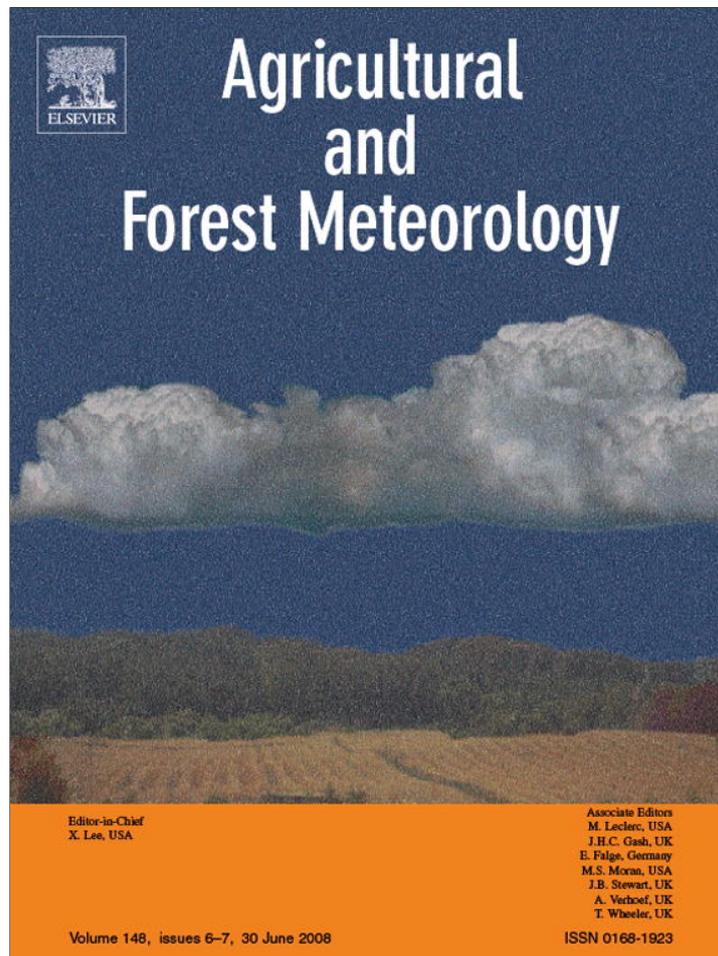


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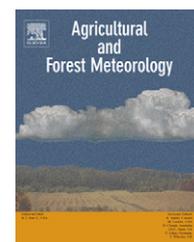


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Elevated carbon dioxide and water stress effects on potato canopy gas exchange, water use, and productivity

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ABSTRACT

Despite the agronomic importance of potato (*Solanum tuberosum* L.), the interaction of atmospheric carbon dioxide concentration ($[CO_2]$) and drought has not been well studied. Two soil–plant–atmosphere research (SPAR) chamber experiments were conducted concurrently at ambient ($370 \mu\text{mol mol}^{-1}$) and elevated ($740 \mu\text{mol mol}^{-1}$) $[CO_2]$. Daily irrigation for each chamber was applied according to a fixed percentage of the water uptake measured for a control chamber for each $[CO_2]$ treatment. We monitored diurnal and seasonal canopy photosynthetic (A_G) and transpiration rates and organ dry weights at harvest. Plants grown under elevated $[CO_2]$ had consistently larger photosynthetic rates through most of the growth season, with the maximum A_G at $1600 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ 14% higher at the well-watered treatments. Water stress influenced ambient $[CO_2]$ plants to a larger extent, and reduced maximum canopy A_G , growth season duration, and seasonal net carbon assimilation up to 50% of the control in both $[CO_2]$ treatments. Water use efficiency increased with water stress, particularly at elevated $[CO_2]$, ranging from 4.9 to 9.3 g dry mass L^{-1} . Larger photosynthetic rates for elevated $[CO_2]$ resulted in higher seasonal dry mass and radiation use efficiency (RUE) as compared with ambient $[CO_2]$ at the same irrigation level. This extra assimilate was partitioned to underground organs, resulting in higher harvest indices. Our findings indicate that increases in potato growth and productivity with elevated $[CO_2]$ are consistent over most levels of water stress. This work can support various climate change scenarios that evaluate different management practices with potato.

