THE EFFECT OF DROUGHT ON THE POTATO LEAF AREA

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The drought affected the size of leaf area in different way in dependence on its action in the growing season. If occurred to full emergence of the stand, it had a positive impact on the size of leaf area. The drought in further period of the development of a plant had a negative influence on its size. The size of leaf area can be compared in different treatments when calculated per stem or hill. More objective indicator is a calculation per stem. Action of drought in different periods of the growing season on the decrease in leaf area varied with varieties. The height of plants was most favourably affected by temporary drought acting in the time of the growth of germs in the soil to full emergence of the stand and the other way round, the drought prevailing in the time of the fastest growth of hills (after emergence of plants to flowering) the most slowed down their growth. As a rule, more leaves with greater leaf area grew on higher stems, even despite reduced number of stems due to drought in emergence of the stand.

potato; drought; leaf area; height and number of stems; number of leaves per stem

INTRODUCTION

Under the conditions of soil water deficit the dry matter production in potatoes decreases (by lower rate of photosynthesis) (Loon, van, 1981). This also limits the development of the crop stand (size of total leaf area), and hence also indirectly dry matter yield. It also speeds up ageing of the stand (Zaag, van der, 1981). The soil water deficit to a decrease in the total amount of intercepted radiation (smaller area of leaves) and effectiveness of photosynthesis. A little lowering in water supply into leaves leads to the reduction in CO_2 uptake by plants (set the stomatal closure). Thus, potatoes are ranked among plants considerably susceptible to the fluctuation of soil water content (Fitter, Hay, 1987). Evidently cultural potatoes have not developed other adaptive system for the regulation of transpiration outlay of water such as control of stomatal openings in leaves (Nečas, Zrůst, 1968). Decrease

in transpiration outlay of water will make difficult an exchange of gases, that is also CO_2, for photosynthesis. The study investigated the effect of stems height and weight and their number, leaf weight and area by intentional reduction in water content in soil in different stages of the vegetation.

MATERIAL AND METHODS

The glasshouse trial comprised nine treatments (Tab. I), 13 vegetation pots in each treatment and was arranged in eight blocks where varieties and treatments were distributed at random (total number of pots in the trials was 468). 10 l vegetation pots were filled with topsoil in the spring before planting (up to 20 cm) from that part of the field where field trials with potatoes were established in that year, in an amount of 14 kg of soil per pot. To provide a good nutrition in a limited space of vegetation pots the following nutrients were added to each pot/hill a week before planting: 0.4571 g N, 0.3017 g P and 0.7589 g K.

I. Survey of treatments

Treatments of soil moisture	Relative soil moisture during development* (%)			
	a	b	c	d
1 (control)	75	75	75	75
2	50	75	75	75
3	30	75	75	75
4	75	50	75	75
5	75	30	75	75
6	75	75	50	75
7	75	75	30	75
8	75	75	75	50
9	75	75	75	30

*Time of development: a – planting to emergence, b – emergence to bud formation, c – bud formation to full flowering, d – full flowering to physiological maturity

Four potato varieties with different length of the growing season and different purposes of potato production were chosen for the trial: Resy – very early, ware, the Netherlands; Karin - early, ware salad, drought proof, CR; Désirée – semi-late, ware, suitable for cultivation in arid regions, the Netherlands; Kamýk – late, commercial, CR.

Relative soil moisture in percentage (RSM) was detected in two- or three-day intervals during the whole growing season by gravimetric method (Novák, 1954). Three vegetation pots of each variety from the first (control) treatments and from those treatments, in which reduced relative soil moisture was maintained, were checked. Pots were watered under condition of water deficit, but only every other day in sunny days with high evapotranspiration.

