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Drought hardening of the potato plant as an after-effect of soil drought conditions at planting

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Zusammenfassung, Résumé p. 190, 191

Summary

A field trial with the potato variety *White Rose* was carried out in order to investigate the influence of soil drought conditions at planting time on the subsequent growth behaviour and on the tuber yield. Drought at planting time delays tuber set, shortens the tuber formation period, increases tuber number, promotes their active bulking and produces a significant increase in yield. When soil drought conditions are permitted to develop at the beginning of the tuberization stage, the tuber formation period is lengthened to the detriment of their number, growth and yield. These detrimental effects almost disappear if planting is carried out under high soil moisture stress. Thus, drought hardening at the critical stage of water requirement would arise as an after-effect of drought at planting time.

Introduction

The potato plant requires an adequate water supply at the beginning of the tuberization stage, as shown by its response to different water regimes applied at various stages of its vegetative cycle (Salter and Goode, 1967). It has, however, proved possible to increase the drought resistance of some cultivated plants (May et al., 1962). Thus, pre-sowing treatments on some species – especially cereals – seem to be particularly effective (May et al, 1962). Positive results have also been achieved with growth retarding substances applied to young plants (El Damaty, Kuhn and Linser, 1965; Halevy and Kessler, 1963).

In the case of the potato plant, drought hardening is claimed to be attained by spraying tubers with several chemical substances – boric acid 0.02%, calcium superphosphate 1.5% (Grecisnikova, 1962) – or by submitting sprouted tubers to a certain water stress before planting (May et al., 1962).

In previous work on the potato (*Solanum tuberosum* L., var. *White Rose*) we have shown the existence of a critical water requirement at the beginning of the tuberization stage (Lis et al., 1964). At the same time drought treatment at planting showed a tendency to increase yield. This fact led us to think that the same drought treatment at planting might induce hardening at the critical water requirement stage. The aim of our work also included the study of the concomitant possibility of morphophysiological changes and their connections with its physiological mechanism. This takes into account the fact that all factors that promote or delay the sprout and/or root growth decrease or increase, respectively, the time to plant emergence; a fact that causes a partial displacement, and eventually can alter, the vegetative cycle growth and senescence of the leaves, flowering, beginning of the tuberization stage and tuber growth (Gifford and Moorby, 1967; Toosey, 1964; van Schreven, 1956). Moreover, potato tuber yield is closely related to the time of tuber set as well as to the modality and length of the growing period of tubers and to the persistence of leaves (Borah and Milthorpe, 1960; Toosey, 1964). It must be remembered that the critical stage of water requirement related to the tuber yield coincides with the beginning of the tuberization stage. Furthermore, if irrigation is supplied at stolon growth stage, early growth and senescence of the leaves is induced, a fact that shortens the bulking period of tubers with a concomitant decrease in tuber yield (Llewelyn, 1962).

Finally, experimental evidence shows that different water status in connection with certain morphological changes can alter, in quality as well as in quantity, the growth behaviour of certain plants. In the onion, drought at the critical stage of water requirement (bulb set) remarkably affects bulb fresh weight and diameter, without affecting the number of leaves and bulb-scales (Lis et al., 1967). On the other hand, drought at the seedling stage induces early bulb formation without affecting yield (Lis, et al., 1967; 1968).

Material and methods

Tubers of the *White Rose* potato variety, of uniform size and weight (80–100 g) were cut longitudinally and used as 'seed'. The vegetative cycle lasted 112 days, from planting (Nov. 23, 1965) to harvest at plant senescence (March 23, 1966). Treatments were set as follows:

0. Control, irrigated throughout the whole growing period;
1. Drought at planting, but irrigated thereafter;
2. Drought at the critical stage of water requirement (tuber set), but irrigated at planting and during the remaining stages of growth;
3. Drought at planting and drought at the critical stage, but irrigated at the remaining stages of growth.

The trial was carried out at the experimental field of the Plant Physiology Department, Facultad de Ciencias Agrarias, Universidad Nacional de Cuyo, Chacras de Coria, Mendoza, Argentine.

