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Effects of moderate drought conditions on crop growth parameters and earliness of six potato cultivars under field conditions

Patrick DEBLONDE, Jean-François LEDENT*

Laboratoire d'Ecologie des Grandes Cultures, Université Catholique de Louvain, place Croix du Sud, 2 bte 11, 1348 Louvain-la-Neuve, Belgium

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Abstract – The main objective of this study was to compare the effects of moderate drought treatments on the intercepted radiation and light conversion coefficient (LCC). Another objective was to determine the impact of such moderate droughts on the evolution of the fraction of dry matter partitioned to the tubers in genotypes of contrasted maturity. Six potato genotypes contrasted for their drought tolerance and their earliness were subjected to three levels of water supply in two field trials in 1995 and 1996. The differential behaviour among cultivars found both years for ground cover duration and intercepted radiation was affected by the level of water supply. Ranking based on tuber yield was consistent with ranking based on intercepted radiation and ground cover duration, showing the interest of these parameters for characterising cultivars and discriminating among them. Stronger reductions of intercepted radiation were observed when the drought was applied early in the season, as in 1996, rather than around the middle of the season, as in 1995 ($-200 \text{ MJ} \cdot \text{m}^{-2}$ in 1996 instead of $-84 \text{ MJ} \cdot \text{m}^{-2}$ in 1995). When drought was applied around the middle of the season as in 1995, the drought treatment significantly reduced LCC but had no significant effect on intercepted radiation. The evolution of the fraction of dry matter which is partitioned to the tubers was not influenced by our moderate drought conditions and therefore did not hasten earliness of maturity. Earlier maturing cultivars showed significantly higher rates of increase in the fraction of dry matter which is partitioned to the tubers than later cultivars.

potato / drought / intercepted radiation / light conversion coefficient / partitioning

Résumé – Effets d'une sécheresse modérée sur les paramètres de croissance et la précocité de six cultivars de pommes de terre en conditions de champ. L'objectif principal de cette recherche était de comparer les effets de sécheresse modérée sur la radiation interceptée et sur le coefficient d'efficience de conversion de la lumière en matière sèche (LCC). Un autre objectif était de déterminer l'impact d'une sécheresse modérée sur l'évolution de la fraction de la matière sèche allouée aux tubercules. Six cultivars de pomme de terre contrastés pour leur précocité et pour leur

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^{*} Correspondence and reprints

ledent@ecop.ucl.ac.be

tolérance à la sécheresse ont été soumis à 3 régimes hydriques d'intensité différente en conditions de champ en 1995 et 1996. Les cultivars se sont comportés différemment selon les régimes hydriques pour la radiation interceptée et pour la durée de couverture du sol qui dans ce cas seraient des critères discriminants. Des réductions plus importantes de radiation interceptée ont été observées lorsque le stress hydrique s'est fait sentir tôt dans la saison comme en 1996 et non au milieu de la saison comme en 1995. La réduction était de –200 MJ·m⁻² en 1996 au lieu de –84 MJ·m⁻² en 1995. La sécheresse appliquée en milieu de saison a significativement réduit LCC mais n'a pas eu d'effet significatif sur la radiation interceptée. L'évolution de la fraction de la matière sèche qui est allouée aux tubercules n'a pas été influencée par nos conditions de sécheresse modérée et par conséquent n'a pas modifié la précocité. Toutefois, les cultivars plus précoces ont montré des coefficients pour l'évolution de la fraction de la matière sèche allouée au profit des tubercules significativement plus élevés que les cultivars plus tardifs.

pomme de terre / sécheresse / radiation interceptée / efficience de conversion de la lumière / répartition

1. Introduction

A major factor which influences the final tuber yield of potato crops submitted to drought conditions is a reduction in the amount of intercepted radiation [5, 6, 11]. The amount of radiation intercepted by the canopy depends on the amount of solar radiation above the canopy and on the fraction of solar radiation that is really intercepted. The effectiveness with which the amount of intercepted radiation is converted into dry matter (LCC, light conversion coefficient defined as the total dry matter production relative to the accumulated intercepted solar radiation [8] is another parameter which may influence final yield but there are discrepancies in the literature about the effects of drought on it: decreases of LCC have been reported by van der Zaag and Doornbos [11] but Jefferies and MacKerron [5] found no significant differences due to drought. The fraction of dry matter which is partitioned to the tubers (FT) was a last component taken into account since we were interested in tuber yield.

Van Heemst [12] showed that the fraction of dry matter which is partitioned to the potato tubers increases linearly through thermal time at a rate of 0.003 per degree-day from the onset of tuber initiation. The rate of increase was not modified by cultivar, soil type, plant density and seed size, but drought stress was not considered. The main difference between earlier and later cultivars was a later onset of tuber initiation in the case of late cultivars whereas the rate of increase through time of the fraction of dry matter invested in tubers did not differ between the two groups of cultivars [12].