Leaf area was measured during the growing season. The number of leaves per stem in 13 hills of each treatment and the number of stems per hill were counted alongside with measuring their height and fresh mass of leaves and stems was weighed. Average hill was taken from each treatment in all four varieties to determine leaf area. More samples could not be processed for working demandingness. Leaf area was measured in accordance with our previous experience that an apprehensible representativeness of these measurements can be achieved in very careful selection of average hill (Nečas et al., 1967; Zrůst et al., 1974; Zrůst, Smolíková, 1980).

Leaf area was measured on the apparatus LI-3100 Area Meter, manufactured by LI-COR (USA), in single term in the Resy variety 49 days from planting, in Désirée 50 days, in Karin 51 days and in the Kamýk variety 58 days, what was on an average of treatments in the Karin variety 6 days, in Resy 8 days, in Désirée 11 days and in the Kamýk variety 14 days from the onset of bud formation. The last two treatments (8 and 9) of nine experimental treatments could not be comprised in the measurements, as these treatments were affected by drought as late as at the end of the growing season (from flowering to physiological ripeness of stands). Leaf area with time was losing its importance for dry matter formation (leaves were turning yellow, drying and falling down). At the end of this period when this measurement could come into question no leaves were available.

RESULTS

The size of leaf area in an average hill in different treatments was affected by the number of stems, their height and number of leaves per stem. In the time from planting to emergence of hills the drought, though reduced the number of stems per hill, stimulated the growth of leaves in such a manner that these hills surpassed the control hills by the size of leaf area growing at 75% RSM (relative soil moisture) during the whole growing season and the plants growing in remaining treatments.

The least leaf area was found on the hills on which the drought acted by 30% RSM in the time from plant emergence to bud formation (treatment 5 –

II. Weight in g and leaf area in cm^2 in one average hill

Variety	Treatment	Leaves					
		weight			area		
		Σ_x	s_x	$\bar{x}$	Σ_x	s_x	$\bar{x}$
Resy	1	101.9	8.139	16.983	2 371.22	151.562	395.203
	2	116.7	8.330	29.175	2 639.75	159.160	659.938
	3	117.5	19.283	23.500	2 693.14	392.840	538.628
	4	95.7	12.419	23.920	2 186.22	245.259	546.555
	5	59.5	4.914	9.916	1 266.19	140.513	253.238
	6	84.2	8.568	14.033	2 079.23	177.330	346.538
	7	87.2	9.554	14.533	1 684.18	204.578	280.696
Désirée	1	117.7	14.457	19.617	2 490.20	273.145	415.030
	2	149.7	26.554	37.425	2 840.13	394.051	710.033
	3	124.7	8.343	41.567	2 330.36	50.359	776.787
	4	100.3	9.778	12.538	2 038.33	182.922	254.791
	5	66.8	8.606	13.360	1 373.32	136.802	274.664
	6	113.9	15.660	18.983	2 375.62	276.472	395.937
	7	86.9	6.505	12.414	1 757.35	113.941	251.050
Karin	1	126.9	12.445	25.380	2 642.22	225.053	528.444
	2	127.3	13.270	25.460	2 513,31	239.121	502.662
	3	146.1	8.316	48.700	2 689.13	112.988	896.377
	4	82.1	8.683	20.525	1 735.53	155.193	433.883
	5	51.7	10.802	12.925	959.36	177.198	239.840
	6	98.9	11.107	19.780	1 903.26	209.639	380.652
	7	95.3	4.284	19.060	1 844.10	72.153	368.820
Kamýk	1	171.2	22.178	34.240	3 741.68	421.918	748.336
	2	164.3	26.169	41.075	3 287.00	480.056	821.750
	3	188.8	18.412	31.467	3 937.24	322.327	656.207
	4	125.5	9.135	15.688	2 956.97	150.459	369.621
	5	126.6	13.212	18.086	2 601.80	241.537	371.686
	6	120.8	10.996	20.133	2 486.44	186.032	414.407
	7	67.8	5.299	8.475	1 661.38	111.649	207.673

varieties Resy, Désirée, Karin) or during the next growing season from the bud formation to full blossom (treatment 7 – the Kamýk variety).