The original edaphic characteristics (loam-clay-silt texture; field capacity 23.5%; wilting point 10.2%) were modified by adding a layer of fine sand, 10 cm thick, later on mixed by adequate cultivation. So modified, the soil proved to have a field capacity of 21%, a wilting point of 7% and an apparent specific weight of 1.3 g/cm^3 (over 60 cm depth average). The profile water holding capacity was 73 mm and 109 mm, up to 40 cm and 60 cm soil depth, respectively. We used a randomized block design, with five replications. At planting time each plot (6 m $\times$ 4.5 m) had 8 rows (80 cm apart) and 48 plants (40 cm apart). At harvest the useful plot (20 m^2) had an average of

30 plants, due to sample lifting and two outside rows discarded in determining yields.

Soil moisture was determined gravimetrically on samples taken every 3–4 days. On the basis of the average soil moisture under all treatments except those under drought, each irrigation was calculated to restore field capacity up to 40 cm soil depth till January 28 and up to 60 cm soil depth from February 4 onwards. Each plot was furrow-irrigated. Hand planting was carried out at 5 cm depth. Four days before it, Treatment 0 and 2 (without drought at planting) were irrigated to field capacity and at planting time they had 65% available soil moisture. The remaining treatments were planted on non-irrigated soil (5% available moisture). In these Treatments (1 and 3) irrigation was started when sprouts emerged. For all treatments, except those under drought, water was replenished by irrigation when it fell to 60% available soil moisture. Under drought treatments irrigation was interrupted at tuber set and resumed after two days of wilting symptoms.

As drought at planting delayed tuber set, the critical stage did not coincide in time for Treatment 2 and 3. Figure 1 records sprouting, emergence, stolon and tuber set for each treatment as well as the irrigation supply and available moisture registered during the whole vegetative cycle. Plant samples (2 for each replication, 10 for each treatment at each sample date) were taken at 9 to 10-day intervals throughout the growing season, beginning on December 20. The statistical evaluation of tuber yield (kg/plot) was carried out by the variance analysis and a 't'-test was preformed to find out the significance of the differences between mean yields.

Results

A. Influence on tuber yield

The data of Table 1 and 2 shows that the highest yields are obtained with Treatment 1 (drought at planting) achieving a significant difference from the control and a

Table 1. Tuber yields.

Replications[1]	Tuber yields (kg/plot)			
	Treatment 0	Treatment 1	Treatment 2	Treatment 3
1	10.5	16.1	3.7	12.5
2	15.6	23.1	7.7	15.1
3	13.0	11.5	8.9	7.5
4	14.4	16.8	11.1	14.8
5	9.2	16.2	4.1	16.5
Mx	12.5	16.7	7.1	13.2

[1] *Wiederholungen – Répétitions* [2] *Verfahren – Traitement*

Tabelle 1. Knollenertrag (kg/Parzelle).
Tableau 1. Rendement en tubercules (kg/parcelle).

Table 2. Significance of the differences between the mean yields.

Treatment[1]	Mx	Significance of the differences between the mean yields			
		Treatment 0	Treatment 1	Treatment 2	Treatment 3
0	12.5	—	*	*	—
1	16.7		—	**	—
2	7.1			—	**
3	13.2				—

[1] Verfahren – *Traitement*
* Significant difference (level 0.05) – *Signifikanter Unterschied (P 0,05) – Différence significative (seuil 0,05)*
** Highly significant difference (level 0.01) – *Hoch signifikanter Unterschied (P 0.01) – Différence hautement significative (seuil 0,01)*
LSD – Kleinster signifikanter Unterschied – Plus petite différence significative

Tabelle 2. Signifikanz der Unterschiede zwischen den durchschnittlichen Erträgen.
Tableau 2. Degré de significance des différences entre les rendements moyens.

highly significant difference from Treatment 2 (drought at the critical stage of water requirement).

