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The effect of drought and cultivar on growth parameters, yield and yield components of potato

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Abstract – Four potato cultivars (*Solanum tuberosum* L.) differing in their precocity and contrasted for their drought tolerance were investigated in the field and in the greenhouse (2 cultivars). They were subjected to two water treatments, well-irrigated and droughted. Our objective was to examine which shoot and leaf characters were related to the decrease in tuber yield. Drought reduced tuber yields by 11% in 53%. Drought stress highly reduced the dry mass of leaves in all cases. Tuber number was reduced only in early cultivars whereas in the later cultivars, leaf area index and leaf area duration were more affected than in the early cultivars. The cultivar which maintained its tuber growth rate better under drought during the first three weeks of tuber bulking also maintained its yield better. No clear common reaction of early versus later varieties to drought was found.

potato / drought stress / cultivar / agro-physiological parameters

Résumé – Effet du stress hydrique et du cultivar sur les paramètres de croissance, le rendement et ses composantes. Quatre variétés de pomme de terre (*Solanum tuberosum* L.) de précocité variable et réputées différentes au niveau de la tolérance à la sécheresse ont été testées, sous deux régimes hydriques (irrigué et stressé) au champ et sous serre. Notre objectif était d'étudier les relations entre l'évolution de différents paramètres de surface foliaire, et de masse (tiges et des tubercules) au cours du cycle et les diminutions de rendement en tubercules. Le stress hydrique a réduit le poids des tubercules de 11 à 53 %. Le stress hydrique a fortement réduit la masse sèche foliaire dans tous les cas. Le nombre de tubercules a été réduit uniquement chez les cultivars précoces, tandis que les cultivars tardifs ont plus été affectés au niveau de l'indice foliaire et de sa durée. Les cultivars qui ont mieux maintenu le taux de croissance de leurs tubercules durant les trois premières semaines de remplissage ont également mieux maintenu leurs rendements. Aucune relation précocité – sensibilité au rendement sous stress n'a été observée.

pomme de terre / stress hydrique / cultivar / paramètres agro-physiologiques

1. INTRODUCTION

Potato is considered to be very drought-sensitive [29, 31, 33] and drought stress even occurs under irrigated potato production [18, 33]. Hence, yields are frequently constrained by drought in most environments, drought stress affecting the development and the growth of shoots, roots and tubers.

The first morphological manifestation of drought effects in the potato is a reduction in leaf size [20]. It results in a reduction in the amount of intercepted radiation and leads to a decrease in tuber dry mass accumulation [17]. Reduced leaf growth and accelerated leaf senescence are indeed common responses to water deficits and could be an adaptation of plants to water deficit [27].

The effect of drought on potato foliar characters, which in turn affects tuber yield, has been studied by several researchers. Jefferies [16] showed that the final size of individual leaves was reduced by drought, but the magnitude of the effect differed significantly between cultivars. There were genotypic differences in the ability to maintain leaf expansion with increasing soil moisture deficit [18]. Drought reduced the number of green leaves up to 22% or 25% in two cultivars, but towards the end of the season, plants affected by drought had a tendency to show similar or even higher numbers of green leaves than in irrigated treatments; leaf lengths of the two cultivars did not respond differently to the treatments [8]. Similar results were reported by different authors cited in the Van Loon's review [33].

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Table I. Field trials' characteristics.

	Field trial (1998)	Greenhouse trials	
		1998	1999
Soil			
% (sand, silt, clay)	6–83–10	23–69–8	20–73–7
Date of planting	May 13	May 20	May 7
Density of planting	3.33 plants/m ²	6.25 plants/m ²	6.25 plants/m ²
Cultivars (a; b; c) ¹	Remarka (ML; ?; VH) Désirée (ML; 8; G) Nicola (ME; 8; VG) Monalisa (E; 6; G)	Remarka Désirée	Remarka Désirée
Seed size (mm)	35–45	40	35–50
Subplot size	4.5 m ² – 14 plants	0.8 m ² – 5 plants	0.8 m ² – 5 plants
Basic dressing	Haspargit: 1500 kg·ha ⁻¹ (3–21–7–21) (45 P ₂ O, 315 K ₂ O, 105 MgO, 315 CaO) in March 150 unit of N, 2 DAP ²	N P K (15–20–26%) 200–260–340 kg·ha ⁻¹ on May 20	N P K (15–20–26%) 120–160–200 kg·ha ⁻¹ on May 7
Nitrogen fertilizing			N P K (15–20–26%) 120–160–200 kg·ha ⁻¹ 48 DAP
Weed control	Defi-Sencor, 10 DAP	Manually	manually
Late blight control	Mancozebe. 7 treatments: 27, 32, 42, 51, 62, 72, and 77 DAP		
Haulm destruction			97 DAP
Tuber harvest	129 DAP	96 DAP	108 DAP

¹ Earliness, drought tolerance and productivity rating (according to Bonthuis and Ebskamp [3]). E, ME and ML: early, mid-early and mid-late, respectively; the number is a drought-tolerance rating, a higher value indicates a higher drought tolerance (maximum 10); ?= unknown drought tolerance. VH, VG and G: very high, very good and good.

² DAP: days after planting.

Drought-stressed crops exhibit slower and lesser canopy expansion and earlier senescence than irrigated crops [20, 21, 34, 36]. A number of researchers have emphasized the importance of the canopy longevity [25]. Wolfe et al. [36] found a high correlation between leaf area duration and final plant dry weight, while Bremner and Taha [4] reported a direct linear relationship between tuber yield and the number of days during which the LAI is maintained at values greater than 3. The effects of drought stress on a plant depend on the timing, but also on the duration and the severity of the stress [18]. Different growth strategies can be followed by the potato plant to adapt to different drought conditions without tuber yield being significantly affected. For example, a lower tuber number may be compensated for by a higher assimilate partitioning to tubers [21], and therefore a higher tuber size [8]. That is why the analysis of the response to drought stress of the cultivars should not be restricted to differences in yield.

Our main objective was to attempt to describe the differences between cultivars' responses to drought in terms of the agro-physiological parameters studied, and to establish which characters were the most related to the yield and/or drought tolerance index.