The objective of this study was first to determine how LCC was affected by early and late moderate drought conditions as commonly encountered in sandy-loamy soils in Belgium and compare the results with the effects of such droughts on intercepted radiation. The effect of moderate drought on other parameters such as harvest index, dry matter content, tuber and biomass yields were also considered. A second objective was to determine the effect of moderate drought on the evolution of the fraction of dry matter partitioned to the tubers and consequently on cultivar maturity. Indeed, the onset of tuberisation is obviously associated with the onset of partitioning of dry matter to the tubers, and both occur earlier in early maturing cultivars. The time taken for the appearance of partitioning coefficients significantly different from zero is therefore related to the earliness of maturity of a cultivar. This applies also to the moment when the partitioning coefficient reaches 100%, i.e. when all the produced assimilates are allocated to the tubers and the increase in weight is only due to the tubers. We wanted to test if drought stress would hasten earliness of maturity.

2. Materials and methods

Two field trials were carried out on a fine silt soil in Nodebais (central Belgium; 50°45'N, 4°44'E). The trials were strip-plots with two factors (cultivar and water status) and four replicates.

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Sub-plot size was 3×9 m. The spaces between tubers within and between the lines were respectively 32 and 75 cm. Certified tuber seeds produced in Benelux were used. Tuber seeds were treated against Rhizoctonia solani before planting with pencycuron (Monceren, Bayer Belgium, 12.5% WP) at a rate of 0.25 $g \cdot kg^{-1}$ tuber seed. Weeds were chemically controlled with linuron (Afalon, Hoechst Belgium, 47.5% WP) and prosulfocarbe (Defi, Zeneca, 800 $g \cdot l^{-1}$). The crop was treated with fungicides as a function of advice from the late blight warning organisation (PAME-SEB). There were five treatments in 1995 and seven treatments in 1996; mancozebe and ofurace (Patafol, Schering, 68.5% WP for mancozebe and 7.15% WP for ofurace) were used and for the two last treatments fentin hydroxyde (Stanex 18 Flow, Protex, 180 $g \cdot l^{-1}$) was added to mancozebe. Fertilisation was as follows: 148 N. 77 P. 151 K in 1995 and 156 N, 72 P, 139 K in 1996. Diseases were kept under control at a low level and there were no obvious physiological disorders except some symptoms of Mg deficiency in some plots with cultivar Claustar. Other characteristics of both field trials are shown in Table I.

In accordance with our objectives we selected six contrasting European cultivars (five of which were present for both years; Tab. I) reported to be different for their drought resistance [1] and showing a range in earliness of maturity.

2.1. Treatments

The plots of the irrigated treatment received water from rainfall plus a limited amount from irrigation (water was sprayed using nitrogen sprayer nozzles; Tab. II). Four (1995) or three (1996) Jet fill tensiometers (Soilmoisture Equipment Corp., Santa Barbara, USA) were placed in two of these plots (replicate 2 and 3; cultivar Désirée) at two depths (15 cm and 60 cm below the seed tuber) to monitor soil water potential. Irrigation was performed in the evening and was triggered when the soil water potential values attained –50 to –60 kPa and this was reached from 100 days after planting onwards. Despite the irrigation (four times in 1995) and three times in 1996), the soil water potential remained sometimes below the triggering value.

	Field trial 1 (1995)	Field trial 2 (1996)
Cultivars	Eersteling $(E; 6)^1$	Eersteling $(E; 6)^1$
	Jaerla (E; 8)	Jaerla (E; 8)
	Claustar (M-E; ?)	Bintje (M-E; 8)
	Krostar (M-E; 5)	Krostar (M-E; 5)
	Nicola (M-L; 8)	Nicola (M-L; 8)
	Désirée (M-L: 8)	Désirée (M-L: 8)
Tuber size (mm)	28/35 for all cultivars except	28/35 for all cultivars except
	cultivar Krostar 28/40	cultivar Krostar 28/40
Date of planting	15 April	12 April
Tuber harvest	129 DAP ² for E and M-E (except Krostar) and 150 DAP for the rest	137 DAP for E and M-E (except Krostar) and 159 DAP for the rest

Table I. Characteristics of field trials.

¹ Earliness and drought tolerance rating (according to Bonthuis and Ebskamp, 1994); E, M-E and M-L: early, mid-early and mid-late, respectively; the number is a drought tolerance rating, a higher number indicates a higher drought tolerance (maximum 10); ?= unknown drought tolerance.

² DAP: days after planting.

