Perspectives of improved tolerance of drought in crops

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Summary

The mechanisms are discussed through which crops suffer yield reductions when water shortage occurs. Cultivars differ in their tolerance of drought but how tolerance is determined, how changes in crop characteristics reduce yields, how crop modeling can be used to explore the potential improvement en whether increased tolerance is associated with negative effects is discussed in this review.

Introduction

Even in a region where it rains relatively abundantly, such as in north western Europe, lack of water is one of the factors most limiting growth and quality of crops. The precipitation deficit during the growing season from April through September, in the Netherlands for instance, usually exceeds 100 mm. Many soils, especially drought sensitive sandy soils, do not have sufficient water storage capacity within the rooted zone to prevent yield losses if crops are not irrigated. Irrigation, is often not possible because of its high costs or because of legal restrictions associated with the extraction of this natural resource from the environment. The efficient use of the available amount of water is of increasing concern to maintain production and quality. The kind of drought which is expected is crucial in the strategy to increase the efficient use of water. Three drought types are distinguished:

- a dry spell at the beginning of the growing season leading to retardation of emergence and early growth;
- a short transient drought period in the course of the growing season, only slightly reducing growth but potentially strongly affecting crop development and quality of the produce;
- a drought which intensifies in the course of the growing season leading to a premature senescence of the crop.

These different types of drought have different effects on crop growth, development and quality of the product. Crops may react in many different ways (and so may producers) to

limit the extent of damage. We review the short and long term effects of drought on processes and morphological properties of the crop. By means of simulation the effect of a change of some crop characteristics on growth is studied as to explore the effects of certain changes in genotype and cultural practices on yields. Potato is used as an example.

Short term effects

Effects on plant water relations and gas exchange

The water relations of a plant cell are described in terms of the water potential (Ψ), an osmotic component (Ψ_o) and a pressure component (Ψ_p) with the equation $\Psi = \Psi_o + \Psi_p$, expressed in MPa. When the moisture content of a cell or a leaf declines because the transpiration rate is slower than water uptake rate by the roots, Ψ, Ψ_o and Ψ_p fall. Moreover the relative water content declines compared to fully saturated tisssue (Dainty, 1976). The osmotic potential in plant cells decreases passively because the concentration of solutes increases but osmotic adjustment may take place as well by an active increase of solutes; the so called osmoregulation. Vos & Oyarzun (1987) reported typical values of potato leaves of PSI and PSIo of -0.5 and -0.8 MPa, respectively, on a clear day with ample supply of water. Stomates form the greatest resistance for transpiration; transport of water from the interior of the leaf to the atmosphere.

Depending on external and internal conditions, plants are able to regulate this stomatal resistance (r_s). Stomatal resistance to CO_2 is 1.6 times as large as to water vapour . Stomatal closure leads to a lower ratio between internal and external CO_2-concentrations and subsequently to a reduced photosynthesis. Vos & Groenwold (1989a) found in potato crops subjected to drought, that stomatal resistance diminished earlier and more than photosynthesis. No consensus exists on the primary site of the reduction in photosynthesis (Kaiser, 1987) or whether photoreactions in the thylakoid membranes or biochemical reactions of the Calvin cycle are most affected (Ogren & Oquist, 1985). In vivo fluorescence signals give information on the light use efficiency and on the rate of electron flow in the thylakoids (Schreiber et al., 1985). Together with gas exchange measurements, analysis of fluorescence signals provides information on rate limitation of processes related to gas phase resistance and to internal photosynthetic processes. The capacity to recover from drought stress in interaction with the developmental stage of the crop, may be as important as functioning during stress itself (Schapendonk et al., 1989). They found in young potato leaves which recovered faster from water stress than old leaves, that mesophyll conductance was greater than in leaves from the control treatment, conductance in the gas phase was smaller leading to stomatal limitation, reduced internal CO_2 and increased transpiration efficiency showing that recovery of the photosynthetic capacity was faster than that of the stomatal regulation mechanism.