2. MATERIALS AND METHODS

Trials were conducted in the field (1998) and in the greenhouse (1998 and 1999). The field experiment was

conducted in Incourt, Belgium. Greenhouse experiments were conducted in square pots (width of 40 cm, depth of 30 cm) at the Université Catholique de Louvain in Louvain-La-Neuve, Belgium. A strip-plot design with two factors (cultivar and water status) and four replicates were used in the three experiments.

The internal temperature in the greenhouse was maintained as close as possible to the external air temperature automatically with a computerized system. The air circulation inside the greenhouse was regulated through openings at the roof level and main door during the daytime. The position of the pots within each block was changed once or twice per week to minimize the effects of light and temperature gradients within the greenhouse, and border effects.

Four potato cultivars (*Solanum tuberosum* L.) reported to be different for their drought tolerance, earliness and showing a range in productivity [3] were investigated in the field; two of them were also tested in the greenhouse. Certified seeds produced in Benelux were used. Each pot was filled homogeneously with 43 l of a mixture of compost (12 kg) and sand (20 kg) after mixing them with a concrete mixer. There were 5 pots per subplot. With 2 treatments, 2 varieties and 4 replicates, the total number of the pots was 80. A planting depth of 5 to 6 cm was used (both in the field and the pots). Other characteristics of the experiments are shown in Table I.

Table II. Water characteristics of the experimentations.

	Field trial (1998)		Greenhouse trials			
	I ¹	S ¹	1998 I ¹	1998 S ¹	1999 I ¹	1999 S ¹
Number of irrigations	5	0	41	15	46	18
Total amount of water (mm) ²						
Rain ³	313	313	0	0	0	0
Effective rain	148	148	-	-	-	-
Irrigation	100	0	128	71	142	83

¹: I: irrigated, S: stressed.²: mm: millimeter: it represents the height of water in the pot or in the field.³: The data related to rain and effective rain were taken from the meteorological station of Pameseb-Incourt.

2.1. Treatments

In the field and in the greenhouse, two contrasting water treatments, well-irrigated (I) and stressed (S), were considered.

Drought stress was induced in the field by withholding irrigation totally, so the drought treatments corresponded to naturally droughted plots versus irrigated controls. The irrigated controls received water from rainfall and irrigation. Irrigation was scheduled, depending on the water balance in the soil, to maintain the plants of the controls near the optimal conditions of water: 20 mm of water was applied by the Sprinkler system five times (26/6, 08/7, 24/7, 07/8 and 17/8).

In the pot experiments, water was applied to irrigated treatments (controls) to maintain soil water potential above -0.3 MPa. The stressed treatment was irrigated only when the soil water potential was lower than -0.8 MPa [1, 22], and it received about 50% of the total quantity of water applied to the controls. Not only the amounts given, but also the frequency, differed between irrigated and stressed treatments.

In the pot experiments, irrigation was applied on average every 2 days for the irrigated treatments and only every 5 to 6 days for the stressed ones (Tab. II).

2.2. Measurements

Soil water potential: tensiometers (Soil Moisture Equipment Corp., Santa Barbara, USA) were used both in the field (at depths of 25 and 50 cm in 2 replications) and in the pots of 1998 (at a depth of 25 cm in 2 replicates) to monitor soil water potential. In 1999, the same pattern of water supply as that of 1998 was used.

Leaf water potential was usually measured on four mature leaves from each treatment in each experiment. Measurements were made weekly with a pressure chamber (P.M.S. Instrument Co., Corvallis, Oregon, USA), following the method described by Scholander et al. [30]. The leaf water potential value was recorded only when vascular sap was clearly forming a small dome of water on the cut surface of the petiole. Bubbles were sometimes visible before this dome appeared but this was not considered to indicate the true value

of water potential. These measurements were performed around midday.

The destructive harvests were done on several dates: on the 29, 41, 57, 78, 91, 111 and 129th DAP in the field, on the 21, 41, 60, 78 and 96th DAP in the pot experiment of 1998 and on the 27, 41, 63, 80 and 108th DAP in the pot experiment of 1999. Each harvest corresponded to one plant per subplot, lifted at random. All studied parameters were recorded on each date.

The measurements concerned were: stem number, tuber number, stem dry mass, leaf dry mass, tuber fresh weight, tuber dry mass and LAI.

Stems, green leaves and shed leaves were separated and oven dried at 80°C for 48 hours before recording the dry masses. Dry mass of leaves integrated both green and shed leaves, but for the LAI calculation, we considered only green leaves.

At each harvest, the LAI measurement was based on 4 leaves per harvested plant both in the field and the greenhouse; the sampling corresponded to 4 leaves per plant \times 4 repetitions per treatment and per variety. For each plant, the leaf area of the sampled leaves was correlated with their dry mass. The total leaf area was deduced from the total dry mass of each plant after multiplying the length by the width and by 0.73 [9].

In the field, tubers were harvested after uprooting the whole plant within a radius of 15 to 20 cm. The tubers were collected by manual digging. Three tubers per plant \times 4 repetitions per treatment and per variety were considered. At the final harvest, 3 tubers of 2 plants (and not only one) were lifted in each repetition for each treatment and each variety. Tuber dry weight content was determined after oven drying at 80°C for 48 hours.

Drought susceptibility was expressed, for each cultivar within years, as corresponding to TDWS (tolerance to a decrease in water supply), tuber dry weight in drought conditions relative to tuber dry weight in irrigated conditions [7, 8]. Statistical analysis was done using the SAS system according to the case and the statistical procedures outlined by Gomez and Gomez [11].

Table III. Soil water potential (in absolute values) (MPa).