Treatment Year	Irriga rainfall ¹ + slig 1995		ated ght irriga 1996	tion	Ambient rainfall only 1995 1996		plasti	Drought during f	ought ing first 8 weeks ² 1996			
Total water supply (rainfall + irrigation, mm) ³	285 + 37		320 + 35		285	320		111+80 ⁴ stemflow: 9mm		nm ste	61+197 ⁴ stemflow: 5mm	
Lowest measured soil water potential (MPa) at two depths	DAP	Ψw	DAP	Ψw	DAP	Ψw	DAP	Ψw	DAP	Ψw	DAP	Ψw
10 to 20 cm 20 to 40 cm	107 107	-0.38 -0.13	102	-0.14	107 107	<-1.5 -0.65			107 107	<-1.5 -0.28	102 102	<-1.5 -0.5
Leaf water potential (MPa)	94	-0.39	112	-0.47			112	-0.6	94	-0.53	112	-0.59

Table II. Characterisation of water supply treatments.

¹ Rainfall of March, April, May and June in 1996 was systematically lower than in 1995. Effect of the ambient treatment was shortened in 1996 because of a heavy rainfall 122 days after planting.

² The plastic sheet mostly limited the supply of rainfall water to stemflow (S) during a period of approximately 8 weeks from 50% emergence onwards + rainfall before and after this period; plastic placing and withdrawal (48–103 days after planting and 54–112 days after planting for 1995 and 1996, respectively).

³ A total of 37 mm and 35 mm was applied in 1995 and 1996, respectively (4 applications between 80–124 days after planting (1995) and 3 applications between 95–115 (1996)).

⁴ Amount of rainfall before and after plastic placing, respectively.

DAP: days after planting.

The ambient treatment received water from rainfall only. The difference between the irrigated treatment and the ambient treatment was especially small for the early cultivars. Indeed in 1996, a heavy rainfall (49 mm) occurred 122 days after planting bringing the irrigated treatment and the ambient treatment to the same level of water supply.

The drought treatment was imposed by placing a strong black plastic sheet (0.2 mm thick) on the soil surface of the plots, the sheet following closely the shape of the ridges and therefore forming gutters between them. Rectangular holes (± 10 cm wide and about 1 m long) were made through the sheet following the top of the ridges to allow plants to protrude. The plastic sheet was placed when 50% of plants of all cultivars had emerged (Tab. II). Most of the rain collected in the gutters formed by the plastic sheet was led outside the field trial through a furrow especially made for this purpose. Soil temperature was measured in the

centre of the ridge, and 20 cm below the top of the ridge, and was not altered either by the plastic sheet nor by cultivars (data not shown). This measure was performed once in 1995 at 3 p.m. after 10 days of high solar radiation (>2000 joules cm⁻²) and high minimum and maximum temperatures (>10 °C and >20 °C, respectively).

We are aware that the plastic sheet did not prevent totally water from rainfall reaching the plants (among other things because of stemflow). The importance of water reaching the soil by stemflow varies as a function of the rain and wind intensity. Saffigna et al. [9] observed that 4 to 23% of the rainfall on potato canopy flowed down the stems during rains of low to high intensity, respectively. The values of the estimated rainfall reaching the soil by stemflow is given in Table II. They were estimated using hourly rainfall intensity data from a nearby meteorological station (at 9 km from the field trial). These data were multiplied by a polynomial function ($y = -0.0006 x^2 + 0.0328 x + 0.032$

0.0027; $R^2 = 0.997$, n = 4) based on the low and high rain intensity data of Saffigna et al. [9] relating rain intensity (mm·h⁻¹) and stemflow proportion.

Thus, three water regimes (irrigated, ambient and drought) were applied on the field trials and the difference between these water regimes was confirmed by the soil and leaf water potentials (Tab. II). The most contrasted treatments were irrigation and drought obtained with plastic sheet covering. The treatment of natural drought (ambient) gave intermediary values.

2.2. Measurements

The emergence percentage was measured twice in 1995 (38 and 44 days after planting) and once in 1996 (46 days after planting). There were differences of emergence between cultivars both years: cultivar Krostar emerged earlier than the other cultivars whereas cultivar Jaerla emerged last. The proportion of ground covered by foliage was determined at 7–11 day intervals with a 90×75 cm frame divided in 100 equal sections $(9 \times 7.5 \text{ cm})$ which was placed over a row and viewed directly from above. The ground cover percentage was obtained by counting the number of sections which were more than half filled with green leaves. Two readings were taken over the central rows of each plot from emergence to 101 and 89 days after planting (in 1995 and 1996, respectively) and one reading afterwards.

We calculated the rate of ground cover development, the length of the period to reach 90% from planting onwards (the latter was preferred to the usual 100% because several cultivars did not reach 100% ground cover in 1996) and ground cover duration which corresponds to daily cumulative ground cover percentage.

