Influence of water stress on photosynthesis and variable chlorophyll fluorescence of potato leaves

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Abstract

Net photosynthetic rate (P_N), productivity and the first phases of the fluorescence induction curve were investigated in leaves of two potato cultivars exposed to water stress. Water stress applied to potato plants at the beginning of their development (planting - bud formation) increased productivity but decreased P_N and variable fluorescence (F_v) of leaves. The short-term influence of water stress on the same plants also diminished the F_v.

Introduction

After previous dark adaptation, intact leaves show as a reaction to irradiation characteristic time-dependent fluorescence changes called fluorescence induction (see Lichtenthaler 1992). One of the characteristics of this phenomenon is the so-called variable fluorescence, F_v (*e.g.* Mohanty and Govindjee 1974, Bradbury and Baker 1984). Depending on the degree of oxidation or reduction of the electron transport chain, F_v is quenched or enhanced. The quinone and plastoquinone pools on the acceptor side of photosystem 2 (PS2) are probably responsible for the fluorescence quenching. In addition, there are further factors (*e.g.* ion concentration, proton gradient on the thylakoid membrane) which affect chlorophyll fluorescence. Quantum yield and fluorescence characteristics thus do not depend only on photochemistry, but on many additional parameters. The fluorescence transient is thus a multiphase process with some important features.

One of the important factors influencing photosynthesis and the final productivity of potato tubers is the relative water content of the plant (RWC). In potato, P_N is reduced under water stress (*e.g.* Van Loon 1981, Bodlaender *et al.* 1986) and Schapendonk *et al.* (1989) has explained water stress reduced P_N of five potato

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cultivars initially as a result of stomata closure, but after 3 d as the direct inhibition of photosynthetic capacity. In potato plants (cv. Désirée) exposed for 24 h to water stress, Prange (1986) found a significant increase in fluorescence transients. Jefferies (1992*a*) found in seven potato genotypes grown under water stress a decline in constant (F_0) fluorescence and F_v in both the irrigated and droughted plants; nevertheless, the decline was larger in droughted plants. The total dry matter production of whole plants was correlated with F_0, F_v (measures of the capacity of primary photochemical events) and especially with the half-lifetime of decay of variable fluorescence ($q_{1/2}$) (Jefferies 1992*b*) that is dependent upon carbon fixation rate.

In order to contribute to the clarification of this complex problem we compared changes induced by drought in P_N (measured as dry matter increment in apical leaf blades - Bartoš *et al.* 1960) with those in the final productivity of tubers and in the F_v of leaves, even though in potato leaves the last method has limitations due to a high local pigment concentration and a high material scattering (Mauro and Lannoye 1989).

Materials and methods

Plants: In measurements done during the years 1986 - 1990, dark adapted (*ca.* 30 min) potato (*Solanum tuberosum* L.) leaves (3rd from top with the same plastochron index) were cut, one leaf half was used for RWC measurement and the second half for F_v measurement. The plant relative water content (RWC) was determined gravimetricaly. Soil water content was determined as a ratio of the actual water content in the soil to maximum capillary capacity according to Novák (1954). The plants were grown in greenhouses in pots and water stress was induced by withholding watering for 3 weeks in the phase emergence - bud formation. The effect of immediate plant rewatering on F_v was also investigated.

P_N of the leaves was determined using the gravimetric method of Bartoš *et al.* (1960) that measures dry mass increment of leaf discs exposed under constant conditions favourable for photosynthesis (saturating irradiance, temperature 19 °C, CO_2 concentration 600 mg m^{-3}). Annular irradiation chamber was used for photosynthesis measurements in leaf disks (Avratovščuková 1973). Final tuber productivity was expressed as the total biomass of all tubers found under the given plant when harvested after physiological maturity.

F_v: Radiation from a 150 W xenon lamp was focused by means of quartz lenses and filtered through two filters (*Jobin-Yvon monochromator H 20*, a neutral filter). In all fluorescence measurements the excitation wavelength was λ_{exc} = 480 ± 4 nm, the excitation irradiance > 100 μW m^{-2}. The measured leaf was fixed in a special holder. The fluorescence was focused on the input slit of the analyzing monochromator *HT 20* with an edge filter and recorder by *PM Hamamatsu R 928*. The electrical signal from PM was processed and recorded in a transient recorder *4 TR 2 M*. A fast electronically synchronized optical shutter in connection with *4 TR 2 M* enabled automatic measurements in the time scale 2.045 ± 0.0005 s. The measurements were performed at room temperature. Our laboratory-made equipment enabled

Table 1. Net photosynthetic rate, P_N [mg(d.m.) m^{-2} s^{-1}] in relation to the water stress treatments (planned) *a, b, c* and soil moisture [%] in pots in the greenhouse experiment of 1989. (*a* control - 75 % during the whole period; *b* - 50 % from emergence to bud formation, *c* - 30 % in the same vegetation phase).

Cultivar	Water stress treatment (planned)	P_N/measured soil moisture 2 May	10 May	15 May	18 May
Radka	*a*	0.3557* / 77.1	0.3402* / 75.4	0.3387* / 73.2	0.3112* / 72.3
	b	0.2943* / 56.7	0.2526* / 49.9	0.2437* / 53.3	0.2640* / 54.8
	c	0.2304* / 35.6	0.2298* / 32.6	0.2569* / 42.4	0.1915* / 30.0
Désirée	*a*	0.4134* / 77.1	0.3729* / 75.4	0.3628* / 73.2	0.3530 / 72.3
	b	0.3512* / 56.7	0.3338* / 49.9	0.3464* / 53.4	0.3668 / 72.0
	c	0.2686* / 35.6	0.2544* / 32.6	0.2276* / 30.4	0.3813 / 74.8

* - measured in vegetation phase from emergence to bud formation

F values from dispersion analysis, significant differences and mean square values of P_N for variants *a*, *b* and *c*.

