7. Simulated effects of elevated carbon dioxide concentration and temperature on the productivity of potato

Interaction with Cultivar Differences for Earliness

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Abstract. The effects of doubled carbon dioxide concentration and elevated temperature were evaluated by means of a crop growth model. Total dry matter production and tuber yield of potato cultivars, growing on a sandy loam were simulated for Dutch weather conditions, considering cultivar differences for earliness and soil moisture content as variables. Averaged over the years 1988–1991, a simulated increase of the carbon dioxide concentration from 350 vpm to 700 vpm increased tuber dry matter production by 22% for late cultivars and 29% for early cultivars. The effects were smaller for late cultivars irrespective of the occurrence of a drought period.

Elevated temperature reduced the positive effect of carbon dioxide because the stimulation of leaf area expansion in the juvenile stage, was upset later in the season due to an early start of foliage senescence. Raised temperature had only a net positive effect for conditions of optimum water supply and high irradiance during the juvenile stage, combined with a severe late drought. Then, the larger foliage prevented a rapid decrease in light interception during senescence.

Introduction

Agricultural productivity will respond to changes in the atmospheric CO_2 concentration and to possibly related changes in temperature. Various studies have shown a positive effect of CO_2 and a counteracting effect of a concomitant elevated temperature. The effects cannot be traced back to one or a few critical physiological and morphological components because the link between plant productivity and physiological characteristics is concealed by feed-back control mechanisms and by the large variance introduced by interactions with other environmental and developmental factors. Simulation models can be helpful to quantify the impact of a hypothetical environment on plant production and to evaluate the best strategy for further experimental research. Several crop growth models have been published for potato, differing in approach and detail (Fishman et al. 1984; MacKerron and Waister 1985; Ng and Loomis 1984). At present, the physiological models have mainly been used as a research tool, especially as a framework in the analyses of experimental results, and in studying the effect of individual processes on crop growth in relation to the environment.

In the present paper, the approach of crop growth modelling will be

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illustrated, first by describing the model in general terms and secondly by showing its usefulness and limitations for management and cultivar choice and its explanatory value for research purposes, especially in the stage prior to expensive experimental activities.

Material and methods

Experimental design

Experimental results were obtained form a field experiment. Sixteen cultivars were grown on a sandy soil in Renkum, near Wageningen, in 1988. The experiment was designed as a split plot in 6 replicates. The experiments were performed to check the general assumption that tuber yield and total biomass are closely correlated with the cumulative intercepted light (Spitters et al. 1989a). Pre-sprouted tubers were planted on 19 April in ridges, 0.75 m apart with a spacing of 0.35 m between plants in a row. Each plot consisted of 40 plants. There were 3 harvest dates: one at the beginning of June to determine the differences in time of tuber initiation, one at the end of July to have an estimate of the maximum haulm weight of each variety and a final harvest in September. At each harvest, dry weight and fresh weight of haulms and tubers were determined for each cultivar. During the whole growth period, the percentage soil cover by green foliage was estimated visually every week as an indicator of light interception.

Description of model for potential production

The light profile within the canopy is calculated from LAI and the extinction coefficients for both the flux of direct solar radiation and that of diffuse sky light. This procedure is followed to calculate the rates of photosynthesis at various heights within the canopy, discriminating between shaded leaf area receiving diffuse radiation only, and sunlit leaf area receiving both diffuse and direct radiation (Spitters et al. 1986).

Leaf area index
Leaf area increment (ΔLAI) is calculated from simulated leaf growth rate (ΔW_{lv}) and specific leaf area (SLA):

$$\Delta LAI = SLA \times \Delta W_{lv} \tag{1}$$

To account for the phenomenon that the early growth of leaf area (LAI < 0.75) is limited by temperature rather than by the supply of assimilates (and thus by radiation), early leaf area growth is described by an exponential function of the temperature sum after plant emergence or after planting (Spitters et al. 1989b):

$$LAI_t = N \times L_o \times exp(RGR_L \times \Sigma \; ^\circ Cd) \tag{2}$$

where the LAI after some temperature sum (Σ °Cd) is calculated from the plant density (N in plants m^{-2}), the initial leaf area per plant at emergence (L_o in m^2 plant^{-1}) and the relative growth rate of leaf area (RGR_L in °C^{-1}d^{-1}). Foliage senescence is calculated from the simulated weight of green leaves (W_{lv}) and a relative death rate (RDR):

$$\Delta LAI = -W_{lv} \times RDR \tag{3}$$

The relative death rate (RDR in d^{-1}) is a function of crop development stage, earliness and temperature (Spitters and Schapendonk 1990).