(a)					(b)		
Irrigated		Drought			Irrigated		Drought
Depth (cm)					Depth (cm)		
Date	25	45	25	45	Date	25	
05 June	0.2	0.19	0.17	0.17	27 May	0.04	0.04
09 June	0.06	0.03	0.07	0.04	29 May	0.06	0.05
18 June	0.08	0.07	0.08	0.05	06 June	0.05	0.38
26 June	0.34	0.23	0.32	0.20	18 June	0.04	0.74
30 June	0.22	0.22	0.37	0.26	30 June	0.04	0.77
03 July	0.27		0.45		05 July	0.05	0.89
06 July	0.35	0.29	0.46	0.34	26 July	0.04	0.87
10 July	0.14	0.23	0.50	0.14	5 Aug	0.06	0.95
17 July	0.11	0.20	0.47	0.40			
07 Aug*	0.43	0.31	0.82	0.48			
12 Aug	0.42	0.31	0.88	0.46			
17 Aug	0.57	0.33	1.07	0.49			
28 Aug	0.10	0.05	0.17	0.61			

a: In the field. b: in the pots in 1998. *Aug: August.

Table IV. Phenological stages.

Stades	Dates		DAP				Code* ¹
	Field 98	Greenhouse	Field 98	Greenhouse			
		98	99	R D N M			
Plantation	13/05	20/05	07/05				220
Emergence	20/05	24/05	15/05	07 07 07 07	0408300	08	300
Stolon initiation	09/06–16/06	07/06	29/05	29 29 34 29	18	22	510
Tuber initiation	23/06–06/07	22/06	16/06	41 41 54 41	33	40	530
Onset. tuber bulking	06/07–17/07	04/07	24/06	54 54 65 54	45	48	
50% yellowing leaves	20/8–30/08			103 107 103 99			650
End. tuber bulking	04/09–15/09	15/08	07/0	125 125 120 114	87	92	560
Maturity	04/09–15/09	24/08	20/08	125 125 114 114	96	105	670
Haulm destruction		-	12/08		-	97	
Harvest	19/09	24/08		129 129 129 129	96	108	

*¹: Jefferies and Lawson [19] code. 98, 99 are 1998 and 1999. R, D, N, M are, respectively, Remarka, Désirée, Nicola and Monalisa. DAP: days after planting. Maturity is noted by total senescence of foliage.

3. RESULTS

3.1. Characterization of drought type

3.1.1. Soil potential

In the field, in the drought treatment, a moderate deficit was observed from the beginning of July and it became markedly

stronger from August 7 on Table III, which corresponds to the bulking stage (Tab. IV). Indeed, the drought stress becomes intense on a potato culture as soon as the soil water potential reaches -0.8 MPa [1, 22]. In the pot experiment of 1998, the stress in the drought treatment was continuous from the beginning of the cycle, and became intense at the start of stolonization (Tab. III). In the pot experiment of 1999, the same irrigation scheduling was practiced and we may

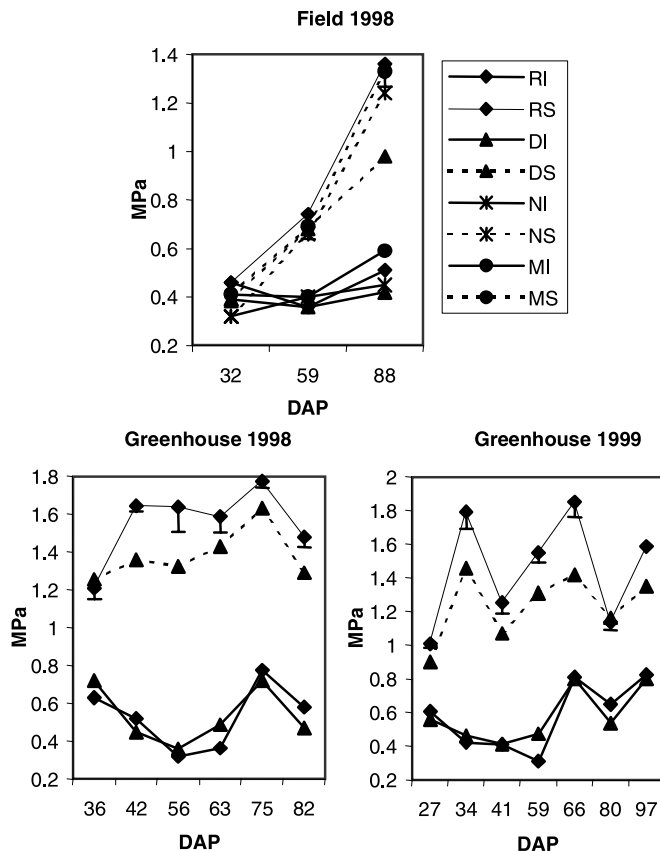


Figure 1. Leaf water potential (absolute value). R, D, N, M are Remarka, Désirée, Nicola and Monalisa. I, S: irrigated, stressed. \perp correspond to the standard errors of water \times cultivar interactions.

reasonably suppose that the drought was similar to that observed the previous year.

3.1.2. Leaf water potential

Figure 1 shows that leaf water potential in the field decreased throughout the drought treatment. Désirée, compared with the other studied varieties, showed less influence on leaf water potential under drought stress, both in the field and in the greenhouse.

Table IV shows that stolon and tuber initiation occurred later in Nicola, contrarily to the other studied cultivars, but the maturity of Nicola was earlier. Nicola formed more foliage initially, and therefore used up the available nitrogen in the pot earlier. We considered, for an earliness criterion, maturity, defined as the total senescence of the foliage.

3.2. Total and mainstem number

Drought stress reduced the total stem number by 28% in the field; it had no significant influence on this component in the greenhouse. No cultivar effect and no interaction water-cultivar were observed for this character. On the contrary, when the mainstem number and not total stem number was considered, there was no effect of drought and no interaction, but varieties differed significantly (Tab. V).

The absence of significant effect of drought on mainstem number does not seem to be a consequence of a late application of stress because in the greenhouse experiments, drought stress was applied early, at the germination stage, and no effect was shown on the mainstem number.

Moreover, the results of 1998 (field and greenhouse) show that for the same variety, the same batch of seeds and similar technical practices, the capacity of a plant to produce a total number of stems was twice as great in the field, where more light was available and the competition for light was less intense. Indeed, besides light absorption by greenhouse glass, there is the effect of density of plantation, which was 6.25 plants/m² in the greenhouses and only 3.33 plants/m² in the field.