The assimilation/transpiration ratio (transpiration efficiency expressed as g CO_2 g^{-1} H_2O exchanged gas) increased when the crop was exposed longer to drought (van Keulen & van Laar, 1986). The much stronger effect of drought on transpiration than on photosynthesis, and the occurrence of hysteresis are represented in Fig. 1 for cv. Saturna. When drought stress continues, assimilation is reduced further by limitation of the photosynthetic capacity (mesophyll limitation (Schapendonk et al., 1989)).
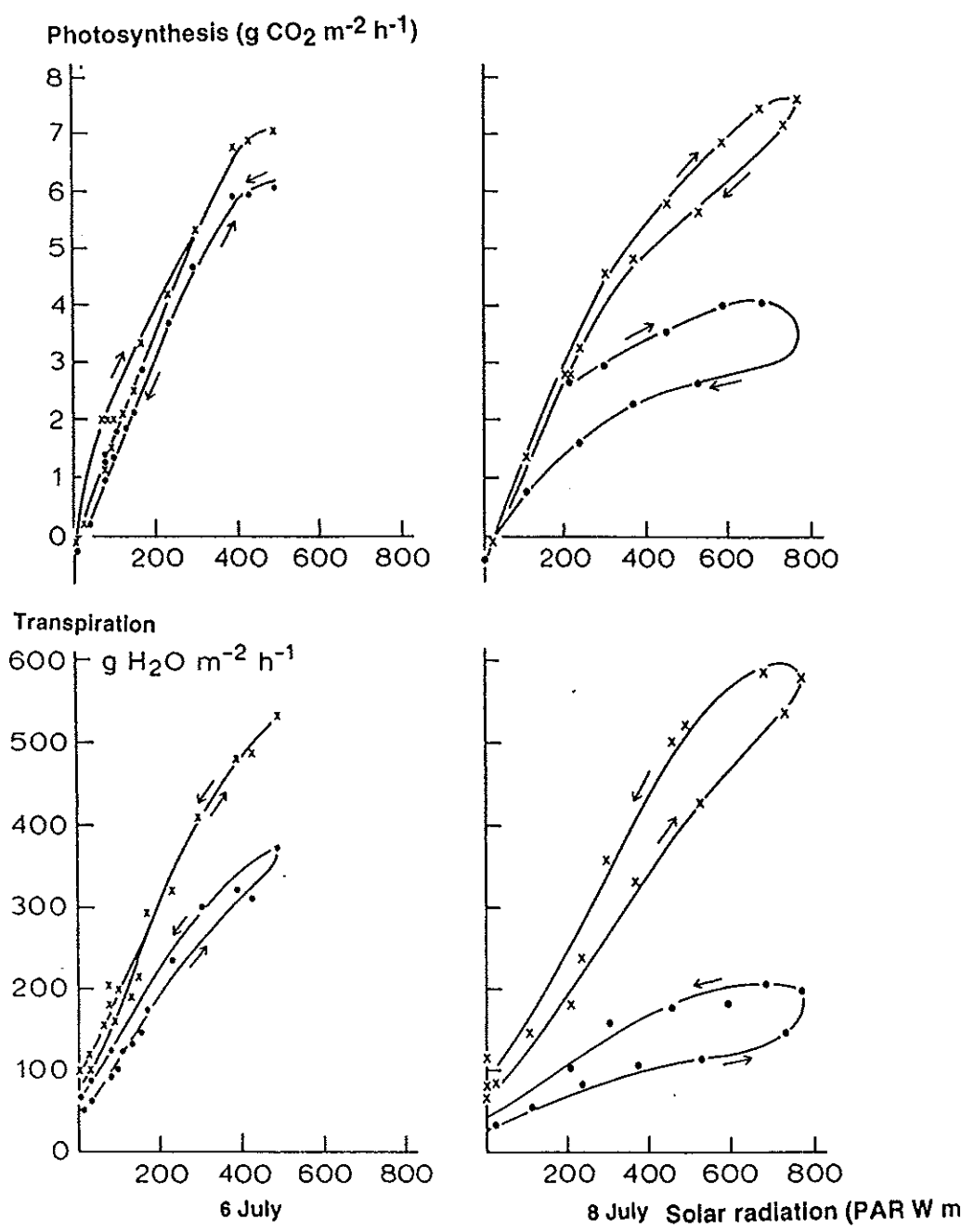
Fig. 1. Light response curves in the course of the day of net photosynthesis and transpiration of a moist (x) and a dry (●) plot of 2 m^2 measured by gas exchange in crop chambers (after data from Bodlaender, Van der Waart & Marinus, 1986).