Dry matter production
Daily dry matter growth rate is calculated from rates of photosynthesis and respiration:

$$\Delta W = C_f \times (P_g - R_m) \tag{4}$$

where ΔW is the growth rate (g DM m^{-2}d^{-1}), R_m the maintenance respiration rate (g CH$_2$O g^{-1} DM d^{-1}), C_f the conversion efficiency (g DM g^{-1} CH$_2$O) derived from average synthesis costs according to the known biochemical synthesis pathways of the chemical components of the dry matter (Penning de Vries and Van Laar 1982). Daily gross canopy assimilation rate (P_g) is obtained from momentaneous photosynthetic rates of individual leaves according to the model of Farquhar et al. (1980) and the light profile in the canopy, integrated by Gaussian integration over LAI and day length (Goudriaan 1986).

Dry matter partitioning
Partitioning factors:

$$\Delta W_i = p_i \times \Delta W \tag{5}$$

Daily dry matter growth of individual tissues (i), expressed on a soil area basis (W_i, g m^{-2}d^{-1}) is calculated from total growth (W, g m^{-2}d^{-1}) using a partitioning factor, which is a function of crop development stage (in °C d after plant emergence or planting).

Total biomass (W) is obtained by integrating the daily growth rates of the tissues (ΔW_i) over time. The harvest index (HI), being the fraction of tuber dry matter in total dry matter, is calculated by dividing tuber dry matter yield by total biomass.

Leaf photosynthesis
Leaf gross CO$_2$ assimilation was simulated according to the biochemical model described by Farquhar et al. (1980) and Von Caemmerer and Farquhar (1981). The model, based on Michaelis Menten kinetics, simulates the kinetics of electron flow and the carboxylation rates. From these relations, effects of temperature, photosynthetically active photon flux density (PPFD) and CO$_2$ concentration on gross leaf photosynthesis can be derived.

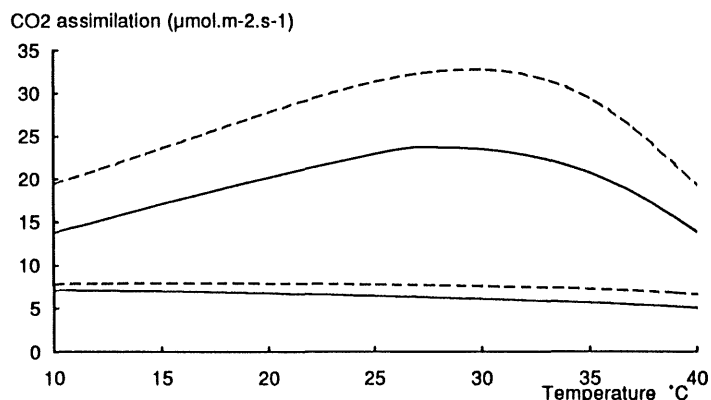Gross leaf photosynthesis is determined by two rate-limiting processes, i.e.

CO2 assimilation (µmol.m-2.s-1)

Figure 1. Simulated temperature dependence of gross CO_2 assimilation at 112 and 900 umol PPFD, lower and upper curves respectively and ambient CO_2 concentrations of 350 (——) and 700 vpm (---).
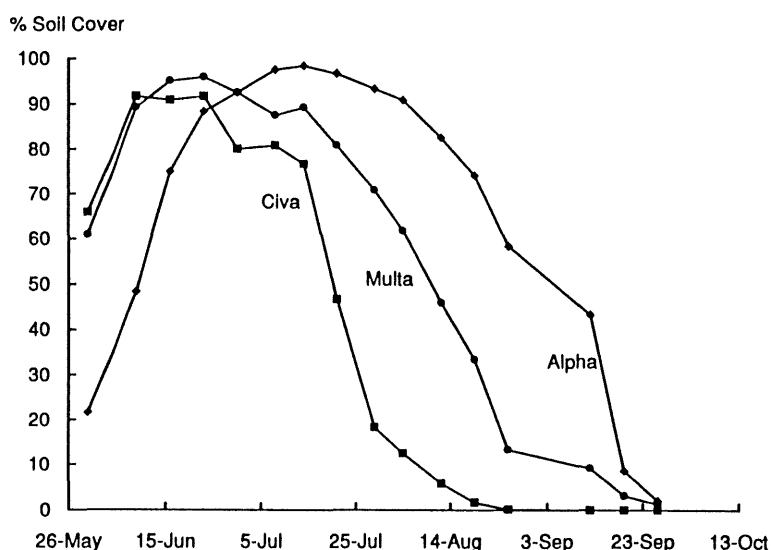