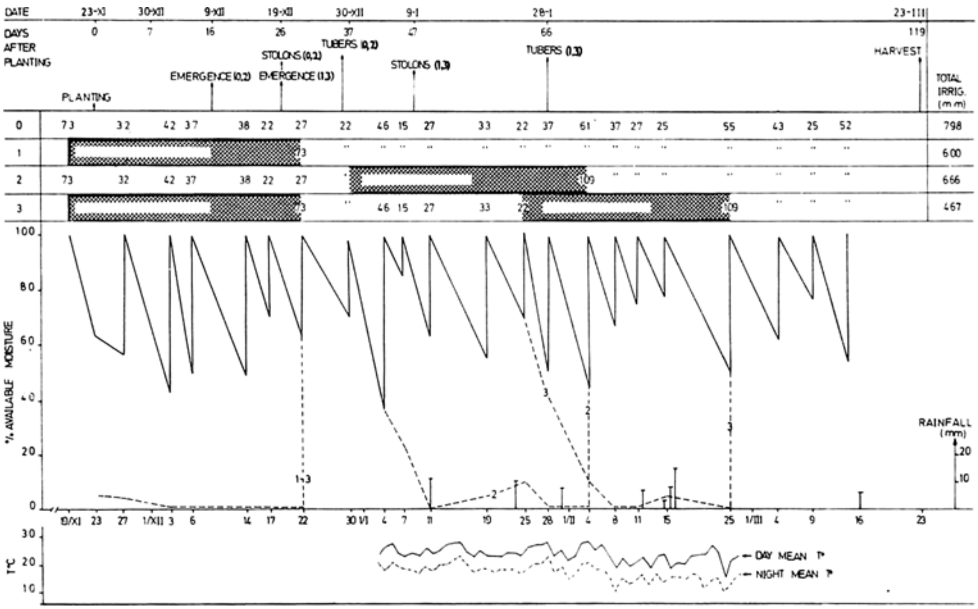
The strong detrimental effect of soil drought conditions at tuber set is confirmed (Lis et al., 1964). This effect is emphasized when we take into account the fact that the yield is significantly different not only from the control but also from the other treatments. The drought hardening effect of high soil moisture stress at planting become apparent through Treatment 3 the yield of which shows a significant difference only from Treatment 2 (drought at the critical stage). This means that the soil drought conditions at planting seem to nullify the detrimental effect of drought at the critical stage. Another important fact to note is the amount of water supplied to each treatment. It is noticeable that Treatment 3, getting 42% less water that the control did. shows no yield difference from the control nor from Treatment 1 (drought at planting), In addition, its yield is almost double that of drought treatment at the critical stage in spite of having received 25% less water.

B. Influence on the vegetative growth behaviour

Sprouting was simultaneously recorded for all treatments but the following vegetative stages were progressively delayed under the two treatments with drought at planting. Thus under Treatments 0 and 2, emergence, appearence of stolons and tuber set proceeded at 8 to 10-day intervals from tuber bud sprouting, while under Treatment 1 and 3 these intervals lengthen to 20 days. This involves a total delay of 30 days for tuber set relative to treatments without drought at planting. Consequently drought at the critical stage (tuber set) could not chronologically coincide for Treatments 2 and 3.

The whole period of tuber growth lasted 53 and 83 days, respectively, for treatments with and without drought at planting. This accounts for the recorded simultaneous plant senescence in all treatments even though the tuber set was not simultaneous.

Fig. 1. Drought treatments, vegetative evolution, irrigation supply, soil water depletion, rainfall data and average day and night temperature during the potato growing season.



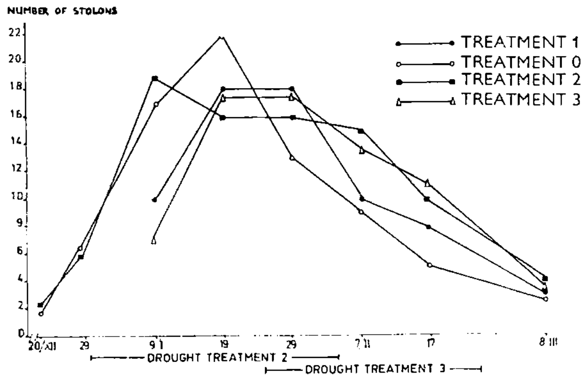
Date – *Datum – Date*
Days after planting – *Tage nach dem Auspflanzen – Jours après la plantation*
Planting – *Pflanzdatum – Plantation*
Emergence – *Auflaufen – Levée*
Stolons emergence – *Auflaufen der Stolonen – Apparition des stolons*
Tubers – *Knollen – Tubercules*
Stolons – *Stolonen – Stolons*
Harvest – *Ernte – Récolte*
Total irrig. – *Bewässerung total – Irrigation totale*
% available moisture – *% verfügbare Feuchtigkeit – % humidité disponible*
Rainfall – *Regen – Pluie*
Day mean T° – *Mittlere Tagestemperatur – Température moyenne diurne*
Night mean T° – *Mittlere Nachttemperatur – Température moyenne nocturne*
Without irrig. – *Ohne Bewässerung – Sans irrigation*

Abb. 1. Trockenheitsverfahren, vegetative Entwicklung, Bewässerungsmenge, Erschöpfung des Bodenwassers, Angaben über Regen sowie über die durchschnittlichen Tages- und Nachttemperaturen während der Zeit des Kartoffelwachstums.
Fig. 1. Traitements de sécheresse, évolution de la végétation, apport par irrigation, déficience en eau du sol, pluie et températures moyennes diurnes et nocturnes pendant la période de croissance.