For potato subjected to drought, Vos & Oyarzun (1988) reported a strong reduction of the leaf water potential from -0.5 to -0.9 MPa. They found a decrease of the internal CO_2-concentration of 29 % and a 58 % reduction in photosynthesis associated with a strong increase of both mesophyll resistance and stomatal resistance.

Vos & Oyarzun (1988) and Haverkort & Schapendonk (1993) concluded that the short term effects mentioned here are not related to the degree of drought tolerance of a genotype. Short term effects appearing rapidly after the onset of drought have the advantage of saving water but the disadvantage of immediate growth retardation. Absence of stomatal closure may lead to a rapid exhaustion of the available amount of water which is disadvantageous when crops are subjected to prolonged droughts.

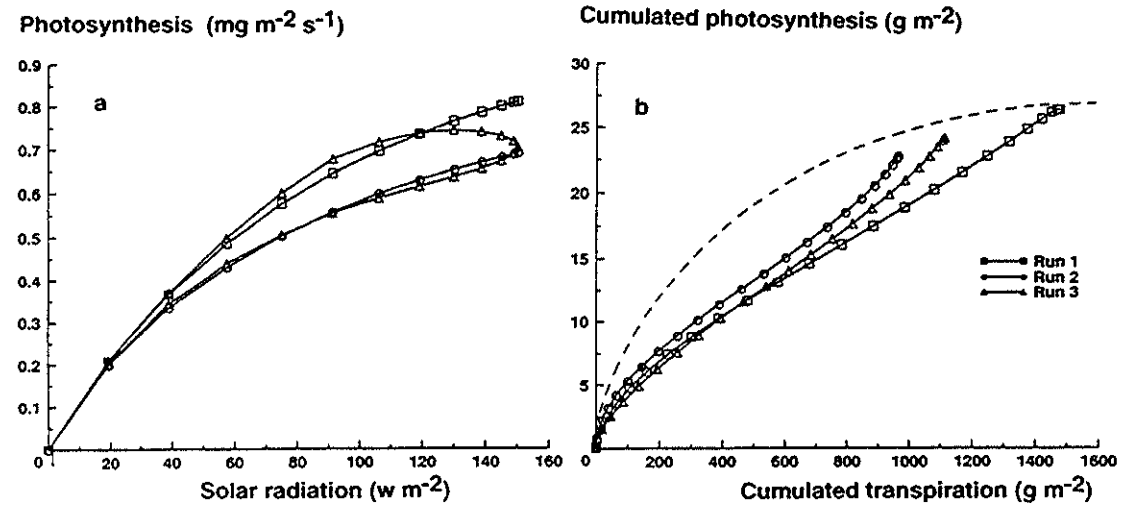*Model calculations of diurnal rythm and stomatal regulation*

Stomatal regulation, beside transpiration, influences photosynthesis as stomatal closure hampers acces of CO_2 to the inner parts of the leaf. Haverkort & Goudriaan (1993) carried out model calculations for the diurnal cycle of photosynthesis of an individual leaf for three types of stomatal behaviour, following lack of water: - stomates remain open with a stomatal resistance r_s=100 s m^{-1};

- stomates are regulated such that they keep the internal CO_2 concentration (c_i) constant during daylight. Stomatal resistance rs is then represented by r_s=(c_a-c_i)/(1.6P_g) with P_g the photosynthetic rate that corresponds with the value of the internal carbon dioxide concentration of ci. In the calculations we used c_i=220 ppm, i.e. about 70 % of the ambient concentration (c_a) and we did not take into account the effect of the resistance of the boundary layer (r_a);
- stomatal response to vapour pressure deficit. It is assumed that stomates open when photosynthesis takes place. They close, however, when the vapour pressure deficit (VPD) and, or the CO_2 concentration of the ambient air increase according to: r_s=a c_a VPD/$P_{g,c}$. Thus air humidity exerts a direct influence on stomatal response and not through the water potential (Ψ) of the leaf or the soil.

The dynamics of photosynthesis and transpiration was calculated for each of the three situations (Fig. 2). The direct reaction on VPD leads to an asymmetric daily cycle in photosynthesis: a higher values in the morning than in the afternoon. The photosynthesis-light response curve then shows a pattern (Fig. 2a) of two loops. The upper one is valid for the situation with open stomates and the lower one for stomates with a c_i-regulation.