Figure 2. Foliage development of three potato cultivars, plotted as soil cover, estimated from visual observations in the experiment of 1988.

the production of reducing equivalents in the electron-transport chain and the rate of carbon fixation in the Calvin cycle. At low PPFD, the electron-transport rate, equivalent to energy delivery is limiting. A high CO_2 concentration has a positive effect due to more efficient energy utilization by suppression of photorespiration. At high PPFD the positive effect is enhanced because the carboxylation rate, linked with the availability of CO_2, is rate-limiting under high light conditions.

The effects of temperature on photosynthesis are complex. Temperature operates on the rates of electron transport and the rates of carboxylation and oxygenation. In addition the affinities of Rubisco for CO_2 and O_2 are affected. Due to a lower activation energy, higher temperatures will promote O_2 binding at the expense of CO_2 binding. At low PPFD, the effect of temperature on gross assimilation will be negative (Figure 1, lower part) due to the increase in

photorespiration. However, at high PPFD, photosynthesis becomes less dependent on energy efficiency and more on the maximum turnover rates of electron transport and carboxylation, which are increased by a higher temperature. CO_2 amplifies this trend (Figure 1).

Earliness

Effects of earliness (m) are expressed by the initiation of tuberization and the onset of leaf senescence. Simulations were made for all cultivars of the 1988 experiment. Figure 2 shows the visual estimates of percentage of ground covered by green foliage for three cultivars. A more accurate but time-consuming method is based on counting the number of grids that were at least filled by more than half with projections of leaves (Khurana and McLaren 1982).

Table 1. Correlation matrix between yield components, measured in 1988

	Eff.	W	HI	Ydry	%DM	Yfresh	m	%CVe	%CVg	Mean	Units
Attribute											
PAR	0.07	0.89	−0.58	0.77	0.71	0.17	−0.96	2.4	13.5	4.9	GJ/ha
Efficiency	1	0.51	0.4	0.65	0.36	0.51	−0.12	4.2	6.1	2.93	g/MJ
Biomass		1	−0.32	0.96	0.78	0.38	−0.88	3.4	16.2	14.3	t/ha
Harvest index			1	−0.04	−0.32	0.38	0.62	1.2	4.6	0.807	−
Tuber yield (dry)				1	0.72	0.51	−0.75	4.1	15.2	11.6	t/ha
Dry matter content					1	−0.22	−0.74	2.4	13.0	0.214	−
Tuber yield (fresh)						1	−0.11	2.7	10.2	54.2	t/ha
Earliness Variety list							1	.	.	.	−

Eff: efficiency of intercepted radiation; W: total dry matter; HI: harvest index; Ydry: dry weight tubers; Yfresh: fresh weight tubers; %DM: dry matter concentration in tubers; m: earliness (Dutch cultivar list); %CVe: percentage environmental variation; %CVg: percentage genetic variation.

Cumulative light interception has been proven to be a reliable determinant of plant production. A correlation matrix for the observed yield components, and the calculated light interception for the same field experiment, is given in Table 1. Most of the variation in cumulative light interception can be attributed to differences in time of foliage senescence as indicated by earliness.