The cumulative intercepted radiation was calculated by multiplying the daily global solar radiation measured in a nearby meteorological station by the proportion of ground cover (ground cover percentage between measurements was obtained by interpolation). The determination of the proportion of ground covered by green foliage with the aid of a grid [2] has the advantage of being quick, non-destructive and allows sampling of large areas.

2.3. Yield

Two plants from the central ridges were lifted fortnightly in each plot (the first harvest started 60 and 67 days after planting in 1995 and 1996, respectively) with the aid of a spade. Thus 14 or 16 plants altogether were harvested for determination of the growth curve. Larger samples were not taken to avoid disturbance of remaining plants within the plot (border effects, effects of gaps due to previous sampling, etc.). Four plants were lifted at final harvest in each plot. Tubers were separated from the rest of the plant and weighed in the field. For each harvest of tubers a sub-sample of 350-400 g was washed and chipped for dry matter determination. The chips were dried in an oven at 105 °C for 72 hours. The rest of the plant which consisted of leaves, shoot and the remaining attached roots and stolons was also weighed. When necessary only a sub-sample of 500-800 g was used for dry matter determination (the part of the shoot which was in the soil was rinsed and shaken firmly afterwards to remove the excess of water).

The light conversion coefficient (LCC) is equal to dry biomass produced per unit intercepted radiation (in $g \cdot MJ^{-1}$) and is equivalent to radiation use efficiency (RUE). The harvest index was calculated as tuber yield at final harvest divided by tuber yield at final harvest plus maximum foliar mass during the season.

2.4. Dry matter partitioning

The fraction of dry matter partitioned to the tubers (FT) was determined by calculating the fraction of the total dry matter increase in the tuber between two successive harvests. We related FT with the accumulated temperature from emergence onwards. Temperature data were obtained from a meteorological station situated 1 km from the field. Since not all temperatures are equally effective, we used a threshold of 7 °C, a maximum of 29 °C and

an optimum of $18 \,^{\circ}$ C [12]. Under 7 and above 29 $^{\circ}$ C the contribution to the temperature sum was considered equal to 0. Between 7 and $18 \,^{\circ}$ C, the contribution was taken as the measured average daily temperature minus the threshold value. Between 18 and 29 $^{\circ}$ C, the contribution was equal to 29 minus the measured average daily temperature [12].

The fraction of roots and stolons which remained in the soil at harvest and dead material (mainly leaves) falling on the ground during the early part of the growing season were not considered in the total dry weight. Thus our partitioning coefficients to tubers were somewhat overestimated but our calculation procedure can be considered to give reliable results as long as these fractions were small. Van Heemst [12] reported the fraction remaining in the soil was relatively negligible in the observed growing period and it never exceeded a few hundred kilograms per hectare. Van Heemst [12] also reported that in well-managed fields there is normally little decay of plant parts during the first seven weeks after emergence. However, severe drought stress could shorten the length of

this period [13]. In the case of our results, the data used for the calculation of the linear regression between the fraction of dry matter partitioned to the tubers and accumulated thermal time were those collected over a period never exceeding eight weeks after 50% emergence.

2.5. Statistical analysis

All data were submitted to analysis of variance per year separately but also over the two years together. Contrasts were calculated and tested to examine in more detail the interactions of cultivars and treatments.

3. Results

3.1. Water deficit and temperature evolution

Figure 1 shows the evolution of the water (rainfall + irrigation) received by the crop in the case of each treatment. The potential cumulative evapo-



Symbols : Ø, potential evapotranspiration ; D, irrigated treatment ; A, ambient treatment ; O, drought treatment



x, maximum ; +, mean ; *, minimum

Figure 1. Accumulated water supply (rainfall and/or irrigation) for all treatments compared to the accumulated potential evapotranspiration for a potato crop (from a nearby meteorological station: Louvain-la-Neuve) and maximum, minimum and mean air temperatures (per decade; from a meteorological station near the field: Beauvechain) in 1995 (left) and 1996 (right). Symbols: \Diamond , potential evapotranspiration; \Box , irrigated treatment; Δ , ambient treatment; \bigcirc , drought treatment; x, maximum; +, mean; *, minimum.

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transpiration is also presented. In the irrigated treatment, the evolution of water received followed fairly closely the potential evapotranspiration in 1995, whereas in 1996 this was not the case from 70 days after planting onwards indicating that if it had been possible irrigation should have been performed more frequently. The effect of the plastic sheet (drought treatment) on the intercepted rainfall was more pronounced and lasted longer in 1995 than in 1996. In the ambient treatment (natural drought) water supply showed through time values between these of the irrigated treatment and the drought treatment. Table II gives also indication of soil and leaf water potentials and confirms the difference between the irrigated treatment and the drought treatment.