The VPD-response follows the upper part of the loop in the morning and the lower one in the afternoon. Thus a hysteresis becomes evident, as actually observed in potato (Fig. 1). Transpiration also follws a loop but in an opposite direction (see arrows Fig. 1) as a result of the driving force of the VPD. This effect occurs for all three types of stomatal behaviour (Fig. 2a). What this means for the daily totals and the resulting efficiency of water use can easily be inferred from the graph of cumulative daily photosynthesis against cumulative transpiration (Fig. 2b). The endpoints of these curves indicate the daily totals and the slopes indicate the relation between assimilation and transpiration (transpiration efficiency). Constantly open stomates lead to the highest photosynthesic rates but at the cost of more water than when stomates are regulated.Absence of regulation (open stomates) tends to occur when the soil is moist and the air is humid. As soon as the plants undergo any water stress, the VPD response is activated, which in practice, is hard to distinguish from a constant c_i regulation. To assess the quantitative importance (Haverkort & Goudriaan, 1993) did some calculations with this model and they found that transpiration efficiencies (g CO_2 per g H_2O) were higher by about

Fig. 2. Simulated (a) photosynthesis - photosynthetically active radiation (PAR) response curve and (b) photosynthesis versus transpiration at three types of stomatal behaviour: (□) constantly open stomates, (o) constant value of c_i and a (∆) response to a vapour pressure deficit (VPD).

Photosynthesis (mg m^{-2} s^{-1})

Cumulated photosynthesis (g m^{-2})

a

b

Run 1
Run 2
Run 3

Solar radiation (w m^{-2})

Cumulated transpiration (g m^{-2})

25% when the 'constant c_i' or 'VPD-response' mechanisms were active as compared to the 'constant r_s" mechanism. This is within the range as actually observed in container experiments as is shown in Table 3.

Long terms effects

Effects on crop growth

The effects of an early dry spell on a restricted number of morphological characteristics of potato cv. Mentor grown in containers under a rain shelter are shown in Table 1. The control plants were watered twice per week to compensate for transpiration. Plants that were kept dry until 43 days after planting (soil water tension had decreased below -0.7 MPa) were watered from then on. Periodic harvests were carried out on day 43, 70 and 92. At the end of the early drought period on day 43, the droughted plants had only half the leaf area of the control plants, mainly because thicker (SLA only 228 cm^2 g^{-1}) and smaller leaves were formed resulting in a 20 % smaller LAR-value. The plants remained stunted (stem length 34 vs 52 cm), had a lower shoot/root ratio and had a 36 % lower tuber yield. Four weeks after the end of the early drought period both treatments had similar weights and areas of leaves. The plants subjected to drought on average still had thicker and smaller leaves but a higher LAR-value showing that leaf expansion in the recuperation period was relatively greater than the accumulation of dry matter. At the final harvest on day 92, the plants that had been submitted to drought still had 14.4 green leaves per stem against 12.0 on plants that had not been submitted to an early drought period. Tuber weights in both treatments did not differ significantly at the final harvest: an early drought initially led to a growth retardation which is overcome later on.

These observations under semi-controlled conditions are in line with those of Krug & Wiese (1972) under field conditions. An early drought, from planting until a few weeks after emergence is less harmful for potato than for cereals because the seed organ (the mother tuber) is much larger than a grain and, moreover, for sprouting and initial growth, a tuber does not depend on imbibition. A short period of water shortage, in general has little influence on total dry matter and tuber production, but it can strongly influence the quality of the harvested product, especially the tuber size distribution and the tuber shape. A short dry spell during stolon and tuber formation strongly reduced the number of stolons per stem but hardly reduced the number of tubers per stolon leading to a strong reduction of the number of tubers per plant (Haverkort *et al.*, 1990).