The correlation between cumulative light interception and earliness, rated according to the Dutch cultivar list (Cv. list) was −0.96. Not only total plant productivity, but also tuber dry matter production were well correlated with cumulative light interception and thus with earliness (Figure 3). This, however, was not true for tuber fresh weight because there was a compensating negative correlation between tuber dry matter concentration and earliness (Table 2).
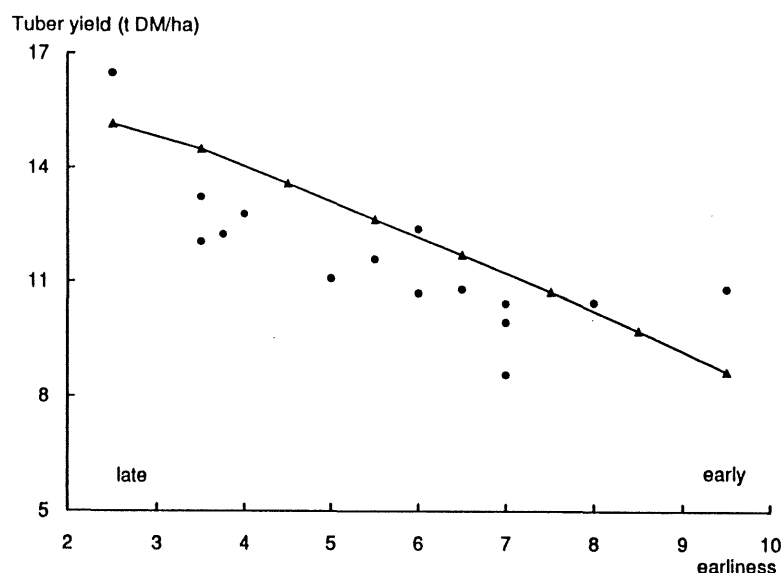
Figure 3. Effect of earliness on tuber yield of 16 potato cultivars in the experiment of 1988. Measured (dots) and simulated data (triangles) at the final harvest.

Table 2. Yield and dry matter concentrations. Harvest 1988

Cultivar	Yfresh	Ydry	%DM	m
Alcmaria	60.23	10.44	17%	8
Alpha	58.09	12.74	22%	4
Bintje	53.65	10.78	20%	6.5
Civa	59.28	10.79	18%	9.5
Karnico	63.83	16.48	26%	2.5
Katahdin	46.54	8.55	18%	7
Kennebec	55.5	10.68	19%	6
Krostar	45.29	10.41	23%	7
Maritta	50.8	12.21	24%	3.75
Multa	61.19	13.2	22%	3.5
Pimpernel	50.3	12.02	24%	3.5
Saturna	50.12	11.56	23%	5.5
Spunta	58.31	9.93	17%	7
Veenster	50.17	12.35	25%	6
Woudster	49.21	11.06	22%	5

Death rate of leaves due to developmental senescence is given by Spitters and Schapendonk (1990):

$$R_{dv} = (T - T_{base}) \exp(-11.7 + 0.48 \, m) \exp((sum(T - T_{base}) - 725)(0.0068 - 0.0005 \, m)) \tag{6}$$

T (average day temperature);
T_{base} (effective temperature for leaf development) = 2 °C;
m (earliness).

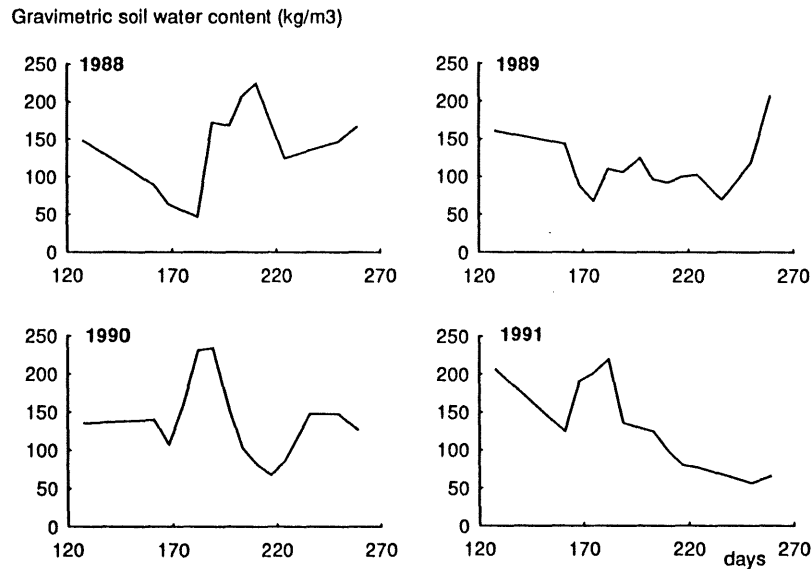Gravimetric soil water content (kg/m3)

Figure 4. Simulated time courses of the gravimetric soil water content in four successive years.