C. Influence on stolon and tuber formation

In all cases we observed only 2–3 cm long primary stolons. Treatment 1 (drought at planting) is the only one registering the same stolon and tuber number. This would imply that all stolons had produced tubers at the tuberization stage. Stolon formation

Fig. 2. Influence of the drought treatments on the number of stolons during the potato growing season.

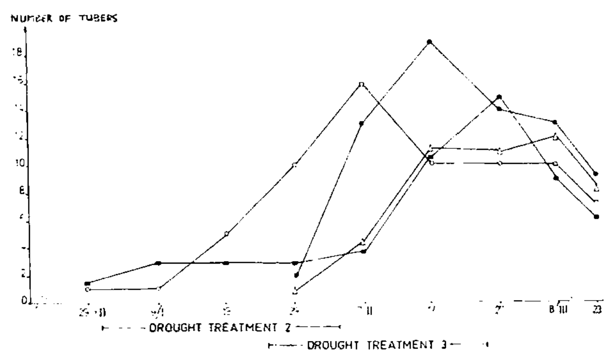


Treatment – *Verfahren – Traitement*
Stolons – *Anzahl Stolonen – Nombre de stolons*
Drought treatment – *Dürre-Behandlung – Traitement de sécheresse*

Abb. 2. Einfluss der Dürre-Behandlung auf die Anzahl der Stolonen während der Zeit des Kartoffelwachstums.
Fig. 2. Influence des traitements de sécheresse sur le nombre de stolons pendant la saison de croissance.

and even new tuber formation are depressed if drought conditions are permitted to develop at the critical stage (Treatment 2). Thus, under this treatment the maximum number of these organs is obtained with 20 days delay compared with the control. Drought at planting caused an opposite effect, delaying tuber set (30 days) but remarkably accelerating the subsequent tuber formation rate. Treatment 1, therefore obtained its maximum tuber number only 10 days after the control did. Treatment 3 shows the delaying effect of drought at planting on stolon and tuber set, while the depressing effect of drought at the critical stage is evidently diminished.

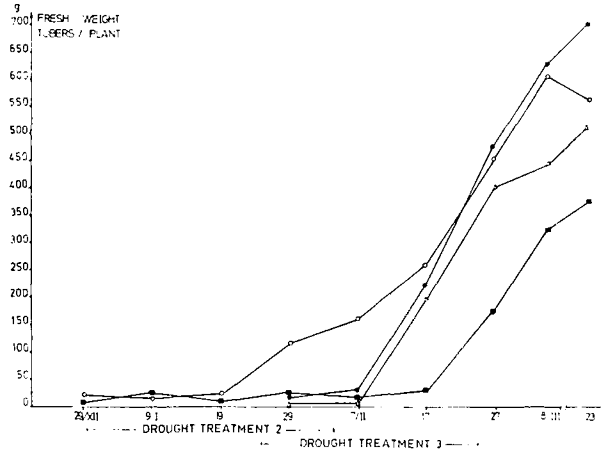
Fig. 3. Influence of drought treatments on the number of tubers during the potato growing season.



Tubers – *Anzahl Knollen – Nombre de tubercules*
Drought treatment – *Dürre-Behandelung – Traitement de sécheresse*

Abb. 3. Einfluss der Dürre-Behandlungen auf die Anzahl der Knollen während der Zeit des Kartoffelwachstums.
Fig. 3. Influence des traitements de sécheresse sur le nombre de tubercules pendant la saison de croissance.

Fig. 4. Influence of drought treatments on the fresh weight of tubers during the potato growing season.



Fresh weight tubers/plant – *Frischgewicht Knollen/Pflanze – Poids frais tubercules/plante*
Drought treatment – *Dürre-Behandlung – Traitement de sécheresse*

Abb. 4. Einfluss der Dürre-Behandlungen auf das Frischgewicht der Knollen während der Zeit des Kartoffelwachstums.
Fig. 4. Influence des traitements de sécheresse sur le poids frais de tubercules pendant la saison de croissance.

