分吸收 能力이 優越하였다.

2. 25℃의 溫度에서 大豆 種子의 發芽期間은 適當한 水分條件 및 −6bars의 土壤水分 狀態에서 2日, −15bars의 土壤水分 條件에서는 5日로 遲延되었고, Essex나 Pickett은 Wayne이나 Bonus에 비해, 그리고 小粒種은 大粒種에 비해 發芽期間이 短縮되었다.

3. 適當한 水分條件에서 發芽初期에 大豆 種子의 水分含量은 60.8%이였으며, 發芽에 必要한 最小 種子의 水分含量은 −6bars에서 50.2%, −15bars에서 50.9%이었다.

4. 發芽期에 있어서 大豆 種子의 滲透圧은 品種 및 浸種時間에 따라 有意的인 變異를 보였으며, 4時間과 8時間 浸種사이에서 急激한 增加를 보였다. 平均滲透圧은 4時間에 浸種에서 −32.0bars, 發芽初期에서 11.2bars의 範圍를 나타냈다.

5. 初期 浸種으로부터 發芽初期 동안의 品種別 全體平均 滲透圧을 보면 Bonus가 −19.4bars, Wayne이 −18.3bars, Essex가 −15.1bars, 그리고 pickett이 −13.2bars이었다.

6. 浸種時間에 따른 草長의 길이와 滲透圧間의 相關係數는 有意性이 없었으며, 이 結果는 大豆 種子의 滲透圧은 初期草長의 生長과 直接的인 關聯이 없는 것으로 推定된다. 그러나 水分吸收와 滲透圧間의 相關係數는 高度의 正의 有意性을 보였다 (r=.98). Bonus나 Wayne에 비해 Pickett과 Essex는 높은 滲透圧을 보였으며, 이것은 水分吸收 試驗結果와 一致하고 있다. 따라서 大豆 種子의 滲透圧은 乾燥狀態에서 發芽能力을 推定하는 하나의 指標가 되리라 생각한다.

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