3.3. Tuber number

3.3.1. Evolution through time

Figure 2 shows that the development pattern of tuber number differed between cultivars but not much between water treatments in the same cultivar. Tuber number remained more or less constant from 78 DAP in the field and 60 DAP in the greenhouse in 1999. But in the greenhouse in 1998, tuber number decreased during the season due to "resorption", although no tuber rot was observed.

In the field, as noted above, Nicola showed the latest tuber initiation, even if its maturity (leaf senescence) occurred at the same time as Monalisa's, and earlier than the other varieties' (Tab. IV). This result differs from those of Deblonde and Ledent [8], who showed that tuber number for cultivar Nicola increased during the season. In this trial, however, the tuber number of Désirée remained relatively stable in the field.

3.3.2. Final tuber number

In all the experiments, there were statistically significant effects of water treatments and cultivars on the final number of tubers per plant. Water-cultivar interaction was significant in the field only, where drought stress reduced tuber number by 7% in Nicola and 27% in Monalisa, but did not affect Remarka and even increased tuber number by 4% (not significant) in Désirée (Tab. V).

In the greenhouse experiments, drought reduced the number of tubers/plant by 41% in 1998 and 29% in 1999 (average of varieties). Moreover, final tuber number, produced in the control treatments, differed between experimental sites (for the same variety) and also, to a large extent, between years (for the same experimental site). Taking into consideration that in 1998, the same batch of seeds was used in the field and in the greenhouse, the number of tubers appears to be influenced by environmental conditions, but also, and especially, by seed tuber characteristics.

3.4. Fresh tuber yield

3.4.1. Growth rate

Fresh tuber growth rate (GR) was calculated as the increase in tuber mass per plant and per day (g/plant/day) (Tab. VI).

Table V. Mainstem number, total stem number, final tuber number, fresh tuber yield, dry matter concentration and harvest index at final harvest.

	Mainstem number (/plant)		Total stem number (/plant)		Final tuber number (/plant)		Fresh tuber yield (g/plant)		Dry matter concentration (%)		Harvest index (HI) (%)	
	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought
Exp. I												
Remarka	3.0	3.0	9.8	6.3	12.5	12.5	2715	1522	19.1	21.1	83.6	77.4
Désirée	3.8	3.5	11.5	9.5	22.2	23.3	2426	2174	20.7	20.5	79.9	80.6
Nicola	5.0	4.3	10.2	9.2	19.7	18.5	2502	2127	20.9	21.6	79.2	82.1
Monalisa	2.8	2.3	10.7	7.8	22.2	16.3	2175	1793	17.6	18.0	82.7	82.4
W	NS		**		*		***		**		NS	
C	***		NS		***		***		***		**	
W × C	NS		NS		*		***		**		***	
Std err	0.27		0.98		0.89		25.86		0.218		0.3	
CV (%)	15.71		20.84		9.67		2.37		2.19		4.18	
Exp. II												
Remarka	3.3	3.3	4.2	4.0	15.3	8.5	335	158	20.7	22.3	62.6	54.9
Désirée	3.9	3.7	4.7	4.0	20.0	12.3	370	223	19.6	21.7	67.6	64.2
W	NS		NS		***		***		**		**	
C	**		NS		**		**		**		**	
W × C	NS		NS		NS		*		*		*	
Std err	0.10		0.14		0.46		3.89		0.06		0.6	
CV (%)	6.00		6.79		6.52		2.87		0.57		2.11	
Exp. III												
Remarka	3.1	3.0	3.2	3.7	23.3	17.5	401	213	17.9	19.3	47.8	45.6
Désirée	3.6	3.3	3.7	3.2	32.5	22.3	389	209	17.4	17.6	47.9	44.2
W	NS		NS		*		***		NS		NS	
C	*		NS		*		NS		NS		NS	
W × C	NS		NS		NS		NS		NS		NS	
Std err	0.12		0.54		1.68		11.64		0.46		2.0	
CV (%)	7.96		30.86		14.15		7.68		5.12		11.16	

Exp I: field experiment (1998). Exp II: greenhouse experiment (1998). Exp III: greenhouse experiment (1999). W: water. C: cultivar. CV: coefficient of variation. Std err: standard error of water × cultivar interactions. *, **, ***: significant differences at the 0.05, 0.01 and 0.001 probability levels, respectively. NS: non-significant difference.

The effect of drought on the growth rate (GR) of fresh tubers varied according to time during the period of tuber bulking and according to the location. Drought affected the cultivars differently only at the beginning of the bulking stage. During the rest of the cycle, drought reduced the growth rate of tubers in similar proportions for the studied varieties. Indeed, in the field, between the 57th and the 78th DAP, when the growth rate is the highest, GR, which for the well-irrigated treatments was between 50 and nearly 60 g/plant/day according to cultivar, was reduced under drought, by 32% for Remarka and 20% for Monalisa, while it remained unchanged under the same drought for Désirée and Nicola. In the greenhouse trials, cultivar Désirée not only maintained its GR under drought during the beginning of tuber bulking (between the 41th and the 60th DAP), but it increased it by 33% in 1998 and multiplied it by more than 3 in 1999 (Remarka also increased its GR during this period in 1998). Thus, the drought affected source-sink relations and seemed to increase the proportion of assimilates allowed to the tubers from the other parts of the plants, at least in some cultivars.

During the following periods, the effect of the interaction water-cultivar on GR in the greenhouse trials was not significant most of the time.

3.4.2. Final tuber yield

Statistical analysis of final fresh tuber yield showed a highly significant effect of cultivar and the interaction water-cultivar in 1998 in the field and in the greenhouse, but those effects were not significant in the greenhouse in 1999 (Tab. V).