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Table 1. *The effect of drought until 43 days after planting on some plant characteristics of potato cv. Mentor. From day 43 onward water supply was restored (after Fasan & Haverkort, 1991)*

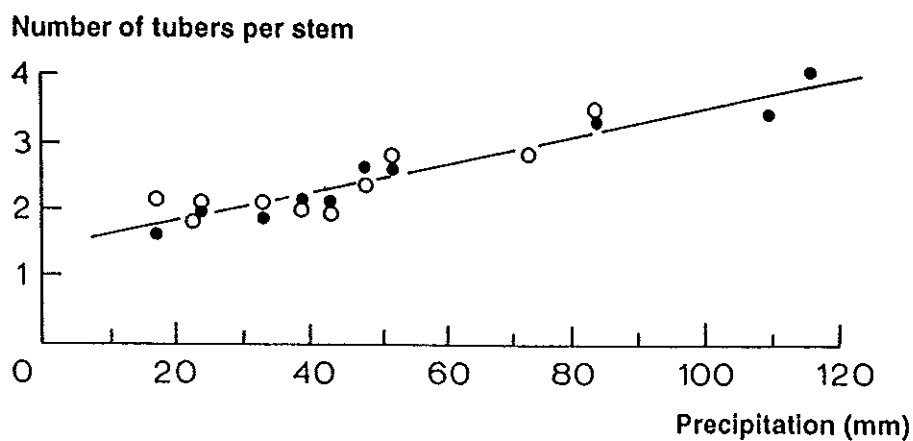| Characteristic	Harvest (days after planting)			
	43		70	
	Treatment		Treatment	
	Control	Dry	Control	Dry
Leaf (dry g per plant)	27.4	20.2	22.6	22.3
Leaf area (cm^2 per plant)	8253	4661	7663	6934
Leaf size (cm^2 per leaf)	150	108	187	140
Specific leaf area (cm^2 g^{-1} dry leaf)	301	228	341	297
Leaf area ratio (cm^2 g^{-1} dry plant)	93.1	74.2	33.8	39.0
Stem length (cm)	52	34	62	54
Tuber dry (g per plant)	42	27	194	140
Shoot/root ratio (g g^{-1})	17.3	15.1	21.4	20.3

Fig. 3. Relationship between the number of tubers per stem and rainfall during the first 40 days after planting, 1975-1988 data, cv. Bintje (•) unsprouted, (o) presprouted seed tubers (after data from Haverkort et al. 1990).

This explains the relationship between precipitation during the first 40 days after planting and the number of tubers per stem (Fig. 3). As a very early dry period does not influence total yield it induces the crop to yield fewer but bigger tubers. In seed potato production it may be advantageous to irrigate early during crop growth, in ware potato production somewhat later. Of an even greater influence on tuber quality, may be a short dry spell during tuber growth stopping both leaf and tuber growth. When growth resumes after rain or irrigation, secondary growth may cause irregularly shaped tubers or even stolons with new tubers (Bodlaender *et al.*, 1964).

Effects on yield components

Long dry spells in the second half of the growing season have the greatest influence on yield. This kind of drought is more frequent than early drought as crop transpiration gets larger and winter rains loose their effect on the soil water content. Crops then form fewer new leaves and accelerate leaf shedding leading to a premature senescence. Because of the linear relationship between intercepted radiation and dry matter production, drought leads to reduced tuber yields. With early (ware potato) varieties, after a few weeks of drought, generally no recovery occurs, even though water supply is resumed. With late (starch potato) varieties, recovery is often possible and longer dry spells can be bridged. The influence of irrigation on ground cover and the relationship between the amount of intercepted radiation and dry matter production is shown in Fig. 4. Both intercepted radiation and the efficiency of dry matter production are negatively influenced by drought.

The most important components that determine tuber fresh matter yield (Y) are the amount of intercepted solar radiation by the foliage (R_i), the efficiency of conversion of R_i into dry matter (E), the Harvest index (H_i) and the tuber dry matter content (C_{dm}) which are summarised in the formula: $Y = R_i \, E \, H_i/C_{dm}$.

In a series of experiments carried out on light sandy soils with four cultivars in 1989 and 1990 which were either irrigated or not, periodic harvests were carried out to determine the value of the yield components of the formula described above. The results are shown in Table 2. The losses due to drought were greatest with the relatively early cultivar Darwina (-45%) and smallest with the latest cultivar Elles (-20%).