D. Influence on size and weight of the tubers

Drought at planting, that shortens by 30 days the tuber formation period, also modifies their growth behaviour, for the lag phase almost disappears and the active bulking period is promoted. This double effect accounts for the high final yields obtained (Fig. 3). Once more the opposite effect of drought at the critical stage Treatment 2) is evident, for the lag phase is lengthened even to 15 days after drought at the expense of the active bulking period and so of final yields. The hardening effect of drought at planting Treatment 3) is enhanced, for tuber weight increase does not stop during drought at the critical stage. Thus, this treatment, under our experimental conditions, gives yields that are practically equal to those of plants normally irrigated during the whole vegetative cycle.

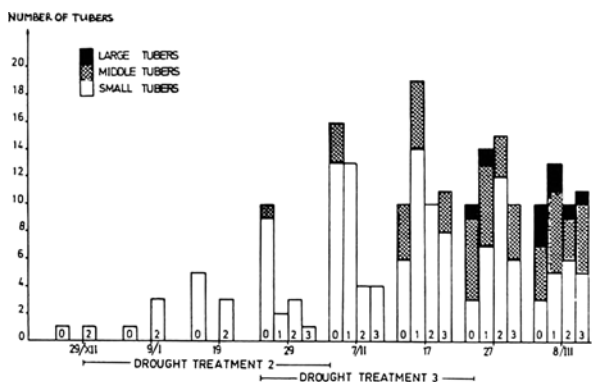
Discussion

From Tables 1 and 2 we can conclude that the potato variety *White Rose* shows, during its vegetative cycle, a different response to water stress. This involves a significant increase (drought at planting time) or decrease (drought at tuber set) in yields, independent of the amount of water supplied. Under our experimental conditions, the *White Rose* variety, submitted to drought from planting to emergence, increased its yield to 33 % above the control yield. On the other hand, the same water stress treatment seems to cause drought hardening at the beginning of the tuberization stage. This hardening effect is closely associated with a different tuberization behaviour in response to drought at tuber set, as is shown by treatments with and without drought at planting time. Thus Treatment 3 shows a progressive increase in tuber number in contrast to the depressing effect of the same drought on Treatment 2 (Fig. 3).

It is claimed that, in the potato plant, all stolons appear almost simultaneously and after a certain period, the length of which is a varietal characteristic, tuber set behaves similarly (Madec et Perennec, 1954; Krijthe, 1955). The curves showing the organ number evolution in our trial suggest two possibities: a. that these organs (stolons and tubers) would appear at a variable rate till the end of the whole vegetative cycle; b. that under our trial conditions the data represented the progressive plant population growth and could not be taken as representative of the growth pattern of individual plants. Neverthless from the comparative analysis of Fig. 1 and 2, it is obvious that while the stolon and tuber number increases with time new organs continue to be formed. In addition, nontuberized stolons outnumber tuberized ones only during the increasing portion of the curve.

The comparative analysis of the data relating to number, fresh weight and size of tubers gives us a hint for interpreting the general behaviour of tuberization. Actually, the lag and exponential phases of fresh weight growth coincide with the increasing period of tuber number, while the linear growth phase begins when this number decreases. This fact indicates that the formation of these organs takes place during the lag and exponential phases of fresh weight growth and their highest increase in fresh weight occurs during the growth of tubers already formed. In addition, the increase in tuber number during the lag and exponential phases seems to be a consequence of the continuous appearance of new organs (see Fig. 5 'small tubers'), while their decrease observed during the active growth period, is perhaps a consequence of a process of tuber resorption (Milthorpe, 1963). Furthermore, the appearance of middle sized tubers indicates the end of the formation period of these organs (see Fig. 5).

Fig. 5. Influence of drought treatments on the size distribution of tubers during the potato growing season.



Tubers – *Anzahl Knollen – Nombre de tubercules*
Large tubers – *Grosse Knollen – Gros tubercules*
Middle tubers – *Mittlere Knollen – Tubercules moyens*
Small tubers – *Kleine Knollen – Petits tubercules*

Abb. 5. Einfluss der Dürre-Behandlungen auf die Grössenverteilung der Knollen während der Zeit des Kartoffelwachstums.
Fig. 5. Influence de traitements de sécheresse sur la répartition de la grosseur des tubercules pendant la saison de croissance.