In the field, the reductions by drought of fresh tuber yields were 11% for Désirée, 15% for Nicola, 18% for Monalisa and 44% for Remarka, in comparison with their respective controls. In the greenhouse trials, these reductions were, in 1998, 40 and 53% for Désirée and Remarka, respectively. In 1999, when the interaction effect was not significant, the same reduction of about 46% was noted both in Désirée and in Remarka. It is also interesting to underline that Remarka led to

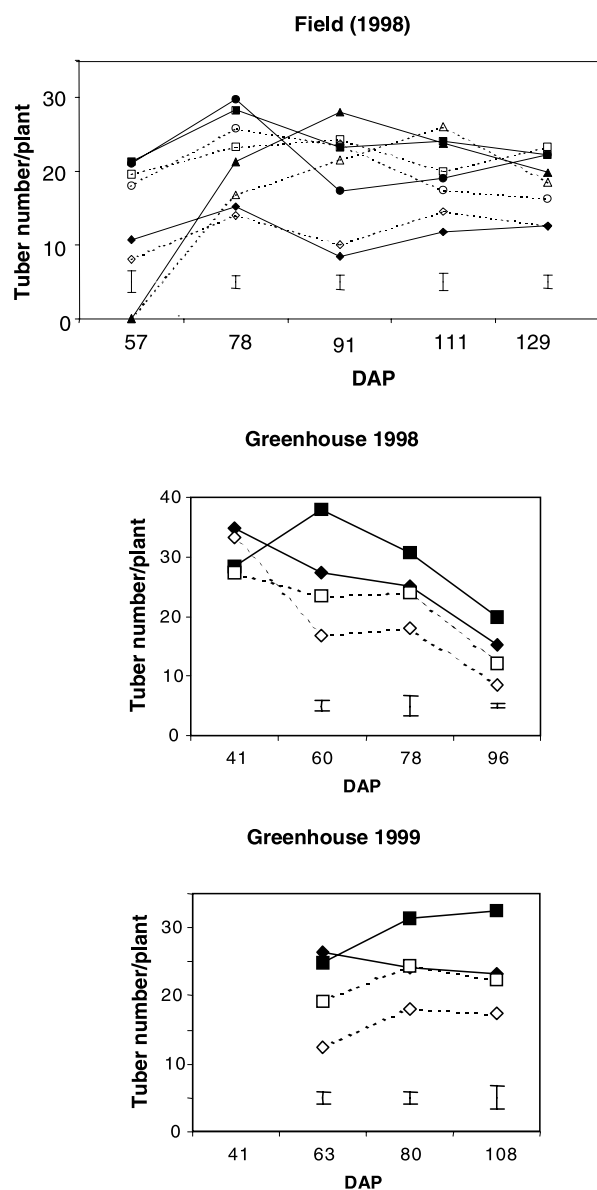


Figure 2. The evolution of tuber number through the season. Full symbols with continuous lines correspond to the irrigated treatments. Empty symbols with discontinuous lines correspond to the droughted treatments. ◆: Remarka, ■: Désirée, ▲: Nicola, ●: Monalisa. \pm correspond to the standard errors of water \times cultivar interactions.

the highest fresh yield in the well-irrigated treatment and to the weakest one under stress.

The final dry yield of tubers was affected in the same manner as fresh yield. In the field, drought decreased dry weight of tubers by 11, 13, 15 and 38% in Désirée, Nicola, Monalisa and Remarka, respectively. In the greenhouse experiment of 1998, the reductions were 33% in Désirée and 49% in Remarka. A similar reduction of about 44% was recorded in each of these two cultivars during the greenhouse

experiment of 1999. Earliness had no effect on fresh or dry yield of tubers.

3.5. Yield and drought tolerance

The drought tolerance index, TDWS (tolerance to a decrease in water supply) is defined as the tuber dry weight in drought conditions relative to the tuber dry weight in irrigated conditions [7, 8].

In the field, TDWS was 61.9% for Remarka, 84.4% for Monalisa, 87.6% for Nicola and 89% for Désirée. According to these results, we can consider that the most resistant varieties were Désirée and Nicola, followed closely by Monalisa, and finally by Remarka. The first three varieties differed little. The greater resistance of Désirée relative to Remarka is confirmed by the greenhouse results of 1998, where Désirée recorded 66.6% versus only 50.9 for Remarka. In 1999, the two cultivars were equally resistant to drought (Fig. 3).

Thus, the general ranking of cultivars according to their drought tolerance index is: Désirée \geq Nicola \geq Monalisa $>$ Remarka. These results (except those of the greenhouse trial of 1999) corroborate the Bonthuis and Ebskamp [3] classification for Désirée and Monalisa. In this reference, Nicola was classified as resistant as Désirée; Remarka was not yet classified. Moreover, TDWS obtained in the greenhouses were weaker than those obtained in the field for the same variety. This is explained by the higher intensity of drought in the greenhouse.

Regarding the relationship between drought resistance (TDWS) and the growth rate, the capacity of each cultivar to maintain its tuber growth rate under drought conditions was calculated as the GR in drought conditions relative to the GR in irrigated conditions and noted as GRM (growth rate maintenance). The calculations were done separately for each time interval, corresponding to successive sampling.

The linear regressions calculated for each trial between the TDWS of the cultivars and the corresponding GRM in each time interval showed significant correlations only in the first interval. Indeed, between the 57th and the 78th DAP in the field, and between the 41st and the 60th DAP in the greenhouse (1998), significant correlations were obtained. No relationship was found in the greenhouse trial of 1999 (Fig. 4).

3.6. Dry matter concentration in tubers

Drought stress generally increased DMC of tubers. For Remarka, the increase was 10% in the field and 8% in the greenhouse in 1998. Désirée was not affected in the field, but its DMC increased by 11% under drought in the greenhouse in 1998. Nicola and Monalisa, tested in the field, had an average increase of 2.5%.

3.7. Leaf area index (LAI)

Drought stress reduced the levels of the leaf area index (LAI) during the whole cycle, both in the field and in the greenhouses. The statistical analysis carried out for the maximum LAI showed a significant effect of the treatment in all the trials. The interaction (W \times C) was significant in 1998,

Table VI. Tuber growth rate (g/plant/day). Fresh weight.