Table 2. *Relative values of yield components of unirrigated versus irrigated plots (mean value of 1989 and 1990, after Haverkort* et al. *1992)*

Cultivar	Y =	R_i x	E x	H_i /	C_{dm}
Darwina	55	62	99	94	105
Desiree	77	88	99	94	105
Elles	80	93	90	95	101
Mentor	73	87	97	97	111

Yield losses were mainly due to a reduction of the amount of intercepted radiation because of earlier senesecence. The light use efficiency wass affected less than intercepted radiation. The cultivar that suffered little losses of intercepted radiation showed a stronger reduction of the light use efficiency (Elles -10 %) than cv. Darwina (-1 %) which reacted mainly to water stress by leaf shedding. Of the total amount of dry matter produced by the crop, about 75%
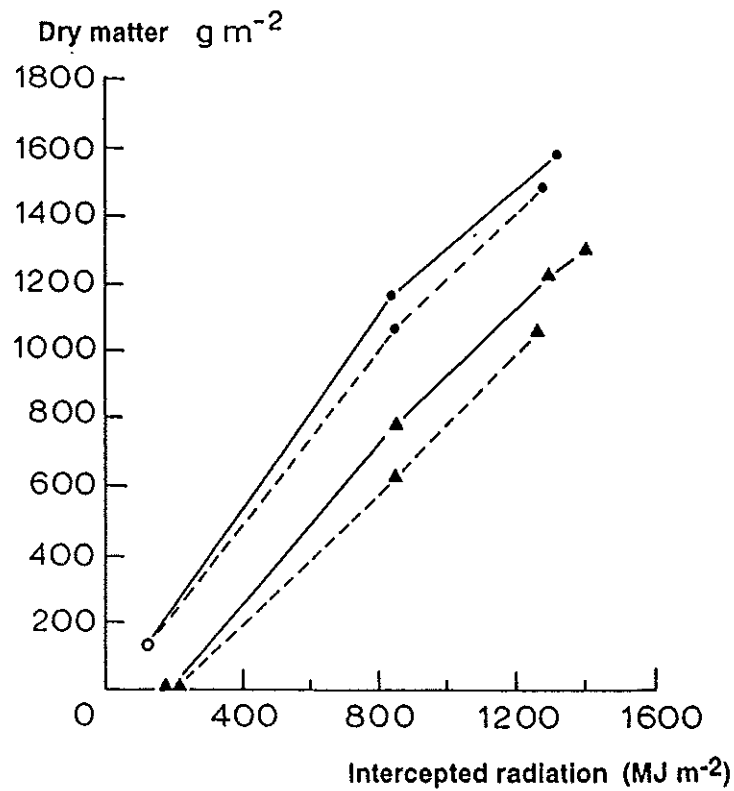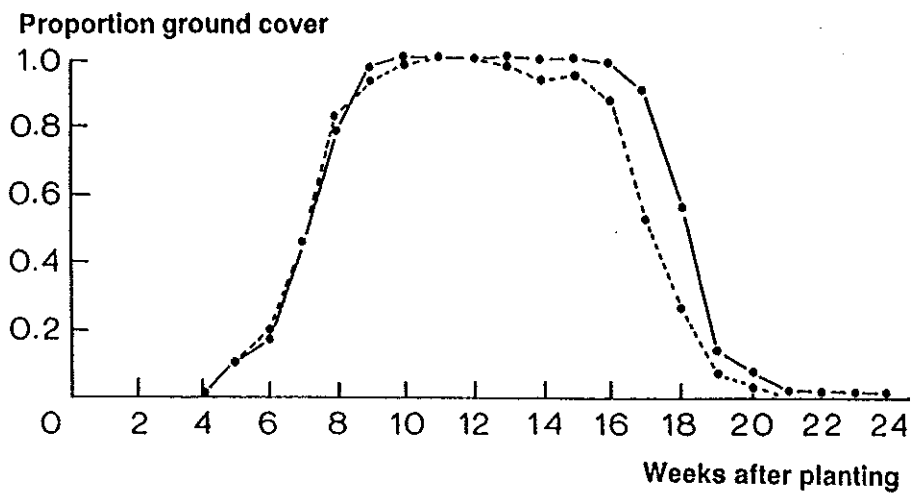
Proportion ground cover

Weeks after planting

Dry matter g m^{-2}

Intercepted radiation (MJ m^{-2})

Fig. 4. Ground cover and the relationship between intercepted radiation and dry matter production (o), total; (△), tuber; (——) irrigated and (-----) unirrigated; after Haverkort , Boerma, Valema & Van de Waart, 1992).