Soil water relations

The soil moisture balance is tracked by a separate subroutine, largely the same as described by Van Keulen (1986). Rainfall is set against percolation of water to the soil layers below the rooting zone and the evapotranspiration rate. When the soil moisture content exceeds field capacity, the surplus water flows to the subrooting zone. Figure 4 shows the simulated soil moisture contents over the years 1988–1991. Evapotranspiration is derived by using a calculated reference value, that quantifies the evaporation from a short grass cover. This reference value marks the potential transpiration and evaporation from daily radiation, temperature and the fractional light interception by the canopy. Next, the actual values for soil evaporation and crop transpiration are calculated. Based on soil moisture balance studies of a sandy soil, the actual soil suction can be derived. Next, an estimated critical volumetric soil water content with a concomitant soil suction is used as a threshold to derive a reduction factor for transpiration (Spitters and Schapendonk 1990).

$$f_{wt} = (p_{wp} - p)/(p_{wp} - p_{cr})$$
$$0 < f_{wt} < 1 \tag{7}$$

p_{wp} (wilting point);

p_{cr} (critical suction; suction of soil moisture above which stomates close and transpiration is reduced);

p (actual suction).

Actual growth of the crop is then given by the product of potential growth and the reduction factor f_{wt} (Haverkort and Goudriaan 1993):

$$\Delta W_a = \Delta W_p f_{wt} (q - 1)/\{(q - 1) f_{wt} + 1\} \tag{8}$$

ΔW_p: potential dry matter production rate;

q: parameter that determines the improvement of the water use efficiency under drought conditions. If q = 1 there is no effect, if q = 2 the maximum increase of the water use efficiency, due to the drought condition, is about 100%.

Carbon partitioning

The partitioning of the assimilated carbon is dependent on the developmental stage of the crop and earliness. Late varieties reach a higher LAI during the season and they maintain a green foliage for a longer time. However, tuber initiation starts later. The effect of stress on dry matter partitioning is often small. However, in seed crops, stress around flowering usually causes an additional yield reduction due to a reduction of sink capacity (empirical relations by Doorenbos and Kassam 1979), which can substantially affect the harvest index. Shortage of soil moisture and/or nutrients favours allocation of assimilates to the below-ground parts at the expense of the above-ground parts, which may significantly affect yield of tuber crops (Seligman and Van Keulen 1981).

For the present application, effects of drought on the specific leaf area and leaf death rate are not implemented, but c.f. Spitters and Schapendonk (1990). In addition the effects of drought and day length on tuber initiation and bulking are neglected despite the evident influence on carbon partitioning (Kooman and Haverkort, implemented in this volume). However, because we only intend to show the basic effects, these interactions are omitted but can easily be inserted into the model.

Interaction with water stress

Water stress induces closure of stomata. The greater resistance of the stomata is reflected in a inhibited rate of photosynthesis. However, photosynthesis is less inhibited than transpiration because the concentration gradient for CO_2 is increased by drought, while that for water remains the same. Therefore, the water-use efficiency is enhanced. However, after a few days, water stress reduces the photosynthetic capacity directly, either by down-regulation of electron transport or by effects on the carboxylation enzymes that lower the mesophyll conductance (Schapendonk et al. 1989) again lowering the water use efficiency. Thus, closure of stomata and the lower mesophyll resistance show a correlated response to water stress, that leads to a constant ci/ca ratio. Therefore, photosynthesis and transpiration are equally reduced and water use efficiency remains the same.

Effects of drought can now be translated into production losses by multiplication of the potential production by the ratio between actual and potential transpiration (Ta/Tp), given a steady-state condition after a few days of a drought period. In general it appears that the immediate effect of drought on physiological parameters is much greater than the integrated seasonal effect, because of the close relation between whole crop transpiration and leaf area (i.e.

growth). In other words, an impaired development of leaf area will save water for later consumption and, therefore, smooth the temporary effects.

Seasonal effects

Photosynthetic light-use efficiency measured early in the season, was low. This was partly due to low photosynthetic rates of individual leaves and partly because a low LAI leads to more light-saturated leaves. Later in the season the light-use efficiency of the canopy increases but gross photosynthesis of single leaves (P_g) gradually decreases mainly due to senescence. The efficiency of net photosynthesis (P_n) decreased even more due to the increasing respiration needed to maintain the standing biomass. This is reflected in an increased respiration/photosynthesis ratio. The declining trend in efficiency of above-ground biomass production (W), is counterbalanced by a gradually decreasing allocation to roots. As a result of all these interactions, the efficiency for above-ground dry matter is rather constant.