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1. Introduction

Potato is sensitive to drought with reductions in yield occurring at even moderate levels of water stress (Jefferies, 1993; Gregory and Simmonds, 1992; Jefferies and Mackerron, 1987; van Loon, 1981). Increased atmospheric carbon dioxide concentration ($[CO_2]$) is known to improve water use efficiency (WUE) (Eamus, 1991), and increase net photosynthetic rate and above and/or below ground biomass (Baker and Allen, 1994) in C3 species. Thus, projected increases in global $[CO_2]$ (Baker and Allen, 1994) may help mitigate the impact of drought on potato

production. Despite the agronomic importance of this crop, studies on the interaction of drought and $[CO_2]$ on seasonal potato growth and development have not been conducted.

Potatoes exhibit a positive response to $[CO_2]$ enrichment, with most research indicating increases in total biomass and/or yield. Schapendonk et al. (2000), Sicher and Bunce (1999), Wheeler et al. (1999), and Wheeler (1991) measured a 27–49% tuber yield increase when $[CO_2]$ was maintained at approximately double that of ambient ($370 \mu\text{mol mol}^{-1}$ versus $740 \mu\text{mol mol}^{-1}$). Goudriaan and de Ruiter (1983) was the one exception to this trend, and observed a slightly negative

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yield response to $[\text{CO}_2]$ doubling. Miglietta et al. (1998) observed a 40% increase in yield, but no significant increase in total biomass, an observation they attributed to relatively low light levels. Lawson et al. (2001) and Miglietta et al. (1998) measured an increase in leaf senescence and flowering, suggesting that elevated $[\text{CO}_2]$ may hasten developmental rate.

Water stress primarily reduces potato canopy expansion (Jefferies, 1995; Vos and Groenwold, 1988) and can delay tuber initiation and bulking (Walworth and Carling, 2002; Bélanger et al., 2001; Costa et al., 1997; Wright and Stark, 1990). Long-term (1–2 weeks or longer) drought reduces leaf area index and canopy longevity (Fleisher et al., 2008; Deblonde and Ledent, 2001; Jefferies, 1993; Jefferies and Mackerron, 1993; Trebejo and Midmore, 1990), resulting in decreased intercepted photosynthetically active radiation (PAR) and net assimilation over the course of the growing season (Susnoschi and Shimshi, 1985). Bélanger et al. (2001) and Trebejo and Midmore (1990) also observed an increase in carbon partitioning to below ground organs (root and tubers) at the expense of above canopy growth in water stressed potato.

Data on potato gas exchange responses to $[\text{CO}_2]$ and water stress are sparse. Ku et al. (1977) found that elevated $[\text{CO}_2]$ reduced transpiration rates and increased photosynthesis and WUE in potato leaves. In an experiment with potatoes grown at 350 and 700 $\mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ in open-top chambers, Schapendonk et al. (2000) measured nearly an 80% increase in the light-saturated rate of canopy photosynthesis with elevated $[\text{CO}_2]$. This differential between $[\text{CO}_2]$ treatments declined over the course of the growing season. Sicher and Bunce (1999) measured increased net photosynthetic rates in the leaves of potato plants grown at elevated $[\text{CO}_2]$ over the entire growing season as compared to ambient $[\text{CO}_2]$ and observed only a moderate amount of photosynthetic acclimation.