The effect of the drought on leaf area size is more precisely expressed by conversion of its value per stem (Tab. II – $\bar{x}$). Obviously, it is more objective indicator, that is in view of the lower number of stems in treatments emerging under reduced soil moisture due to the drought. Early in the growing season the Désirée variety (the variety resistant to droughts) responded most positively to the drought in accordance with this indicator. In the above variety the leaf area in average hill in the stand in the treatment water to 30% RSM increased to 187.2% compared with the control and in the treatment watered to 50% RSM increased to 171.1%. The same with the Karin variety, resistant to drought, had greater leaf area in the treatment 3 by 169.6% compared with the control. In remaining two varieties the plants watered from the beginning of the growing season to 50% RSM had the greatest leaf area. Hills growing in the control were mostly placed by the size of leaf area between these two treatments or behind them.

A decrease in leaf area due to the drought acting in the remaining growing seasons varied by different varieties. The order of treatments by the size of leaf area (from treatment 4) was in conformity with the varieties Désirée and Kamýk, the order of treatments on the last three positions was identical for the varieties Resy and Karin. Varieties with shorter growing season (Resy, Karin) had the smallest leaf area converted per stem in the time when the drought acted from stand emergence to bud formation, and varieties with longer growing season (varieties Désirée and Kamýk) at the drought starting in the time of initiation of tubers and continuing in initial growth of tubers.

Comparison of the effect of drought on the size of leaf area of whole hills from emergence of plants to bud formation (treatments 4 and 5) and from bud formation to full blossom (treatments 6 and 7) showed stronger negative effect in the first period (emergence – buds) in the Karin variety, while in the second period (buds – flower) in the Kamýk variety. In remaining two varieties greater stress (30% RSM) affected from plant emergence to bud formation stronger negatively than in further period (buds – flower).

Leaf weight in different treatments was relatively in good congruency with leaf area (Tab. II) what allowed to the use fast destructive method to determine leaf area.

As mentioned above, both the number and height of stems play a decisive role in the leaf area size of the whole potato hill. Their number affects, except variety, storing regime of planting tubers and soil temperature after planting (particularly in tubers in dormancy), above all water regime in soil during emergence. The drought affects negatively on the number of stems from tuber planting to crop stand emergence. It was confirmed in selection of average

III. The number of stems, their height in cm and weight in g

Variety	Treatment	Stems						
		number	height			weight		
			Σ_x	s_x	$\bar{x}$	Σ_x	s_x	$\bar{x}$
Resy	1	6	122.0	1.94	20.33	42.4	1.869	7.067
	2	4	108.0	2.68	27.00	53.8	3.487	13.450
	3	5	123.5	4.03	24.70	54.5	6.918	10.900
	4	4	77.5	3.25	19.38	32.5	1.387	8.125
	5	5	54.5	2.25	10.90	25.2	1.884	5.040
	6	6	99.5	1.39	16.58	33.7	2.218	5.616
	7	6	125.5	3.81	20.92	57.1	2.872	9.516
Désirée	1	6	127.5	6.36	21.25	73.5	8.240	12.250
	2	4	112.0	1.96	28.00	89.2	9.051	22.300
	3	3	117.0	0.50	39.00	91.2	1.709	30.400
	4	8	95.5	2.77	11.94	51.9	4.185	6.488
	5	5	71.5	2.84	14.30	31.1	2.680	6.220
	6	6	152.5	2.60	25.42	72.4	4.710	12.067
	7	7	116.5	5.52	16.64	51.7	3.262	7.386
Karin	1	5	138.0	2.90	27.60	72.0	3.937	14.400
	2	5	152.0	2.49	30.40	84.3	5.298	16.860
	3	3	89.5	2.26	29.83	68.8	2.715	22.933
	4	4	63.0	2.26	15.75	31.1	0.918	7.775
	5	4	37.5	1.97	9.38	17.2	2.736	4.300
	6	5	112.5	6.71	22.50	57.8	6.057	11.560
	7	5	96.5	2.41	19.30	49.0	1.733	9.800
Kamýk	1	5	153.0	2.88	30.60	78.9	7.045	15.780
	2	4	105.0	4.29	26.25	62.8	8.153	15.700
	3	6	190.5	3.09	31.75	100.8	5.292	16.800
	4	8	196.0	2.84	24.50	83.6	3.782	10.450
	5	7	124.5	4.98	17.79	54.2	4.661	7.743
	6	6	123.0	1.41	20.50	51.7	2.023	8.617
	7	8	164.0	4.52	20.50	45.2	2.783	5.650