It was stated that the environmental conditions prevailing during the first two weeks of the tuberization stage determine the behaviour of tuber growth, apparently closely related to the foliar area attained up to that moment. In order to lengthen this growth period and obtain an increase in yields, early planting has been suggested (Borah and Milthorpe, 1960). However, the effectiveness of this technique seems doubtful, for these early plantings lead to less active growth and early foliar senescence with a detrimental effect on tuber growth (Radley et al., 1961). The results of our trial show that the prevailing soil water conditions at the time of sprouting and tuber set stages influence remarkably the tuberization behaviour. Thus, when sprouting of seed tubers takes place under high soil moisture stress, at last under our trial conditions, the time of tuber set is delayed, the tuberization period is shortened, the number of tubers is increased and their active growth period is enhanced. All these facts seem, in turn, to result in high final yields. On the contrary, when the same drought conditions occur at tuber set, the whole tuber formation period lengthens to the detriment of tuber number, growth and yield. The response to the combined treatment (drought at planting and drought at tuber set) shows that the water status during sprouting of seed tubers has a decisive influence on the tuberization behaviour. Hardening to drought at the critical stage appears as an after-effect of drought at planting. This hardening seems evident taking into account the disappearance of the detrimental effects caused by drought at the critcal stage on the tuber growth and yield. The possibility cannot be excluded that the high soil water stress at planting could have modified the soil temperatures round the tubers under drought and, as a consequence, their physiological status. With regard to this, it has been shown that, in certain varieties, the incidence of high temperatures on seed tubers before planting increases yield (Tizio and Montaldi, 1953; Tizio et al., 1955). Lastly, the fact of non-simultaneous tuberization under Treatment 2 and 3 suggests the incidence of an additional factor. Indeed, the delay in tuber set delays, in its turn, the whole growing period of the tubers which as a consequence, takes place under different, and probably more favourable, environmental conditions (Yamaguchi et al., 1964).

Summing up, the hardening effect of drought at planting in connection with the critical stage of water requirement (tuber set) could imply the simultaneous or subsequent incidence of two factors: a. Metabolic changes, not here studied, which could arise from high soil water stress at sprouting, and b. Environmental conditions perhaps more favourable at the tuber formation stage delayed as a consequence of drought at planting.

Acknowledgment

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Abhärtung der Kartoffelpflanze gegenüber Trockenheit als Nachwirkung der Bodentrockenheit zur Zeit des Pflanzens

Ziel der Arbeit war es, die Einwirkung einer strengen Bodendürre zur Zeit des Pflanzens auf die Art des Wachstums und den Ertrag der Kartoffelpflanzen der Sorte '*White Rose*' zu untersuchen. Der Versuch wurde auf dem Versuchsfeld des Departementes für Pflanzenphysiologie der landwirtschaftlichen Fakultät der staatlichen Hochschule (Universidad Nacional de Cuyo) in Mendoza, Argentinien, durchgeführt. Die Parzellen (6 × 4,5 m) wurden in Blocks mit zufälliger Anordnung mit 5 Wiederholungen angelegt. Jede Parzelle bestand aus 8 Reihen mit einem Abstand von 80 cm zwischen den Reihen. Die bei der Ernte benutzte Parzelle betrug 20 m^2 mit durchschnittlich 30 Pflanzen. Es wurden die folgenden Behandlungen angewandt: 0 = Kontrolle, d.h. Normalbewässerung während des ganzen vegetativen Zyklus; 1 = Dürre während des Pflanzens, nachher normale Bewässerung; 2 = Dürre während der kritischen Zeit des Wasserbedarfs (Beginn der Knollenbildung) und normale Bewässerung während des Pflanzens und der restlichen Zeit des vegetativen Zyklus und 3 = Dürre während des Pflanzens und der kritischen Zeit und normale Bewässerung während des restlichen vegetativen Zyklus (Abb. 1).