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is found in the tubers by the time of crop senescence (Hi=0.75). Drought reduced the harvest index only slightly and no differences between cultivars were found. Drought increased the dry matter content of all plant parts (Haverkort & Fasan, 1991), also of the tubers (Table 2) and especially so with the relatively early cultivar Mentor (+11%) and least with the late cultivar Elles (+1%). The tolerance of the cultivar Elles for drought lies in its abundant formation of foliage associated with its lateness. Whereas drought reduced its light use efficiency, the cultivar effectively overcame relatively long periods of absence of precipitation.

Transpiration efficiency

The long term transpiration efficiency (amount of dry matter formed per kg of water taken up) can be calculated from the dry matter yield at a (periodic) harvest and the total amount of water taken up by the crop. In the experiment described in Table 1, the total amount of water supplied was recorded by weekly weighing the containers. The efficiencies obtained are represented in Table 3. The transpiration efficiency which was about 8 g kg^{-1} in the control increased to about 9 g kg in the early drought period and up to almost 12 g kg^{-1} in the late drought period. The decrease of the transpiration efficiency between 70 and 90 days after planting in the control was due to senescence of the crop. The crop subjected to an early dry spell senesced later which resulted in relatively higher values of transpiration efficiency. These data show that beside plant age (ambient conditions may have played a role as well), transpiration efficiency depends on the severity of drought stress.

Table 3. *Transpiration efficiencies (g kg^{-1}) of cv. Mentor subjected to an early drought period until 43 days after planting (dap) and by a late drought period (50 % water of the control from 43 dap onward) After Haverkort & Fasan, 1991*

Period (dap)	Control	Early drought	Late drought	LSD$_{0.05}$
0-43	7.34	9.19	7.34	0.60
0-70	8.35	8.69	9.09	0.72
0-92	7.71	8.40	9.41	0.51
43-70	9.06	8.86	10.62	0.82
70-92	5.90	7.52	11.78	0.64

Another effect of stomatal closure beside the increased assimilation/transpiration ratio, is an increase of the proportion of stable isotope ^{13}C within the plant (Farquhar *et al.*, 1982. Farquhar, O'Leary, Berry & Richards, 1984) related decreased ^{13}C discrimination as a consequence of decreased internal CO_2 concentration in wheat to increased transpiration efficiency values. Vos & Groenwold (1989b) compared six optimally watered genotypes (of which three were also subjected to a drought treatment) of potato. Fig. 5 shows the linear relation between the two parameters. This relationship, however, is not stable as ^{13}C-discrimination increases with plant age, is lower in plant parts closer to the roots (from green

to yellowing leaves, to stems, stolons roots and tubers), possibly due to relatively enhanced ^{13}C extrusion in the process of respiration (Haverkort & Valkenburg, 1992).
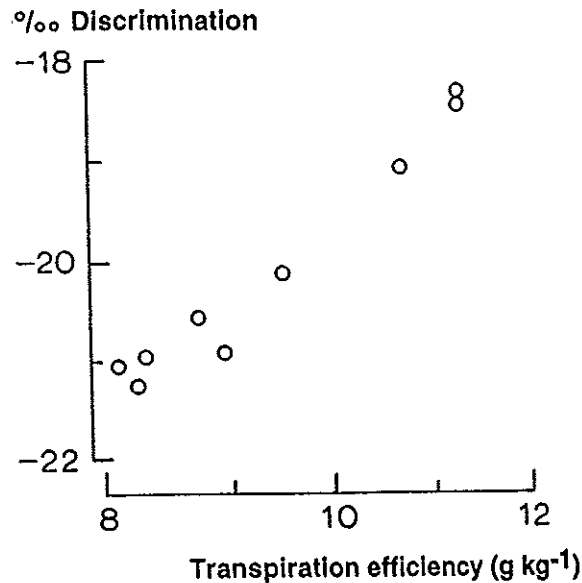
‰ Discrimination

Transpiration efficiency (g kg^{-1})

Fig. 5. Relationship between ^{13}C-discrimination and transpiration efficiency of different genotypes of potato. After Vos & Groenwold, 1989b.

Although an increase of the transpiration efficiency and a decrease of ^{13}C-discrimination indicate that the plant more efficiently uses available soil moisture,plant ^{13}C-status is not a good predictor of genotypic ranking in drought tolerance. On the contrary, genotypes which are not tolerant of drought may even have a higher transpiration efficiency if they show drought symptoms earlier due to a lower water uptake capacity in combination with earlier stomatal closure.