Cultivar	Interval of time (DAP)							
Exp. I	57–78		78–91		91–111		111–129	
	Irrigated	Drought	Irrigated	Drought	Irrigated	Drought	Irrigated	Drought
Remarka	50.15	33.83	39.88	16.92	38.38	18.29	6.94	0.37
Désirée	53.86	51.14	25.56	11.29	17.74	16.85	19.50	22.49
Nicola	58.52	57.94	28.71	15.33	32.49	23.03	13.92	13.94
Monalisa	59.75	47.61	29.98	36.85	15.33	–0.23	–0.76	5.90
W	***		*		*			NS
C	***		NS		*			*
W × C	*		NS		NS			NS
Std err	2.36		6.42		5.74			5.57
LSD (W)	3.78		10.27		9.18			8.92
LSD (C)	5.35		14.53		12.98			12.61
CV %	9.17		50.25		56.74			10.89
Exp. II	41–60		60–78		78–96			
	Irrigated	Drought	Irrigated	Drought	Irrigated	Drought		
Remarka	5.12	6.80	7.24	9.44	3.31	1.41		
Désirée	0.36	1.72	8.90	8.92	0.7	0.58		
W		***		NS		***		
C		***		*		NS		
W × C		*		NS		NS		
LSD		0.8		0.9		0.6		
Std err		0.25		0.29		0.17		
CV %		14.43		6.73		31.12		
Exp. III	41–63		63–80		80–97			
	Irrigated	Drought	Irrigated	Drought	Irrigated	Drought		
Remarka	6.38	6.10	3.45	6.04	7.22	5.43		
Désirée	0.57	2.03	5.02	4.42	4.10	3.18		
W		***		NS		***		
C		**		*		**		
W × C		*		*		NS		
LSD		0.55		1.05		2.11		
Std err		0.17		0.33		0.66		
CV %		9.28		13.96		16.18		

Exp I: field experiment (1998). Exp II: greenhouse experiment (1998). Exp III: greenhouse experiment (1999). DAP: days after planting. W: water. C: cultivar. CV: coefficient of variation. Std err: standard error of water × cultivar interactions. *, **, ***: significant differences at the 0.05, 0.01 and 0.001 probability levels, respectively. NS: non-significant difference.

both in the field and in the greenhouse, but not in 1999 (Tab. VII).

In the field, drought stress reduced the maximum LAI by 29, 14, 2 and 6%, respectively, in Remarka, Désirée, Nicola and Monalisa. In the greenhouse trial of 1998, drought reduced this parameter by 63% in Remarka and by 40% in Désirée. In 1999, Remarka and Désirée registered an equal reduction of about 40% each.

The relationship between the maximum LAI and the tuber yield was highly significant in all the experiments. The variations in yield were associated to 32, 85 and 64% (R^2) with those of LAI in the field, in the greenhouse in 1998 and in the greenhouse in 1999, respectively (Fig. 5).

3.8. Leaf area duration (LAD)

Leaf area duration (LAD) integrates LAI and the length of time foliage remains photosynthetically active on the plant. It was calculated as: $LAD = \int LAI dt$.

The water effect and the interaction water-cultivar were significant on the LAD in all the experiments (Tab. VII).

Drought stress reduced LAD in the field by 60, 42, 11 and 17 days, respectively, in Remarka, Désirée, Nicola and Monalisa. In terms of percentage, compared with their respective controls, the reductions in LAD by drought in the field were 17, 11, 4 and 6%, respectively, for Remarka, Désirée, Nicola and Monalisa. Thus LAD reductions were higher in earlier cultivars. In addition, the reductions were

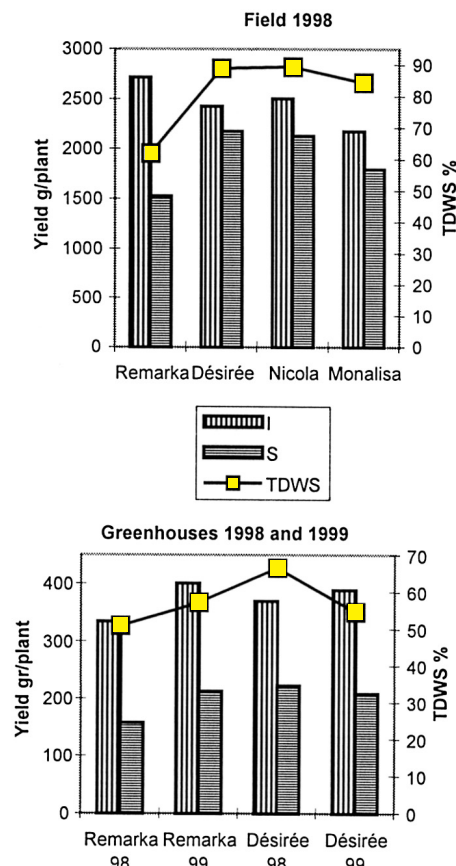


Figure 3. Tuber yields (g/plant) and the TDWS. TDWS is defined as tuber dry weight in the drought treatment relative to the irrigated treatment. I: irrigated. S: stressed.

more severe in the greenhouse and had reached 183 and 134 days in 1998, and 151 and 104 days in 1999 for Remarka and Désirée, respectively.

No significant correlations were found between LAD and tuber yields.

3.9. Harvest index (HI)

In 1998, both in the field and in the greenhouse, the interaction water-cultivar concerning HI was significant (Tab. V). In the field, the effect of drought stress on the HI was very dependent on the cultivar tested. Drought reduced HI by 8% in Remarka and increased it by 4% in Désirée while it had no effect on the HI of Nicola and Monalisa. In the greenhouse trial of 1998, the HI was decreased by 13 and 6%, respectively, in Remarka and Désirée.

In 1999, there were no significant differences, but similar trends were observed (Tab. V).

No clear relation was shown between the earliness of the studied cultivars and the effect of water shortage on HI. But, if we consider only the affected varieties, the HI appeared to be increased for the earliest variety, Nicola, and was decreased for the latest one, Remarka.