Source of variation	F value	d.f.	mean square	significance
Replication	1.025	5	0.002	
Water stress	290.406	2	0.245	**
Date	10.584	3	0.013	**
Cultivars	310.442	1	0.131	**
Water stress × date	10.914	6	0.028	**
Water stress × cultivars	16.047	2	0.014	**
Date × cultivars	26.205	3	0.033	**
Water stress × date × cult.	20.804	6	0.053	**
Error		115	0.048	

** significant at 0.01 probability level measurements in the range of 0.1 - 3 s, in the period when fast electron processes decay and slower transport processes start. This time interval was characterized by $F_v = F_P - F_0/F_P$ and reflected both the photochemical and nonphotochemical fluorescence quenching (F_0 and F_P are expressed in relative units, F_P is the fluorescence signal after 2 s).

Table 2. Relative productivity of potato cultivars Radka and Désirée which were exposed to water stress at different periods of their development (greenhouse experiment, average of years 1986-1989).

Water stress applied during the period	Soil moisture [%]	Final mass of tubers [g] Radka	Désirée
Planting - emergence	50	359.5	416.2
	30	373.5	406.8
Emergence - bud formation	50	342.0	378.9
	30	352.2	351.5
Bud formation - flowering	50	306.1	337.0
	30	272.1	286.8
Flowering - physiological maturity	50	323.9	352.1
	30	288.1	283.3
Control - mean of the whole development	75	347.5	380.3

F values from dispersion analysis, significant differences and mean square values of tuber masses [g] for corresponding probes with different water stress:

Source of variation	F value	d.f.	mean square	significance
Replication	0.382	7	3096.415	
Water stress	88.467	8	819467.500	**
Cultivars	81.067	1	93865.641	**
Years	779.964	3	2709305.172	**
Water stress × cult.	5.192	8	48094.875	**
Water stress × years	12.365	24	343608.000	**
Cultivars × years	2.285	3	7936.630	
Water s. × cult. × years	3.201	24	88964.542	**
Error		497	575464.460	

** significant at 0.01 probability level

Results and discussion

In both tested cultivars, P_N decreased with increasing water stress (Table 1). Nevertheless, after a certain time the plant adapted to soil dryness and P_N rose again. The tuber mass was decreased by the severe water stress (30 % soil moisture) applied from bud formation to full flowering and from flowering to physiological maturity of the crop (Table 2), but there were highly significant differences between the cultivars.

During the period plant emergence - bud formation the values of F_0 decreased with increasing water stress (Table 3). These values corresponded to those of P_N and productivity of corresponding plants (Tables 1 and 2). Water stress in the period of bud formation increased final potato productivity (Genkel 1956), indicating that the plant has adapted to drought by increased root density and better water utilization. In the case of variable fluorescence we measured fluorescence kinetics at a given wavelength; that means that the fluorescence values obtained on dark adapted leaves represent fluorescence changes after excitation in period of approximately 10^{-2} - 10^{-1} s. In this time interval the values of F_0 might reflect the decay of radiative deexcitation between the plastoquinone pool and thr reaction centre of PS2 ground state (after Allakhverdiev and Klimov 1990); the lifetime of the excited acceptor Q_A is about 150 μs. In stressed plants we can thus expect a decrease of F_0 due to increased photochemical efficiency of the leaves investigated or to the occurrence of other deactivation processes. Excitation energy transfer to pigment pools having a lower quantum yield fluorescence is also possible.

Table 3. Relative values of F_0 at 300 K of potato leaves (λ_{exc} = 480 ± 4 nm, and variable fluorescence F_v measured at 685 ± 4 nm). Three different treatments of plants were compared: *a* - control plant, fluorescence measured 36 d and 44 d after plant emergence and during the whole period the soil moisture was 75 %; *b* - medium water stressed plant, in the time interval from from emergence to bud formation, the soil moisture was 50 %; *c* - severe water stress applied during the same period as in *b*, the soil moisture was 30 %. After the first measurement (10 May 1989) the plant was watered in the pot and second measurement was performed 8 d later. RWC (relative water content) values in the plants [%] are in brackets

Cultivar	Date of measurement	F_0 *a*	*b*	*c*	F_v *a*	*b*	*c*
Radka	10 May	39 (78)	31 (56)	27 (52)	0.75 (78)	0.71 (56)	0.74 (52)
	18 May	48 (70)	46 (63)	40 (60)	0.74 (70)	0.64 (63)	0.53 (60)
Désirée	10 May	38 (78)	34 (56)	19 (46)	0.77 (78)	0.76 (56)	0.75 (46)
	18 May	33 (65)	25 (63)	29 (60)	0.71 (65)	0.69 (63)	0.69 (60)

As concerns the short-time (several days) effects of water stress in the period of bud formation (vertical columns of Table 3), F_0 increased and F_v slightly decreased with decreasing RWC. The decreasing value of F_v indicated the diminishing plant photosynthetic activity with short time water stress. Fluorescence quenching during the induction curve was probably also dependent upon the metabolic status of the leaf tissue.

In agreement with Jefferies (1992*a*, *b*), we have showed that variable chlorophyll fluorescence provides a method for the study of changes in the photosynthetic capacity of the potato in response to water stress. Our results also indicate that measurements of F_0 and F_v may also provide rapid indicators of changes in current plant productivity in response to water stress.

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