The effects of drought on potato leaf level photosynthesis are small compared with stem and leaf elongation rates (Tourneux et al., 2003; Jefferies, 1995; Vos and Groenwold, 1988), suggesting that the main effect of drought on canopy photosynthesis may be due to reduced leaf area production and duration (Jefferies, 1993, 1995). Costa et al. (1997) observed reductions in canopy photosynthetic rate that were correlated with irrigation treatment, with the highest rates occurring with well-watered plants. However, these measurements were limited to flowering and tuber maturation stages and sink strength is known to affect photosynthetic rates (Basu et al., 1999). Vos and Groenwold (1989) measured canopy gas exchange parameters on droughted potato and concluded that the rate of photosynthesis, relative to a non-water stressed control, was suitable for assessing the degree of drought impact on productivity. However, additional gas exchange studies are needed to further quantify the effects of $[\text{CO}_2]$ enrichment on water stressed potato during an entire growing season.

The effect of $[\text{CO}_2]$ and water stress on potato gas exchange and productivity was investigated using six different levels of irrigation at ambient (370 $\mu\text{mol mol}^{-1}$) and elevated (740 $\mu\text{mol mol}^{-1}$) $[\text{CO}_2]$ in soil-plant-atmosphere-research (SPAR) chambers. The objectives were to (1) quantify trends in canopy photosynthesis, seasonal net assimilation rate,

seasonal and diurnal transpiration and water use patterns in response to differences in irrigation amount, (2) assess how these trends were influenced by $[\text{CO}_2]$, and (3) relate these responses to end-of-season productivity, including dry matter production and radiation and water use efficiencies. Research results are important for evaluating production and management practices of potato under future climate change scenarios.

2. Materials and methods

2.1. SPAR chambers

Two experiments, one at 370 $\mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ and the other at 740, were conducted concurrently each using six soil-plant-atmosphere-research (SPAR) chambers at United States Department of Agriculture-Agricultural Research Service (USDA-ARS) facilities in Beltsville, MD, USA in the summer of 2005. The SPAR chambers consist of transparent chamber tops, 2.2 m \times 1.4 m \times 2.5 m (length \times width \times height) constructed of 0.0127 m thick Plexiglas and are similar to systems at the University of Florida (Pickering et al., 1994), Corvallis, OR (Tingey et al., 1996), and Mississippi State University (Reddy et al., 2001). Each SPAR chamber top is mounted to a steel soil bin measuring 2.0 m \times 0.5 m \times 1.0 m (length \times width \times depth). A dedicated Sun SPARC 5¹ workstation (Sun Microsystems Inc., Mountainview, CA, USA) logged environmental data (air and soil-media temperatures, relative humidity, $[\text{CO}_2]$, and PAR above and below the canopy) every 300 s. Additional physical description and methods of operation and monitoring of these SPAR chambers have been described previously (Baker et al., 2004).

Each chamber formed a semi-closed system for measurement of $[\text{CO}_2]$ flux. $[\text{CO}_2]$ leakage rates were estimated daily for each chamber using an N_2O tracer gas system (Baker et al., 2004). Each chamber was fitted with its own infrared gas analyzer (model #LI-6262, Licor Biosciences, Lincoln, NE, USA). Pure CO_2 supplied from a compressed gas cylinder to mass flow controllers (Omega Engineering Inc., Stamford, CT, USA) located in the air ducting in each chamber was coupled with a feed-forward, feed-back PID (proportional-integral-derivative) control algorithm in order to maintain chamber $[\text{CO}_2]$. The amount of $[\text{CO}_2]$ injected, the amount of $[\text{CO}_2]$ leaking from the system, and the amount of $[\text{CO}_2]$ injected but not taken up by the plants were all used to calculate the $[\text{CO}_2]$ exchange rate (CER, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at 5-min intervals. Condensate was collected from the cooling coils of each chamber and weighed every 15-min (Timlin et al., 2007; Baker et al., 2004). This condensate represented whole-canopy transpiration as a vapor barrier was placed over the soil surface to minimize evaporation.