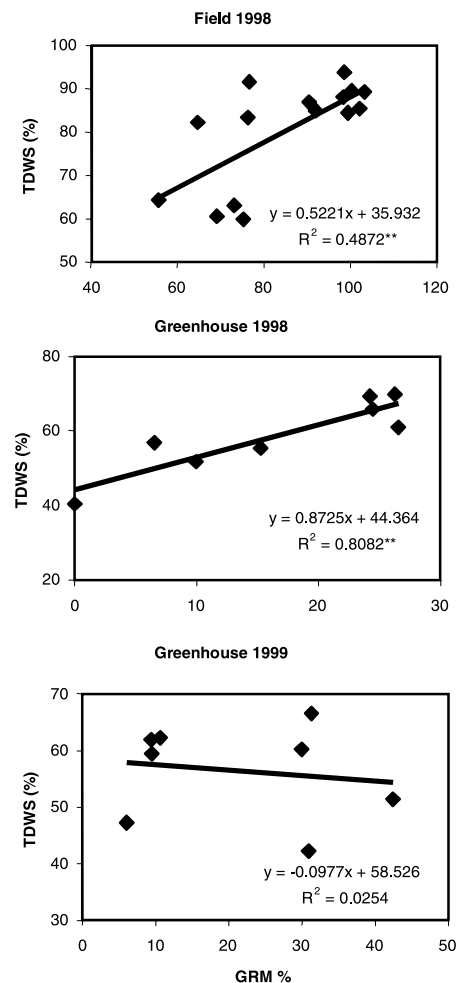


Figure 4. Relationship between tuber growth rate maintenance (GRM) (between the 57th and the 78th DAP in the field, and between the 41th and the 60th (or 63 in 1999) DAP in the greenhouses) and TDWS (defined as tuber dry weight in the drought treatment relative to the irrigated treatment) for all cultivars in each repetition.

4. DISCUSSION

Among all the parameters investigated in this study, only mainstem number was never affected by drought. Indeed, drought reduced total stem number, tuber number, fresh and dry tuber yield, total aerial biomass, dry mass of leaves, leaf area index (LAI), leaf area duration (LAD) and the harvest index (HI) of some cultivars, while drought increased dry matter concentration of tubers. For the majority of these characters, the interaction water-cultivar was significant; the cultivars tested were not affected to the same degree by water shortage, except for the greenhouse trial in 1999 where the reductions observed did not statistically differ between the studied varieties, Remarka and Désirée. This can be explained by the great fluctuation between the samples (high coefficients of variation and standard errors) which made the statistical

Table VII. Dry aerial biomass, leaf dry mass, LAI and LAD.

	Dry aerial biomass (g/plant)		Leaf dry mass (g/plant)		Maximum LAI (cm ² /cm ²)		Cumulated LAD (days)	
	irrigated	drought	irrigated	drought	irrigated	drought	irrigated	drought
Exp. I								
Remarka	101.6	93.7	50.51	35.24	7.31	5.18	349	288
Désirée	125.7	107.2	72.63	54.61	7.48	6.44	392	350
Nicola	137.5	100.1	94.11	59.88	5.46	5.34	287	275
Monalisa	80.2	68.9	39.95	24.48	4.57	4.10	303	286
W	***		***		*		***	
C	***		***		***		***	
W × C	**		*		*		**	
Std err	3.47		3.86		0.25		6.00	
CV (%)	6.80		14.31		9.60		3.79	
Exp. II								
Remarka	41.2	28.8	26.3	15.0	5.82	2.17	305.0	121.9
Désirée	34.7	26.9	20.4	15.6	5.11	3.09	292.9	158.1
W	**		**		***		***	
C	*		*		NS		NS	
W × C	*		*		***		**	
Std err	0.66		0.76		0.03		1.03	
CV (%)	5.50		7.93		1.66		5.33	
Exp. III								
Remarka	78.7	48.8	34.2	24.2	6.61	4.00	285.4	133.7
Désirée	73.9	46.4	26.4	20.7	6.59	3.81	231.8	126.9
W	*		NS		**		**	
C	NS		NS		NS		NS	
W × C	NS		NS		NS		*	
Std err	5.12		2.50		0.53		8.25	
CV (%)	16.53		16.53		20.3		10.15	

Exp I: field experiment (1998). Exp II: greenhouse experiment (1998). Exp III: greenhouse experiment (1999). W: water. C: cultivar. CV: coefficient of variation. Std err: standard error of W × C interactions. *, **, ***: significant differences at the 0.05, 0.01 and 0.001 probability, respectively. NS: non-significant.

differences not significant. The different behavior in the 1999 greenhouse trial would be due to a large variability in tuber seed size (Tab. I). However, the general tendencies were often in the same direction as those of the greenhouse trial of 1998.

Responsiveness to drought in terms of fresh and dry tuber yield varied greatly between the different varieties. In the field, the most affected variety is a later variety, Remarka (−44, −38% for fresh and dry yield, respectively), and the least affected one is also a later variety, Désirée (−11% each for the fresh and the dry yield). In our experiments, in the chosen interval of precocity, the earliness criterion had no effect on sensitivity of fresh or dry yield to drought (early drought in the greenhouse, or later in the field). One will therefore question the correlation between yield under drought and precocity. In 1998, in the greenhouse and field trials, Remarka was also more reduced by drought than Désirée, although both have similar earliness.

If we compare the two groups of earliness, according to the most affected parameters in each, our study showed that in the earlier cultivars, tuber number was more affected. In the later cultivars, the maximum leaf area index (LAI) and the total leaf area duration (LAD) were more affected. The sensitivity of the

other studied characters did not show differences according to the earliness criterion.

Since total stem number was influenced only by drought and the mainstem number only by cultivar, as reported before by Iritani [15] and Lynch and Taï [22], a compensation of the main stems by secondary stems takes place in relation to environmental conditions. Total stem number was indeed shown to be affected by factors like ambient temperature [13] or growth regulators [26]. The mainstem number appears to be a varietal character, as reported by Lynch and Taï [22]. But it is also affected by other factors such as the length of pre-sprouting period [2], size of seed tuber [14, 37] and physiological age [15].

Both in the field and in the greenhouse trials, the dynamics of tuber development was little affected by drought but differed between cultivars. It would be genetically controlled and little modified by management or environment [6]. The tubers initiated were more numerous in irrigated than in drought conditions. A wetter fore-season is beneficial for tuber number initiation [8, 28, 33]. Our field results indicate that for the earlier cultivars, Nicola and Monalisa, a surplus of tubers, which were going to disappear later, were initiated both in irrigated and dry conditions.