Simulation of seasonal drought effects

For simulation of long term effects of drought on crop growth we chose a potato crop which was made to emerge on day of year 130, grown in climate conditions of De Bilt (centre of the Netherlands) averaged over the period between 1960 and 1990. There were three treatments of water supply: ample supply, no rain until day 170 and a late drought (no rain from day 170 onward). We used the crop growth model SUCROS92 (van Laar, Goudriaan & van Keulen, 1992) with dry matter distribution, developmental and leaf senescence rates after Spitters & Schapendonk (1990) and Bessembinder (1991). Modifications (Haverkort & Goudriaan, 1993) regard switching of leaf growth from exponential sink limited growth to source limited growth

and crop earliness depending on maturity class as defined by the temperature sum at which leaf senescence starts. This temperature sum deceases when actual/potential transpiration is less than 1 (Bessembinder, 1991)

The influence of increased leaf death was small for the late drought but much larger for the early drought period. When subjected to drought, leaf senescence was advanced by 30 days in the late cultivar and by about 20 days in the early cultivar which prevented recover in the second half of the growing season. The simulation results for these conditions are shown in Table 4. An early dry spell affected the tuber of an early cultivar more than that of a late cultivar, whereas a late dry spell more affected the yield of the late cultivars more strongly as they could not escape the drought. The late drought strongly reduced both tuber yield and harvest index as hardly any dry matter was partitioned to the tubers.

Table 4. *Simulated results of a SUCROS potato model*

Parameter	Drought					
	none cultivar		early cultivar		late cultivar	
	early	late	early	late	early	late
Total biomass (t ha^{-1})	28.9	16.4	13.6	5.5	13.3	9.1
Tuber dry matter (t ha^{-1})	22.4	13.2	10.2	3.7	7.4	6.0
Harvest index	0.78	0.81	0.75	0.67	0.55	0.65
Highest LAI value	7.4	3.8	4.8	2.5	7.4	3.8
Transpiration (mm)	471	283	239	105	238	166
Transp. efficiency (g kg^{1})	6.33	5.99	5.92	5.52	5.95	5.85

The only adaptation to drought that was included in the model so far, was through reduced total transpiration with a proportional effect on assimilation. When a functional adaptation such as improvement of the assimilation/transpiration ratio was added, rising by up to a factor two under extreme drought conditions, the tuber yields under dry conditions still increased still not more than by about 15%.

Conclusions

Measurements of plant water relations, gas exchange, transpiration efficiency and stable isotope fractionation give insight into the degree of drought stress a plant is (or has been) subjected to. However, each of this methods on its own cannot be considered as a suitable instrument to predict the degree of tolerance of genotypes. A small reaction to drought may be indicative of a luxurious use of water and a strong reaction on the other hand may point at a insufficient ability of the root system for water uptake. Moreover, these characteristics also depend on the physiological age of the crop which on its turn may be affected by drought. Lateness of a cultivar is the major factor determining tolerance of short transient or of late prolonged dry periods. Late cultivars develop a lush that is able to loose mor leaf area before interception of solar radiation is affected. An early cultivar may be more suited to (Mediterranean) conditions in which drought gradually increases towards the end of the

growing season. Increasing dry matter partitioning to the tubers leads to an escape from drought. Drought has a larger effect on the total amount of intercepted radiation than on the relatively conservative light use effeciency. Therefore determination of light interception is a proper tool to determine the accumulated effect of drought. Breeding for stress tolerance may inadvertantly lead to a lower productivity under optimal conditions. For instance, cultivars with a low harvest index which produce abundant foliage are more tolerant of drought but have lower yields under optimum conditions than genotypes that produce less foliage. Model explorations showed that improved plant characteristics (e.g. a higher transpiration efficiency) under dry conditions may be less effective (as growth is strongly reduced then) than improved plant characteristics under optimum conditions. Crop reactions to drought stress may be modelled with simple (light interception and light use efficiency) or with complex (SUCROS) models but complex models imply (as in reality) such a large number of feedbacks that in order to arrive at the optimal set of parameter values for a given set of growing condition, the use of optimisation techniques should be considered.

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