Der grösste Ertrag wurde bei der Behandlung 1 (Dürre beim Pflanzen) erzielt mit signifikanten und hochsignifikanten Unterschieden im Vergleich zur Kontrolle bzw. bei Behandlung 2. Behandlung 3, bei welcher am wenigsten Wasser gegeben wurde (42% weniger als bei der Kontrolle), zeigte keine signifikanten Unterschiede, weder zur Kontrolle noch zur Behandlung 1 (Dürre beim Pflanzen). Ausserdem wurde bei Behandlung 3 um 25% weniger Wasser gegeben als bei der Behandlung 2 (Dürre während der kritischen Zeit); trotzdem wurde der Ertrag praktisch verdoppelt (Tabellen 1 und 2, Abb. 1).

Die Einwirkung der Dürre während des Pflanzens verzögerte den Beginn der Knollenbildung um 30 Tage im Vergleich zur Kontrolle, regte aber dann nicht nur den Knollenwuchs an, sondern führte auch zu einer Verkürzung der Zeit der Knollenbildung (ebenfalls um 30 Tage im Vergleich zur Kontrolle). Wenn die Bodendürre bei Beginn der Knollenbildungsperiode angewandt wurde, so verlängerte sich diese, und Zahl, Wuchs und Endertrag der Knollen nahmen ab. Diese nachteiligen Wirkungen verschwanden praktisch ganz und gar, wenn das Pflanzen unter strengen Bodendürre-Bedingungen stattfand (Abb. 2, 3, 4 und 5). Daraus folgt, dass die Dürreabhärtung während der kritischen Zeit des Wasserbedarfs möglicherweise direkt oder indirekt als Nachwirkung der Bodendürre während des Pflanzens stattfindet. Der Mechanismus, durch den sich dies ereignet, ist zur Zeit unbekannt.

Résistance à la sécheresse de la plante de pomme de terre comme arrière-effet des conditions sèches du sol à la plantation

On a cherché à déterminer l'influence de conditions de sécheresse édaphique sévère au moment de la plantation sur la croissance et le rendement de la pomme de terre, variété *White Rose*. L'étude a été menée à la Station Expérimentale du Département de Physiologie Végétale de la Faculté des Sciences Agraires de l'Université Nationale de Cuyo, Mendoza, Argentine. Les parcelles (6 m × 4,5 m) étaient réparties au hasard au sein de blocs; il y avait cinq répétitions. Chaque parcelle comprenait huit rangs à 0,80 m de distance. La partie utile de chaque parcelle avait une surface de 20 m^2 et comportait 30 plantes environ. Les traitements appliqués furent les suivants: 0 = Témoin, irrigation normale pendant tout le cycle végétatif; 1 = Sécheresse à la plantation et irrigation normale pendant tout le reste du cycle végétatif; 2 = Sécheresse pendant la période critique de besoin en eau (début de la tubérisation) et irrigation normale à la plantation et pendant le reste du cycle végétatif et 3 = Sécheresse à la plantation, de même pendant la période critique, mais irrigation normale pendant le reste du cycle (Fig. 1). Les rendements les plus importants ont été obtenus avec le Traitement 1 (sécheresse à la plantation) et les différences étaient respectivement significatives et hautement significatives par rapport au témoin

et au Traitement 2 (sécheresse au moment de la période critique de besoin en eau) (Tableaux 1 et 2). Le Traitement 3, qui apporte la plus faible quantité d'eau d'irrigation (42% en moins que le témoin), n'a pas montré de différences significatives par rapport au témoin et au Traitement 1 (sécheresse à la plantation). D'autre part, ce traitement qui a apporté 25% d'eau en moins que le Traitement 2 (sécheresse pendant la période critique) a, néanmoins, presque doublé le rendement de celui-ci (Tableaux 1 et 2; Fig. 1). Le traitement de sécheresse à la plantation a retardé le début de la tubérisation (30 jours par rapport au témoin) mais, par après, il a stimulé la croissance des tubercules et a raccourci la période de tubérisation (30 jours par rapport aux Traitement 0 et 2). Quand la sécheresse édaphique coïncide avec le début de la période de tubérisation, celle-ci s'allonge, tandis que diminuent le nombre de tubercules, leur croissance et le rendement final. Ces effets négatifs disparaissent presque entièrement si la plantation a lieu dans des conditions de sévère sécheresse édaphique (Fig. 2, 3, 4 et 5). Les auteurs concluent que l'induction de la résistance à la sécheresse pendant la période critique de besoin en eau pourrait être la conséquence directe ou indirecte de la sécheresse édaphique. Le mécanisme de ce phénomène est encore inconnu.

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