The soilbin of each SPAR chamber was filled in layers (approx 0.15 m thick and 2 \times 0.50 m in area) and wet thoroughly as each layer was added. The soil type was 75% coarse sand and 25% vermiculite (Grace Construction Pro-

¹ Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the USDA and does not imply the exclusion of other available products.

ducts, Cambridge, MA, USA) by volume. Fifteen 30 cm-long TDR waveguides (three rod) were installed horizontally in each soilbin perpendicular to the widest dimension. These were installed at three horizontal positions at five soil depths. A calibration relationship between water content and dielectric constant was developed using soil from the chambers. Water contents from air dry to saturation were used. Additional information on the TDR system and soil characteristics can be found in Timlin et al. (2007).

2.2. Plant culture

Time release fertilizer (Osmocote 14-14-14, The Scotts Company, OH, USA) was incorporated in the top 5 cm of the soil in each chamber at a rate of 60 g m⁻² prior to planting. On 27 May 2005, certified potato (*Solanum tuberosum* cv. Kennebec) seed tubers (54.9 ± 10.04 g mean fresh weight) were planted at a depth of approximately 5 cm in six rows (12 plants m⁻²) in SPAR chambers. All SPAR chambers were maintained at a constant day/night 16 h/8 h thermoperiod of 23/18 °C. The average seasonal relative humidity of the air during the respective two parts of the thermoperiod was 58 ± 8.1 and 58 ± 8.8% which provided an air vapor pressure deficit of 1.3 ± 0.26 and 0.97 ± 0.2 kPa. Daytime [CO₂] was controlled at either 370 and 740 μmol mol⁻¹ for the six SPAR chambers in each [CO₂] level. Night-time [CO₂] was uncontrolled, but varied between 461 and 635 μmol mol⁻¹ with an average of 536 ± 55.7 μmol mol⁻¹ for all chambers during the course of the experiment. Photoperiod averaged 14.1 h during the course of the experiment (27 May through 21 October 2005) and average daily light integrals over the course of the experiments are provided in Table 1. Chamber soil volumes (270 L) were soaked with tap water prior to planting; however, during the growing season, irrigation was controlled so that the bottom layer did not saturate to prevent drainage of water from the soil (Timlin et al., 2007). Irrigation was not supplied again until 3 weeks after emergence (see below), at which point volumetric water content was approximately 130 L for each chamber. After emergence, potato plants were pruned to allow only the growth of a single main stem and transparent plastic film (4 mil thickness) was used to cover the top of the soil around each plant to minimize evaporation from the soil surface. Shade curtains were added at 21 days after emergence (DAE) to maintain the production area and minimize border effects.

Irrigation was supplied in the form of 1/2 strength Woody's solution (Robinson, 1984) and distributed by drippers arranged in three 2.0 m rows with 0.20 m spacing between rows in each chamber. The drippers were spaced at 0.10 m intervals. Irrigation treatments were initiated at 21 DAE (days after emergence), corresponding to main stem flowering. Varying amounts of irrigation was provided to each SPAR chamber on a daily basis according to 90, 75, 50, 25 and 10% of the daily water uptake (computed from TDR system as described below) measured from the control chamber (100%). Separate control chambers were used for the 370 and 740 μmol mol⁻¹ [CO₂] experiments. Irrigation was applied after 22:00 h for each chamber. Harvest times (Table 1) were selected when canopy photosynthetic rates dropped to below 50% of their peak value.

2.3. Data collection

Hourly TDR water contents were multiplied by soil volume for each layer to obtain total volume of water in the soilbin of each chamber for each hourly measurement. The hourly water volumes were averaged by depth and summed to obtain a daily total water volume in the soilbins. Water uptake per day was obtained as the difference between the 06:00 and 21:00 h water contents, and seasonal water uptake was calculated as the sum of the daily uptake values. Additional information on the TDR system operation may be found in Timlin et al. (2007).