Effects of elevated CO_2

Light use efficiency

We measured a higher light use efficiency, for a canopy with a higher leaf area index (LAI). In accordance with these results, Figure 5a shows the calculated light use efficiencies of cultivars varying in earliness. Thus late cultivars are more efficient, mainly due to the overall higher leaf area that leads to less light-saturation in the canopy. The relative effect of elevated CO_2 is just opposite. It is slightly higher for early than for late cultivars. This is due to the CO_2 effect on the light response curve which is higher in the light saturated region and thus under conditions with low LAI, i.e. early cultivars, where individual leaves, on average, receive more light. Caution should be taken to generalize this statement because analyses showed that the light use efficiency varies considerably from day to day. However for longer periods of time (e.g. a 14-day period), the application of an average light use efficiency for above-ground dry matter production is satisfactory.

The relative effect of CO_2 on tuber yield is greater then on the light use efficiency because tuber bulking of early cultivars has an additional benefit from CO_2 due to the enhanced rate of leaf expansion, so that the tuber filling later in the season becomes less vulnerable to drought stress (Figure 5b).

Basic trends

Sink-source interaction. The reported effects of CO_2-enrichment on the yield of potato vary between a slightly negative effect (Goudriaan and De Ruiter 1983) and a maximum positive effect of 39% for a doubling of the CO_2 concentration from 350 to 700 vpm (Wheeler et al. 1991). The yield increase, predicted by the present model is on average 26%, which is in agreement with Wheeler et al. (1991). When the yield of potato is limited by CO_2-assimilation, i.e. when the source of carbohydrate is limited, effects of CO_2 on
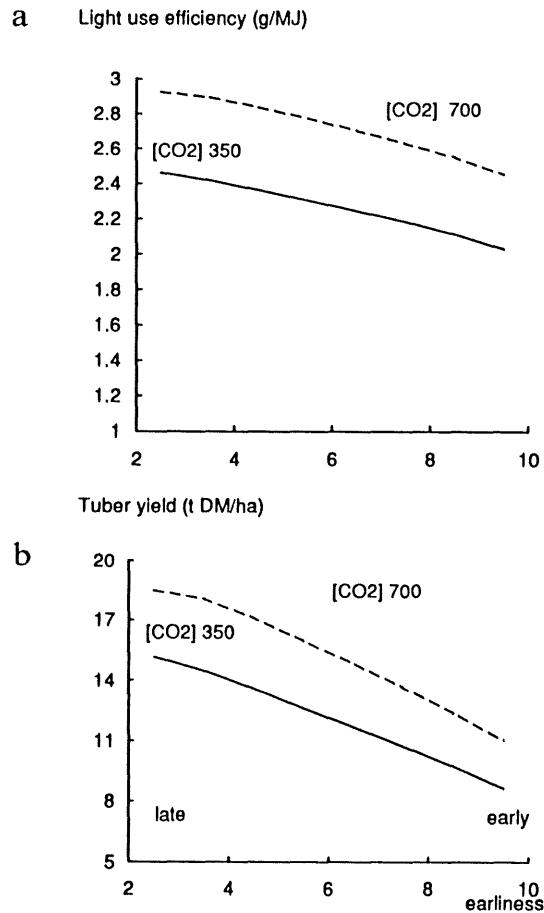
Figure 5. The efficiency of absorbed irradiance (a) and the tuber yield (b) plotted as a function of earliness at two different CO_2-concentrations.

photosynthesis will be important. However, in the case of sink limitation, increasing the CO_2 concentration may have no effect. Wheeler et al. (1991) demonstrated that doubling the CO2 concentration resulted in an increase of 32% in tuber dry matter under 12-h photoperiods but no increase under 24-h photoperiods. This difference was attributed to earlier tuberization under the shorter photoperiod, providing a greater sink for assimilates. Sink limitation may decrease photosynthetic rate or even result in an irreversible damage of the chloroplasts due to starch accumulation (Goudriaan and De Ruiter 1983) and thus it can inhibit photosynthesis physically.

Photosynthesis in general, responds to a sink limitation by a decreased quantum efficiency. In that way assimilate supply and demand are tuned. However, there are exceptions. For instance, the mesophyll resistance of the late cultivar Kennebec, in our experiments, hardly responded to drought-induced growth limitation. This implies a poor operational control of photosynthesis. Indeed it has been noticed that carbohydrate levels in the leaves of this cultivar increased to injurious levels under elevated CO_2 and high irradiance (Wheeler and Tibbitts 1985).