In 1995 maximum air temperatures were maintained at a high level (more than 25 °C per decade) during five decades and in three of them maximum temperatures were above 27.5 °C. Such high temperatures were not observed in 1996. High temperatures are known to stop development and reduce growth in potato crops. Sands et al. [10] reported a maximum of 30 °C above which development ceased. Thus on the basis of temperature, final yield could be expected to be lower in 1995 compared to 1996 but this could be offset by the lower rainfall during the season in 1996 (until 122 days after planting).

3.2. Ground cover

For the values of ground cover reached (through time), the effects of treatments and more specifically the difference between the drought treatment and the irrigated treatment were generally higher in 1996 (Fig. 2, Tab. III) due to the less favourable



Figure 2. Ground cover evolution in 1995 and 1996 (average over cultivars). DAP: days after planting.

	1995					1996							
Treatment	DAP ¹	89	100	107	121	94	101	111	122	132	138		
Irrigated	Eersteling	93.8	95.3	87.0	37.0	97.0	79.5	75.5	70.3	51.5	31.8		
•	Jaerla	96.0	93.8	94.3	36.5	95.5	83.3	79.3	77.5	49.3	35.8		
	Krostar	94.1	98.0	93.0	47.8	99.1	93.5	89.0	86.8	86.8	79.3		
	Nicola	98.0	98.8	99.3	93.5	99.9	99.4	99.5	95.3	89.3	81.7		
	Désirée	94.0	99.0	96.8	87.8	98.1	94.5	95.3	97.0	92.3	93.0		
Drought	Eersteling	88.5	91.0	79.5	51.3	88.5	67.3	49.8	47.8	29.8	23.3		
-	Jaerla	93.1	93.3	81.8	30.8	81.1	58.6	26.8	23.3	6.8	8.0		
	Krostar	74.1	74.0	73.0	32.3	92.0	82.1	70.0	67.3	69.0	64.3		
	Nicola	94.4	92.0	90.3	81.0	93.8	93.0	92.5	91.0	86.5	80.7		
	Désirée	93.6	97.5	94.5	89.0	90.0	86.9	87.5	86.3	78.0	77.3		
Analysis	Cultivar	*	**	**	**	**	**	**	**	**	**		
5	Treatment	NS	**	NS	NS	**	**	**	**	**	**		
	$C \times T$	**	**	**	*	**	*	**	**	**	*		
	C.V. (%)	5.0	3.5	6.9	22.7	3.2	5.5	8.3	10.6	12.8	14.4		
	s.e.	2.33	1.63	3.04	5.88	1.52	2.35	3.25	3.90	4.12	4.21		

Table III. Ground cover values.

¹ DAP: days after planting.

*, **: significance at 0.05 and 0.01 probability levels, respectively. NS: not significant.

conditions in the fore-season of that year (86 mm rainfall from March until end of May in 1996 instead of 202 mm in 1995). In the case of the drought treatment no cultivar, and especially early cultivars, ever reached full cover in 1996. On average 90% ground cover was reached 71 and 80 days after planting in 1995 and 1996 (Fig. 2). Toward the end of the season of 1996 ground cover in the drought treatment became significantly higher than in the ambient treatment. Significant cultivar differences for ground cover were found as expected for almost all measurement dates. Cultivar Krostar was mainly responsible for the cultivar by treatment interactions in 1995 whereas, in 1996, this could generally be attributed to cultivars Jaerla and Nicola. Cultivar Krostar characterised by longer stems was sensitive to strong winds which led to lower ground cover values and also longer periods of recovery after such events.

The rate at which ground cover develops was significantly slower in 1996 than in 1995 (significant year effect at the level P < 0.01; 2.42 and

3.15% increase in ground cover per day, respectively).

In 1995, ground cover duration of cultivar Krostar showed significantly (P < 0.01) stronger decrease in the drought and ambient treatments (difference with the irrigated treatment) than all other cultivars (Fig. 3). In 1996, Jaerla was the cultivar most affected by the drought treatment whereas Nicola gave better (P < 0.05) ground cover duration under these conditions than the other cultivars. The ambient drought treatment did not reveal any differential behaviour that year.

3.3. Intercepted radiation

Intercepted radiation expressed relative to the irrigated treatment, appears as the measured parameter most influenced by drought, and to a lesser extent by the ambient treatment, especially in 1996. The analysis within years shows significant (P < 0.01) cultivar by treatment interaction both years (Tab. IV), showing that cultivars responded



Figure 3. Ground cover duration in 1995 and 1996. ^T: represents standard error of interaction.

differently to the various levels of water supplies. In the case of the drought treatment the low values of intercepted radiation obtained for Krostar (both years) and Jaerla (only in 1996) were in contrast with the high values of Nicola both years.