hills in the stand in all four varieties, with exception of treatment III with 30% RSM in the Kamýk variety (Tab. III). It was probably due to lower number of stems in the hill chosen from the control than was the average number in this treatment.

Potato plants respond to direct influence of drought by retardation of stem growth. Greater stress is induced by stronger growth retardation and lower stems have, as a rule, less leaves. Differences in response of potato plants to drought in various periods of the growing season were recorded.

The drought, being effective from emergence to bud formation, consequently, early in the growing season, when increase in mass of above-ground parts of hills are the greatest and the growth is approximately linear, had the greatest long-time negative influence on the height of stems. Plants in these treatments (4 and 5) were the smallest also in further period of the growing season when watering was converted to optimal values (75% RSM) compared with plants in remaining treatments.

Plants responded to drought in different way when it occurred in pre-emergence growth (treatments 2 and 3). Soon after emergence these hills were the lowest compared with other treatments, not reaching the half of their height (especially at 30% RSM). Under conditions of optimal irrigation the loss of height was overcome very quickly and these hills were higher than in other treatments.

Plants of the treatments 6 and 7 were maintained in this irrigation regime from bud formed to flowering one to two weeks before the leaf area size was determined. This short time of drought affected the hill height less than in previous treatments in which drought was during the whole specified period.

There were great differences in the height of stems (stems of one hill) in each treatment (Tab. III). When the highest stems were measured in each hill, significant differences were found between hill height within treatment in all four varieties. Results acquired in the Resy variety towards the end of April (three weeks before leaf area measuring – Tab. IV). Watering in treatments 2 to 5 was changing in that time. Another change of watering in treatments 6 to 9 in the first decade of June induced characteristic differences in stem height (Tab. V).

Similar differences between treatments were found also in their weight (Tab. III). These differences were more significant when expressed in per cent. Treatments (2 and 3) affected by drought were distinct considerably in the time of emergence (varieties Désirée and Kamýk compared with the control).

The number of leaves per stem was not in close correlation with stem height. The order of treatments was not in congruency in both investigated indicators. The trend of stem height and number of leaves on them were

IV. Variance analysis of hill height of the Resy variety of April 26, 1991

Source of variability	*N*	Sum of squares	*F*-test	Significance
Replication	12	519.979	7.038	**
Treatment	8	960.885	19.508	**
Error	96	591.060		
Total	116	2 071.923		

Order	Treatments	Average in cm	Percentage compared with control
1.	7	10.462	114.3
2.	1	9.154	100.0
3.	9	8.077	88.2
4.	5	7.808	85.3
5.	8	7.769	84.9
6.	6	7.000	76.5
7.	4	6.077	66.4
8.	2	3.308	36.1
9.	3	0.577	6.3

** significant at the level of $P = 0.01$ (the same applies to other tables)
Significant differences for treatments at the level (Turkey's test): $P = 0.05 - 3.098$, $P = 0.01 - 3.627$

V. Variance analysis of hill height of the Resy variety of June 6, 1991

Source of variability	*N*	Sum of squares	*F*-test	Significance
Replication	12	1 834.701	3.852	**
Treatment	8	2 916.068	9.184	**
Error	96	3 810.376		
Total	116	8 561.145		