During the daytime, CER values represent canopy net photosynthesis, A_N. Two mean values for dark respiration, R_D, at day and night temperatures, were estimated for each 24-h period. Daytime R_D was obtained by averaging CER values at the day temperature between 20:00 and 22:00 h when PAR was zero, and nighttime, or dark period, R_D was estimated at the night temperature between 01:00 and 04:00 h. Resulting R_D values were added to A_N to estimate gross photosynthesis, A_G, as in Eq. (1). Although R_D does not account for photorespiration and may be affected by [CO₂], this method has successfully been used to relate carbon assimilation to dry matter (van Iersel and Kang, 2002; Reddy et al., 1989; Dutton et al., 1988) from growth chamber data:

$$A_G = A_N + R_D \quad (1)$$

where A_G is the gross instantaneous photosynthetic rate (μmol CO₂ m⁻² s⁻¹), A_N the net instantaneous photosynthetic rate (μmol CO₂ m⁻² s⁻¹), and R_D the dark respiration (μmol CO₂ m⁻² s⁻¹).

Canopy gas exchange data were averaged at 15-min intervals. A rectangular hyperbola (Eq. (2)) (Acock et al., 1976), was fit to the relationship between A_G and incident PAR in order to analyze light-response curves for each day of interest:

$$A_G = \frac{\alpha I \tau C}{\alpha I + \tau C} \quad (2)$$

where A_G is the gross photosynthetic rate (μmol CO₂ m⁻² s⁻¹), I the incident PAR above the canopy (μmol PAR m⁻² s⁻¹), τ the canopy conductance to [CO₂] transfer (m s⁻¹), α the canopy light utilization efficiency (μmol CO₂ μmol⁻¹ PAR), and C the [CO₂] (expressed as μmol CO₂ m⁻³).

The NLIN procedure in SAS statistical software (The SAS system for Windows, 8.02, SAS Institute Inc., Cary, NC, USA) was used to obtain parameter values using the Gauss-Newton nonlinear least squares iterative method.

At harvest, all senesced leaf material was gathered and recorded for each chamber. Root weights were estimated on a chamber basis from root cores that were taken at five different depths at four horizontal positions in each soil layer and included stolon weights. Plants were separated according to stem, remaining green leaf, and tubers. All plant material was dried to constant weight in air forced ovens at 70 °C.

2.4. Evaluation of experimental approach

At the end of the growth season, the total irrigation to each chamber, expressed as a percentage of the control amount at

Table 1 – Harvest date (days after emergence, DAE), seasonal irrigation and water uptake, and average daily light integral expressed as photosynthetically active radiation (PAR) per irrigation treatment at 370 and 740 $\mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ from planting through harvest

Irrigation (% of control)	Harvest date (DAE)		Seasonal irrigation (L) ^{a,b,c}		Seasonal uptake (L) ^b		PAR (mol PPF m ⁻² day ⁻¹)	
	370	740	370	740	370	740	370	740
100	126	132	737	637	714	640	35 ± 13	35 ± 13
90	134	98	664 (90)	443 (88)	668	559	34 ± 13	38 ± 11
75	119	110	516 (71)	416 (74)	542	485	37 ± 12	37 ± 12
50	91	91	248 (50)	225 (48)	331	380	38 ± 11	38 ± 11
25	81	81	103 (24)	100 (26)	242	221	39 ± 12	39 ± 12
10	74	74	37 (10)	33 (9)	193	122	39 ± 11	39 ± 11

Standard deviations are indicated where appropriate.

^a Values in parenthesis are the seasonal irrigation amounts expressed as a percentage of the control for ambient (370) and elevated (740) $[\text{CO}_2]$.

^b Computed using the TDR system.

^c Soil volume was saturated prior to planting with approximately 170 L of water not included in this column.

the time of chamber harvest, is indicated in parenthesis in Table 1. These actual percentages match closely with the desired treatment amounts. There was approximately 170 L of water available to the plants in the soil compartment at the start of the irrigation treatments. Thus, total uptake exceeded total irrigation for the less well-watered treatments (Table 1).