Statistical analysis of data obtained over years at final harvest shows significant (P < 0.05) two-way interactions and a triple interaction (year × treatment × cultivar; Tab. IV). Thus the effect of treatments and the behaviour of cultivar was modified across years (P < 0.01).

3.4. Tuber and biomass yield

Across years there was also a difference among cultivars for tuber and biomass dry weight at final harvest (Tab. IV). Within years main effects were observed but there was no differential behaviour of cultivars between treatments (not significant cultivar by treatment interaction). However, in 1996, the contrast method showed that the drought treatment reduced significantly less (P < 0.01) tuber dry weight in the mid-late cultivars Nicola and

Table	IV.	Intercepted	radiation,	light	conversion	coefficients,	harvest	index,	dry	matter	content,	tuber	and	biomass
yield.														

Treat- ment	Cultivar	Interce radiati (MJ·m	epted on 1 ⁻²)	Light conver coeffic (g·MJ ⁻	sion ient ¹ 1)	Harvest index		Dry matter content (%)		Tuber (kg·m ⁻	yield ⁻²)	Biomass yield (kg·m ⁻²)	
		1995	1996	1995	1996	1995	1996	1995	1996	1995	1996	1995	1996
Irrigated	Eersteling	1067	1077	1.13	1.19	0.78	0.80	23.7	21.4	1.05	1.08	1.20	1.23
	Jaerla	1019	1013	1.18	1.35	0.79	0.82	20.2	20.0	1.03	1.18	1.20	1.35
	Krostar	1234	1400	1.08	1.12	0.79	0.78	24.4	24.9	1.17	1.35	1.33	1.55
	Nicola	1478	1399	0.95	0.90	0.71	0.73	20.2	19.9	1.14	1.08	1.41	1.32
	Désirée	1400	1373	1.02	1.04	0.77	0.73	20.6	20.7	1.17	1.14	1.42	1.41
Mean		1240	1252	1.07	1.12	0.77	0.77	21.8	21.4	1.11	1.17	1.31	1.37
Ambient	Eersteling	1070	948	1.17	1.15	0.79	0.77	23.0	22.7	1.09	0.83	1.26	0.98
	Jaerla	1003	911	0.96	1.21	0.75	0.79	20.7	20.9	0.83	0.93	0.96	1.08
	Krostar	1093	1230	1.10	1.02	0.78	0.76	25.0	24.0	1.09	1.05	1.21	1.23
	Nicola	1440	1276	0.99	0.88	0.70	0.72	21.0	19.5	1.13	0.88	1.42	1.09
	Désirée	1341	1275	1.04	1.06	0.76	0.76	20.6	20.4	1.14	1.16	1.39	1.47
Mean		1189	1128	1.05	1.06	0.76	0.76	22.1	21.5	1.06	0.97	1.25	1.17
Drought	Eersteling	1043	888	0.97	1.12	0.77	0.77	24.1	22.5	0.84	0.78	1.00	0.96
	Jaerla	962	674	1.04	1.48	0.81	0.80	21.8	22.2	0.87	0.82	1.00	0.96
	Krostar	1033	1165	0.90	1.07	0.76	0.79	24.4	25.5	0.83	0.99	0.93	1.20
	Nicola	1385	1314	0.91	0.90	0.71	0.77	20.7	20.8	0.98	0.97	1.26	1.23
	Désirée	1355	1216	1.00	1.00	0.77	0.79	20.8	21.1	1.09	0.98	1.36	1.20
Mean		1156	1051	0.96	1.11	0.76	0.78	22.4	22.4	0.92	0.91	1.11	1.11
Analysis	Y ³	1	NS	*		NS		NS		NS		NS	
over	С	:	**	**	:	**		2	**	*		*	
years ²	Т	:	**	NS	5	Ν	1S		*	*	**	**	
	$Y \times C$:	**	**	:	Ν	1S		*	*		*	**
	$Y \times T$:	**	NS	5	Ν	NS	Ν	IS	N	IS	N	IS
	$C \times T$	1	NS	NS	5	Ν	IS	Ν	IS	N	IS	N	IS
	$Y \times C \times T$		*	NS	5	Ν	NS	Ν	IS	Ν	IS	N	IS
Analysis	C ³	**	**	NS	**	*	**	**	**	*	*	**	**
within	Т	NS	**	P < 0.057	NS	NS	NS	NS	*	*	**	*	**
years4	$\mathbf{C} \times \mathbf{T}$	**	**	NS	NS	NS	NS	NS	*	NS	NS	NS	*
	s.e.	23.1	23.4	0.08	0.06	0.01	0.02	0.53	0.37	0.077	0.052	0.08	0.06
												8	0

¹ Light conversion coefficient for biomass dry weight.
² Analysis performed with the five cultivars present both years (i.e. without Claustar and Bintje).
³ Y: year; C: cultivar; T: treatment.
⁴ Analysis performed with the six cultivars present within a year.
*, **: significance at 0.05 and 0.01 probability levels, respectively. NS: not significant.