Order	Treatments	Average in cm	Percentage compared with control
1.	3	41.154	124.1
2.	2	40.154	121.1
3.	8	36.077	108.8
4.	9	35.462	107.0
5.	1	33.154	100.0
6.	6	32.308	97.4
7.	7	29.462	88.9
8.	5	29.077	87.7
9.	4	24.923	75.2

Significant differences for treatments at the level (Turkey's test): $P = 0.05 - 7.867$, $P = 0.01 - 9.208$

VI. Variance analysis of the number of leaves per stem of the Resy variety of April 26, 1991

Source of variability	*N*	Sum of squares	*F*-test	Significance
Replication	12	220.137	3.874	**
Treatment	8	183.812	4.852	**
Error	96	454,632		
Total	116	858.581		

Order	Treatments	Average of the number of leaves	Percentage compared with control
1.	1	8.23	100.0
2.	8	8.23	100.0
3.	7	7.85	95.3
4.	5	7.69	93.5
5.	4	7.54	91.6
6.	6	7.39	89.7
7.	9	7.39	89.7
8.	2	6.23	75.7
9.	3	4.00	48.6

Significant differences for treatments at the level (Turkey's test): $P = 0.05 - 2.72$, $P = 0.01 - 3.18$

VII. Variance analysis of the number of leaves per stem of the Resy variety of June 6, 1991

Source of variability	*N*	Sum of squares	*F*-test	Significance
Replication	12	23.368	1.088	
Treatment	8	87.915	6.138	**
Error	96	171.863		
Total	116	283.145		

Order	Treatments	Average of the number of leaves	Percentage compared with control
1.	2	12.62	106.5
2.	3	15.54	105.8
3.	8	12.00	101.3
4.	1	11.85	100.0
5.	5	11.62	98.1
6.	9	11.46	96.8
7.	4	10.85	91.6
8.	6	10.23	86.4
9.	7	10.08	85.1

Significant differences for treatments at the level (Turkey's test): $P = 0.05 - 1.67$, $P = 0.01 - 1.96$

maintained in the treatments. It is documented by the results in the Resy variety in terms when corresponding values were measured and calculated (Tabs. VI and VII).

DISCUSSION

The drought persisting from tuber planting to crop emergence reduces the number of stems per hill and consequently the leaf growth is stimulated. It can be explained by compensation for lower number of stems and action of growth-regulation endogenous substances, cytokinins above all. The drought in this time has favourable effects on the growth and number of roots which positively affect supply of water, nutrients and production of cytokinins, important for the utilization of proteins needed for leaf growth and their longer vitality.

The drought acting after stand emergence in any stage of the growing season has negative influences on the leaf area and decreases the stem height and leaf number per stem. Thus, it affects also leaf area index and spatial distribution of the total leaf area. Dying-off of the parts of leaves leads to premature defoliation. This all results in lower values of leaf area duration.

The response of varieties to drought by decrease in assimilative area is different. A decisive role is played by the time of the growing season in which drought acts and its intensity.

The results acquired in the trial confirmed the previous experience (Zrůst et al., 1991) that the soil water deficit in late in the vegetation causes faster loss of leaves. Later in the growing season this deficit appears, irreversible effects are more frequent, and this has negative impact on growth and development of the stand. In early stages of the development the drought has not such unfavourable effects if replaced by the period with ample precipitation. Potatoes can regenerate leaf area by another growth from vegetation apexes and buds in leaf axils.

In most cases the reduction in leaf area caused by drought has serious consequences for the potato growth. The stress induced decreases the rate of photosynthesis (Zrůst et al., 1994) and retards the conductance (Bodlaender et al., 1986). Together with restriction of radiation intercepted by the stand by lower leaf area (Burstall, Harris, 1983) affects negatively the stand production (Engel, 1965; Allen, Scott, 1980; Khurana, McLaren, 1982).