A comparison of end of growth season cumulative net assimilation ($\text{mol CO}_2 \text{ m}^{-2}$) versus total dry mass production (including all senesced leaf material) was made in order to evaluate the accuracy of the gas exchange measurements over the entire growth season (Fig. 1). The inverse of the slope of the regression line indicates a carbon content of 0.41 g C g^{-1} biomass for $370 \mu\text{mol mol}^{-1} [\text{CO}_2]$ and 0.46 g C g^{-1} biomass for $740 \mu\text{mol mol}^{-1} [\text{CO}_2]$. Assuming a 41% carbon content for potato (Wheeler et al., 1996), these results indicate a slight over-prediction in cumulative net photosynthetic rate at elevated $[\text{CO}_2]$. However, Stitt and Krapp (1999) and Long et al. (1996) described increased carbohydrate contents in leaves of plants grown with elevated $[\text{CO}_2]$ (possibly due to increased nitrogen use efficiency by elevated $[\text{CO}_2]$), a finding that may explain the larger carbon content estimated in this experiment. Potential sources of error likely include carbon loss during harvesting procedures, including loss of senesced leaf material and respiratory losses during initial oven drying (Monje, 1993).

2.5. Data analysis

Regression was used to analyze the responses of canopy gross photosynthetic rate at high irradiance ($1600 \mu\text{mol PAR m}^{-2} \text{ s}^{-1}$), seasonal and specific respiration, radiation and water use efficiency, transpiration, and dry matter production versus irrigation amount expressed as a percentage of the control chamber. Irrigation amount was treated as a continuous variable and $[\text{CO}_2]$ as qualitative. SAS (The SAS system for Windows, 9.01, SAS Institute Inc., Cary, NC, USA) Proc GLM was used to determine the appropriate regression form (linear or nonlinear), calculate the coefficients of the regression, and test for common slopes and intercepts between $[\text{CO}_2]$ levels. Regression lines and/or coefficients that were not significantly different from one another between $[\text{CO}_2]$ levels were noted in the appropriate tables and figures.

A modified form of the Gompertz growth equation (Eq. (3)) (Thornley and Johnson, 1990) was used to describe the relationship between cumulative net assimilation versus time. The maximum net assimilation rate was taken as the difference in assimilation rate between 20 and 80% of the time required to reach the final assimilation X_f :