Désirée than in the other cultivars (the reduction is calculated in comparison with the irrigation treatment). In the ambient drought treatment, only cultivar Désirée maintained the yield level of the irrigation treatment (P < 0.01). The differential behaviour observed for biomass yield was due to the same cultivars and treatments as for tuber yield. We take the difference in tuber dry weight in $g \cdot m^{-2}$ between the irrigated and the drought treatments as a measure of sensitivity to water shortage. The classification from the most tolerant to the least tolerant on the basis of sensitivity values obtained in 1996, and indicated between parentheses, is as follows: Nicola (109), Désirée (163), Bintje (255), Eersteling (300), Jaerla (359) and Krostar (362).

3.5. Light conversion coefficient (LCC), harvest index and dry matter content

In 1995, a tendency of the drought treatment to show lower LCC values was observed (significant only at P < 0.057 in 1995; Tab. IV), and this was confirmed by the significant contrast between drought and irrigation (P < 0.05; data not shown). Therefore that year LCC was significantly reduced by drought whereas intercepted radiation was not. In 1996, LCC was not significantly modified by drought treatments but early cultivar Jaerla had significantly higher LCC than the mid-late cultivars (especially cultivar Nicola). Both years, cultivar by treatment interactions were not significant.

The harvest index was not influenced by the drought treatments, and different behaviour of cultivars between treatments was not observed. However, the analysis over years showed that cultivar Nicola had a significantly lower harvest index than the other cultivars. The contrast method showed also that early cultivars (Eersteling and Jaerla) had a significantly higher harvest index (P < 0.05) than Krostar, Nicola and Désirée.

Dry matter content percentage (DMC) was not influenced by the drought treatment in 1995 whereas in 1996 it was significantly increased (Tab. IV). In 1996, a differential behaviour of cultivars was observed (cultivar by treatment interaction). The increase of DMC in Jaerla was indeed higher than in the other cultivars whereas DMC of Bintje was not affected.

3.6. Yield evolution in relation with intercepted radiation

Figure 4 presents the relationship between intercepted radiation and tuber dry weight during the season for all cultivars except Désirée. In the case of Jaerla, the lack of intercepted radiation towards the end of the season was the main reason for the tuber dry weight reduction associated with the drought treatment (compared to irrigation) in 1996, whereas in 1995 this was not the case as LCC played a greater role in the tuber yield reduction than the intercepted radiation. In the case of cultivar Nicola, intercepted radiation and LCC were hardly affected by drought both years. This figure and the results of the statistical analysis of intercepted radiation and LCC (Tab. IV) show that differences of LCC between treatments were greater in 1995 (although not statistically different but at the limit of the signification: P < 0.057), whereas the effect on intercepted radiation over the whole season was stronger in 1996.

The ranking of cultivars on the basis of the intercepted radiation shown in Table IV gives the following result for 1996 (from the most tolerant to the less tolerant cultivars; the value between brackets gives the difference of intercepted radiation in $MJ \cdot m^{-2}$ between the irrigation and the drought treatments): Nicola (85), Bintje (122), Désirée (157), Eersteling (189), Krostar (235) and Jaerla (339). The comparison of this classification with the tuber dry weight classification indicates that both classifications are quite similar and well in accordance: Nicola was the most tolerant cultivars whereas cultivar Krostar and Jaerla were the least tolerant ones.

3.7. Dry matter partitioning

The fraction (FT) of dry matter which is partitioned to the tubers increased through time. The rate of increase (bFT) was on average 0.0030 (sb =



Figure 4. Relation between intercepted radiation and tuber dry weight for two treatments (irrigated and drought treatments) and four cultivars.

0.00032) per degree-day (mean over cultivars, treatment and years; Tab. V). Statistical analysis gave a significant cultivar effect on bFT while other main effects and interactions were not significant. FT values increased faster through thermal time in earlier maturing cultivars (Eersteling and Jaerla) than later cultivars. At the first harvest after all cultivars had tuberised, cultivar Eersteling was the only cultivar which had in both years a significantly higher FT than cultivar Nicola, the cultivar reported as most tolerant to drought.

4. Discussion

For all measured and calculated parameters, except for harvest index, we observed a significant

year by cultivar interaction. This indicates that one or more cultivars behaved differently according to the year conditions. This could be due to differences in physiological age of the mother tuber. Another reason was that years differed mainly by their fore-season which was relatively drier in 1996.