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Vliv sucha na velikost listové plochy bramboru.

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Ve skleníkovém pokusu o rozsahu devíti variant (tab. I) bylo sledováno ovlivnění plochy listů, výšky a hmotnosti stonků a počtu a hmotnosti listů záměrným snižováním obsahu vody v půdě v rozdílných fázích vegetace. Do pokusu byly vybrány čtyři odrůdy brambor s rozdílnou délkou vegetační doby i užitkového směru pěstování (Resy, Karin, Désirée, Kamýk). Listová plocha byla měřena na přístroji LI-3100 Area Meter, fy LI-COR (USA) v jednom termínu, destruktivní metodou, za 49 až 58 dnů

po výsadbě. Od každé odrůdy byl proměřován jeden trs. Ostatní parametry byly zjišťovány v týdenních intervalech u 13 trsů od každé odrůdy.

Sucho v době od výsadby až do vzejití trsů sice omezilo počet stonků na trs, stimulovalo však růst listů takovou měrou, že velikost listové plochy většinou předčila jak kontrolní trsy, tak i rostliny rostoucí v ostatních variantách (tab. II). Přesnějším vyjádřením vlivu sucha na velikost listové plochy je přepočet její hodnoty na stonek ($\bar{x}$ – tab. II), který je zřejmě objektivnějším ukazatelem, a to vzhledem k suchem zaviněnému nižšímu počtu stonků ve variantách vzcházejících za snížené půdní vlhkosti. Na sucho z počátku vegetace reagovala podle tohoto ukazatele nejvíce odrůda Désirée (odrůda odolná přísuškům), u níž se listová plocha zvětšila u průměrného trsu v porostu ve variantě zalévané na 30 % relativní půdní vlhkosti (RPV) na 187,2 % oproti kontrole a ve variantě zalévané na 50 % RPV na 171,1 %. Rovněž odrůda Karin, odolávající přísuškům, měla ve třetí variantě zvětšenou listovou plochu o 169,6 % vůči kontrole. Zmenšení listové plochy v důsledku sucha působícího ve zbývajících obdobích vývinu bylo rovněž odrůdově odlišné. Hmotnost listů v jednotlivých variantách poměrně dobře souhlasila s plochou listů (tab. II).

O velikosti listové plochy celého bramborového trsu rozhoduje také počet a výška stonků. Sucho působí v období od výsadby hlíz do vzejití porostů na počet stonků negativně (tab. III). Rostliny brambor reagují při bezprostředním zásahu sucha rovněž zpomalením růstu stonků. Větší stres vyvolává silnější retardaci růstu. Nižší stonky jsou zpravidla osazeny menším počtem listů. Sucho, působící od vzejití do tvorby poupat, tedy na počátku vlastní vegetace, kdy jsou přírůstky nadzemních částí trsů nejvyšší a růst je přibližně lineární, nejvíce ovlivňovalo výšku stonků dlouhodobě negativně. Jinak reagovaly rostliny na sucho působící v průběhu prorůstání klíčků hrůbky (var. 2 a 3). Zpočátku po vzejití byly tyto trsy v porovnání s trsy v ostatních variantách nejnižší, nedosahovaly ani jejich poloviční výšky. Při optimální závlaze (75 % RPV) však výškovou ztrátu velice rychle dohnaly a přerostly trsy v ostatních variantách (tab. IV a V).

Podobné rozdíly mezi variantami byly také v jejich hmotnosti. Tyto rozdíly byly ještě výraznější při procentuálním vyjádření. Počet listů na stonku nebyl v těsné korelaci s výškou stonků. Pořadí variant nebylo souhlasné u obou zjišťovaných parametrů. Tendence u výšky stonků a počtu listů na nich však byly ve variantách zachovány (tab. VI a VII).

brambor; sucho; listová plocha; výška a počet stonků; počet listů na stonek

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