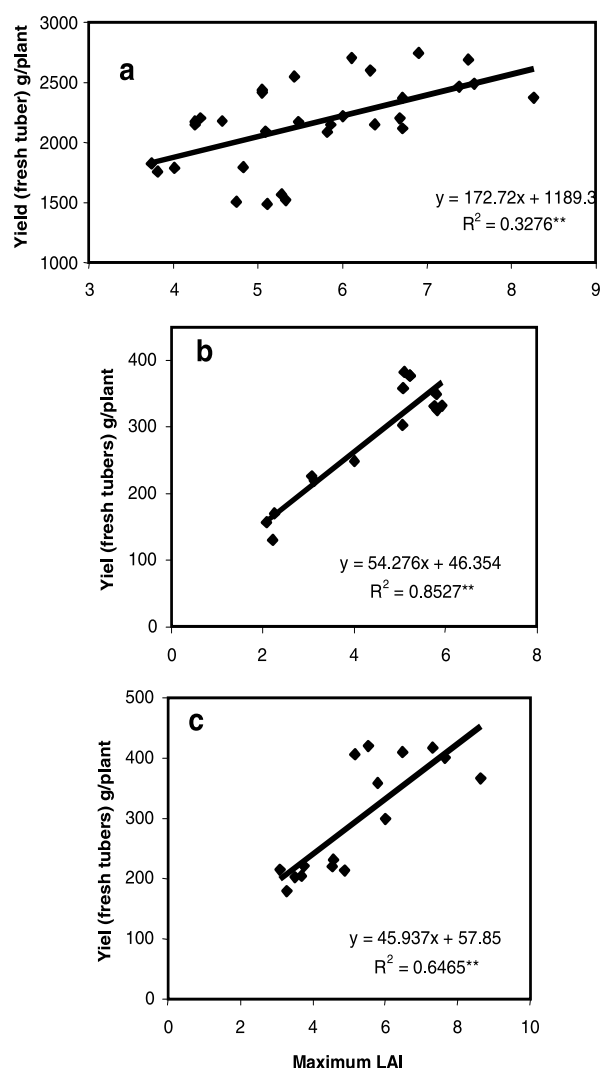


Figure 5. Relation between the maximum LAI (leaf area index) and the fresh tuber yield. a: Field 1998. b: Greenhouse in 1998. c: Greenhouse in 1999.

The differential behavior of the same cultivars according to the growth conditions (field versus greenhouse) shows that an early drought (greenhouse) reduces the number of tubers per plant in all varieties tested. The effect of a later one, beginning at tuber initiation (field), differs according to the variety and is more pronounced in the early cultivars. This may explain the different results found in the literature. Deblonde and Ledent [8] did not find differences between the two groups of earliness for final tuber number in response to drought. Mackerron and Jefferies [23, 24] showed that in Maris Piper, the number of tubers per stem was reduced by water shortage imposed very early in the season, but not later.

The maximum LAI (which was reached around the onset of tuber initiation) was determinant for fresh tuber yield in the three experiments, while no relationship was found between yield and total cumulated leaf area duration (LAD) in all of the three trials. Thus, the quantity of leaves developed before tu-

ber initiation was determinant, directly or indirectly (through association with other plant characters determined during the pre-initiation period) for tuber yield levels; differences in leaves developed after this stage were less related to tuber yield in our conditions. Root density and LAI before 49 DAP, but not later, are determinant for yield [10]. At the end of the season, there is no relation between the number of green leaves and yield; the drought treatments have a tendency to give a similar or even higher number of green leaves [8].

In many cases, LAD has been reported as being a major determinant of potato yield [5, 32, 34, 35] and a main limiting factor in early cultivars [12]. LAD and therefore tuber yield may be limited (suboptimal) by insufficient maximum LAI values and/or duration as such of the leaves formed. In our case, there was a tendency for leaf mass to be limiting for tuber yield in drought conditions but not in irrigated conditions. The early and later varieties behaved similarly in terms of yield. Thus, early varieties were more efficient, since more days in the later varieties did not mean more tuber yield, either in drought or in irrigated conditions.

According to the drought tolerance criterion, TDWS (tolerance to a decrease in water supply), defined as tuber dry weight in the drought treatment relative to the irrigated treatment, Désirée was the most resistant cultivar. In the field, it yielded under drought conditions nearly 90% of its control. The least resistant cultivar was Remarka, with less than 62% of the corresponding control. The TDWS of Nicola and Monalisa were 87.6 and 84.4%. A clear gap exists between Remarka and the other three cultivars. The greenhouse trials corroborate these results, at least in 1998.

GRM (growth rate maintenance) during the first three weeks of tuber bulking accounted for 49% of the drought tolerance index (TDWS) variation in the field, and for 80% in the greenhouse in 1998, while no relation was found in the greenhouse trial in 1999. Indeed, during the first three weeks of tuber bulking, when the rate of tuber growth is the highest, the most resistant cultivars, Désirée and Nicola, maintained their growth rate (GR) under drought conditions, contrarily to the reductions of 32 and 20% in Remarka and Monalisa, respectively. In the greenhouse, an increase in GR was even recorded for Désirée during the first weeks of tuber bulking under drought treatments. Thus, maintaining or increasing the early growth of tubers may be one of the strategies for maintenance of tuber yields in conditions of drought.

5. CONCLUSION

Except for mainstem number, all agro-physiological parameters studied were sensitive to drought and for most of them, the interaction water-cultivar was significant.

An early-maturing cultivar was more affected than a later-maturing cultivar in terms of tuber number, whereas the opposite occurred for LAI and LAD. The other studied characters did not show differences according to the earliness criterion. Therefore, in our conditions and in the few cultivars studied, the longer cycle of the later-maturing cultivars did not

result in a yield increase and, in this aspect, they do not have an advantage relative to earlier varieties.

The cultivars with the highest tuber yields in favorable conditions may not be the most productive ones when one of the conditions becomes limiting. This was the case for cultivar Remarka.

GRM during the first three weeks of tuber bulking accounted for 49% of the drought tolerance index variation in the field and for 80% in the greenhouse in 1999. Thus, the cultivars which maintained their tuber growth rate better under drought during the first three weeks of tuber bulking also maintained their yield better.

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