Over years, early cultivar Eersteling had a higher ground cover development rate than later cultivars. The results of 1996 showed that towards the end of the season ground cover was maintained at a higher level in the drought treatment. This demonstrates the capability of potato crops to produce new leaves (either on the top of the main stem or on the above ground lateral branches) and to maintain ground cover. This may enable the crop

Table V. Regression coefficients in degree-day of the linear relation between the fraction of dry matter increase invested in tubers (bFT) and the temperature sum for the five cultivars present both years (mean over years).

Cultivar	Irrigated	Drought
Eersteling	0.00316	0.00310
Jaerla	0.00322	0.00342
Krostar	0.00291	0.00316
Nicola	0.00315	0.00291
Désirée	0.00252	0.00266
Y1]	NS
С	;	*
Т]	NS
Y×C]	NS
$Y \times T$]	NS
$C \times T$]	NS
Y × C × T]	NS

¹Y: year; C: cultivar; T: drought treatment.

*: significance at 0.05 probability level. NS: not significant.

to produce after drought stress has been alleviated or suppressed.

Ground cover duration and intercepted radiation were the only parameters for which cultivars showed differential behaviour between treatments in both years. Moreover, within each year, the rankings of cultivars on the base of these closely related parameters were identical (with no inversion of position). More importantly these rankings were consistent with those according to tuber yield. These two parameters should therefore be useful criteria to characterise genotypes and to discriminate among them. Cultivar Krostar showed both years strong reductions in intercepted radiation and may therefore be considered as sensitive to this parameter. Jaerla appears to be sensitive to drought applied early in the season (as in 1996), whereas cultivar Nicola was the most tolerant cultivar in this regard.

The light conversion coefficient was affected by the drought treatment only in 1995. These results on LCC and those of intercepted radiation indicate that in 1995 LCC was the parameter most affected by drought whereas intercepted radiation was not significantly reduced. This is in contrast with the results of Jefferies and MacKerron [5] who found that only intercepted radiation was affected by drought, and those of van der Zaag and Doornbos [11] who found that LCC played a role equivalent to the role of the intercepted radiation in explaining yield differences when drought stress occurred in the middle of the season or when there was a lack of nitrogen supply. Cultivar Krostar in 1995 was the only case giving a result in agreement with the findings of van der Zaag and Doornbos (Tab. IV). The lower LCC values in the drought treatment of 1995 might be explained by the combination of normal canopy development in the beginning of the season (because of the wet fore-season) and strong drought stress around the middle of the season which obliged the crop (with abundant foliage) to reduce transpiration. This was likely done through reduced stomatal aperture in a first step leading to reduced photosynthesis and LCC. van der Zaag and Doornbos [11] showed that late cultivars had a tendency to exhibit lower light conversion coefficients than earlier cultivars. This appears to be statistically confirmed in our results with late cultivar Nicola having a lower LCC than cultivar Jaerla whereas the other cultivars showed intermediate values.

Our moderate drought conditions did not influence the harvest index. This is in contrast with the data on effects of severe stress reported by Jefferies [4]. Jefferies and MacKerron [7] showed that the harvest index under severe drought was lower than in control.

The drought treatment increased slightly dry matter content percentage with significant main effects and interactions only in 1996. The dry matter content increase in the drought treatment did not play an important role in the response of the potato crop to the moderate drought.

The rate of increase bFT of the fraction of dry matter which is partitioned to the tubers (FT) was 0.003 per degree-day. It was not influenced by our moderate drought conditions, and was equal to the value obtained by Van Heemst [12]. We are aware that our treatment 1 was not a real well irrigated treatment and this may have prevented us showing P. Deblonde, J.-F. Ledent

a drought effect on this parameter. Earlier cultivars showed higher bFT than later cultivars, a result in contrast with that of Van Heemst [12] who did not found any difference between cultivars in that respect. This discrepancy can be explained by the calculation of a constant slope for fitting the FT data in Van Heemst's trials because of the lack of confidence in the individual data points. Our result would imply that the shorter life cycle of earlier cultivars is not only explained by an earlier onset of tuber initiation (as it was shown by Van Heemst [12] and Burton [3]) but also by a faster increase of the partitioning of dry matter to the tubers through thermal time.

5. Conclusions

The intercepted radiation and the closely related ground cover duration were the parameters most affected by our moderate drought treatments. These parameters were more affected when drought was applied early in the season, as in 1996 (combination of dry fore-season and placement of a plastic sheet). The differential behaviour of cultivars between treatments for intercepted radiation makes it useful for screening and breeding purposes, as the classification based on intercepted radiation was consistent with the tuber yield classification.

The light conversion coefficient (LCC) played a role when drought was applied in the middle of the season and canopy development of the crop in the beginning of the season was not hampered by drought (as in 1995).

The slope bFT of the relation between the fraction of dry matter which is partitioned to the tubers and thermal time was cultivar dependent but was not influenced by our drought conditions. Thus moderate drought seemed not to modify the earliness of maturity of cultivars.

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