The broad variation of responses to elevated CO_2 emphasizes the existence

of genetic variation in both source and sink limited processes. On the other hand, the close correlation between the cumulative light absorption and dry matter production (Table 1), favours the idea of a prevailing source limitation.

Interaction with temperature

Gross CO_2 assimilation responds to temperature by changes in electron-transport, turn-over of Rubisco and the affinity of O_2 and CO_2 to Rubisco. Temperature enhances the CO_2-effect because it induces higher rates of enzyme turn-over, that are amplified by CO_2-induced suppression of photorespiration (Figure 1). This is valid for high and low PPFD. At high PPFD, limitation of carboxylation will be less at elevated CO_2 concentrations, which provides an additional advantage.

At temperatures above 35 °C, irreversible damage of the electron carriers in the chloroplasts and denaturation of Calvin cycle enzymes cause a sharp decline of the maximum electron transport- and carboxylation rates. It has been shown that the combined effects of high temperature and drought severely impair photosynthetic electron transport (Schapendonk et al. 1989).

The effects of temperature on respiration depend on the developmental stage of the crop. Initially respiration is proportional to growth and therefore it remains a fixed fraction of photosynthesis. However, with increasing biomass, maintenance respiration of the crop will take an increasing share of the total respiratory costs. At leaf area ratios above 4, the maintenance may consume substantial amounts of energy, and higher temperatures will have a negative effect on net photosynthesis and increase the light-compensation point of the crop. The simulated results show losses of about 11 and 15% for total biomass production and tuber yield, respectively when the temperature rises 3 °C (Table 3). The year 1991 was an exception. High temperature and abundant water in spring caused rapid leaf expansion, that compensated partly for the late drought in the summer and autumn. Further, the temperature was low in the summer of 1991 and so the simulated yield increased by 6–7%, when the temperature was raised by 3 °C. In general there was no interaction between CO_2 concentration and temperature on yield or evaporation (Table 3). The momentaneous effects are apparently counteracted by long-term effects, most likely through indirect effects on the leaf area duration (LAD).

Conclusions

- A doubling of the CO_2 concentration is expected to stimulate the yield of potato, ranging from 20% for the late varieties to 30% for the early varieties. The effects can be attributed to increased light use efficiency and a positive effect on the amount of intercepted light.
- The positive effect of CO_2 is greatest for early varieties and early-drought conditions. The effect of drought on late cultivars is smaller and independent of the period in the year. However one should recall the fact that effects of

Table 3. Simulated data on transpiration, total dry weight and tuber yield. The figures between brackets show the relative effect of a temperature increase by 3 °C

year	350 vpm	T = (+3 °C) (%)	700 vpm	T = (+3 °C) (%)
Cumulated transpiration (mm)				
1988	139	*(−10.4)*	144	*(−9.9)*
1989	134	*(−3.7)*	145	*(−4.5)*
1990	177	*(−1.4)*	186	*(−1.5)*
1991	138	*(+4.3)*	142	*(+3.6)*
Cumulated total dry weight (t/ha)				
1988	13.14	*(−14.1)*	16.31	*(−12.9)*
1989	14.17	*(−10.0)*	17.92	*(−11.0)*
1990	16.83	*(−11.4)*	20.81	*(−11.5)*
1991	12.04	*(+4.3)*	14.88	*(+3.6)*
Cumulated tuber dry weight (t/ha)				
1988	11.83	*(−17.7)*	14.78	*(−17.0)*
1989	11.10	*(−17.1)*	14.14	*(−17.2)*
1990	13.79	*(−14.3)*	17.14	*(−14.3)*
1991	8.59	*(+7.0)*	10.72	*(+6.0)*

- CO_2 and temperature on time of tuber initiation are not accounted for in the presented model.
- The amount of water transpired over the whole growth period is not changed by an elevated CO_2 concentration because an increased water use efficiency is compensated by an increased LAI.
- A temperature increase of 3 °C has a negative effect on the yield. This is mainly due to an effect on leaf senescence. The simulated data for both high and low CO_2 are practically identical, which means that in the long term there is no interaction between CO_2 concentration and temperature.

Acknowledgements

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