$$X = X_0 e^{[\ln(X_f/X_0)(1-e^{-Dt})]} \quad (3)$$

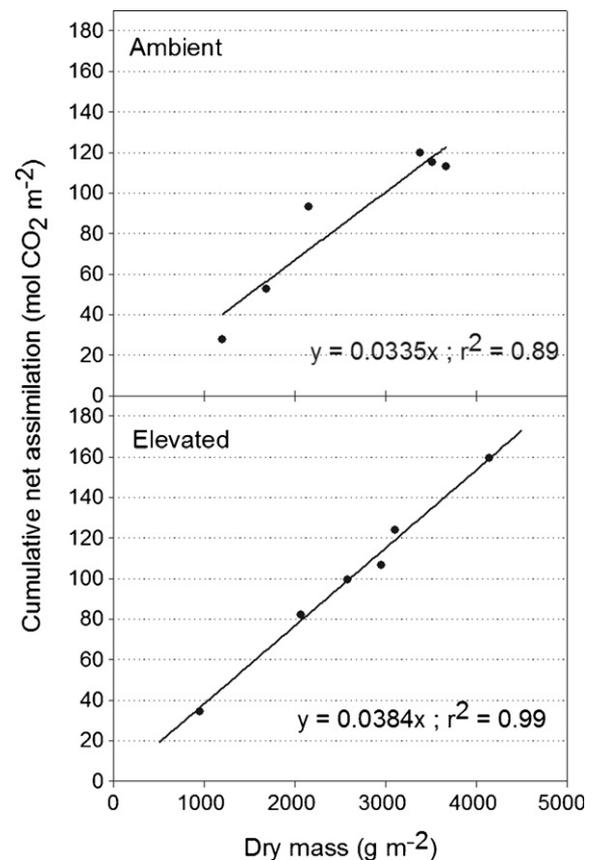


Fig. 1 – Cumulative net assimilation ($\text{mol CO}_2 \text{ m}^{-2}$) versus end of season dry matter production (g dry mass m^{-2}) for potatoes grown at $370 \mu\text{mol mol}^{-1} [\text{CO}_2]$ (ambient) and $740 \mu\text{mol mol}^{-1} [\text{CO}_2]$ (elevated).

where X_0 is the initial net assimilation at 0 days after emergence (i.e. $t_d = 0$) ($0.05 \text{ mol CO}_2 \text{ m}^{-2}$), X_f the final cumulative net assimilation at harvest ($\text{mol CO}_2 \text{ m}^{-2}$), X the cumulative net assimilation at current time increment ($\text{mol CO}_2 \text{ m}^{-2}$), D the cumulative net assimilation at current time increment ($\text{mol CO}_2 \text{ m}^{-2}$), t_d the days after emergence (days).

3. Results

3.1. Canopy photosynthesis, respiration, and radiation use efficiency

Light response curves for 3 days with full sunlight (i.e. little or no cloud cover) (DAE 29, 45, and 65) were selected to assess irrigation and $[\text{CO}_2]$ effects on gross photosynthetic rates at different times during the growth season. Parameters from fitting Eq. (2) to this data were shown in Table 2. Canopy light use efficiency (α) and τ were at their highest values for both $[\text{CO}_2]$ levels at DAE 65 for irrigations above 25% of the control. On DAE 45 and 65, α was smaller at decreasing irrigation amounts, likely a result of smaller canopy size. Conductance to $[\text{CO}_2]$ transfer (τ) decreased with irrigation on all DAE. This trend was particularly evident when comparing 10 and 25% irrigation values versus 50 through 100%. This response was presumably due to increased stomatal resistance with the less watered plants. No consistent differences in α between $[\text{CO}_2]$ levels were apparent. However, τ was clearly smaller for elevated versus ambient $[\text{CO}_2]$ at most irrigation treatments.

Fig. 2 illustrated these responses with light response curves at 45 and 65 DAE. Despite the decline in τ between $[\text{CO}_2]$ levels, elevated $[\text{CO}_2]$ gross photosynthetic rates were still higher than ambient $[\text{CO}_2]$ at a given PAR level during most days of the growth season, with no clear indication of acclimation occurring (Fig. 2).

Weekly averages for canopy A_G at $1600 \mu\text{mol PAR m}^{-2} \text{ s}^{-1}$ ($A_G\text{-}1600$) during the course of the growth season for several irrigation treatments at each $[\text{CO}_2]$ treatment were shown in Fig. 3. Polynomial regression parameters were summarized in Table 3. Maximum $A_G\text{-}1600$ values were smaller with at the lower irrigation treatments for both $[\text{CO}_2]$ levels. This result followed from the observation that α and τ terms declined with DAE, particularly between 10 and 25% versus the more well-watered treatments (Table 2). Maximum $A_G\text{-}1600$ values were also not clearly different between 50, 75, 90 and 100% irrigation treatments (Fig. 3, 75 and 90% not shown for clarity). However, the duration of time for which this value was maintained was clearly influenced by irrigation and largely due to differences on leaf area production and persistence over the course of the growth season.

Total seasonal respiration declined linearly with irrigation for both $[\text{CO}_2]$ levels (Fig. 4A). This result was due to higher net assimilation rates (and thus, larger biomass) as irrigation increased. Respiration for the 10%, 370 $[\text{CO}_2]$ treatment was relatively high, particularly when expressed on a dry mass basis (Fig. 4B). A comparison of seasonal net assimilation and the estimated total C fraction of end of growth season biomass for that treatment indicated that biomass was under-

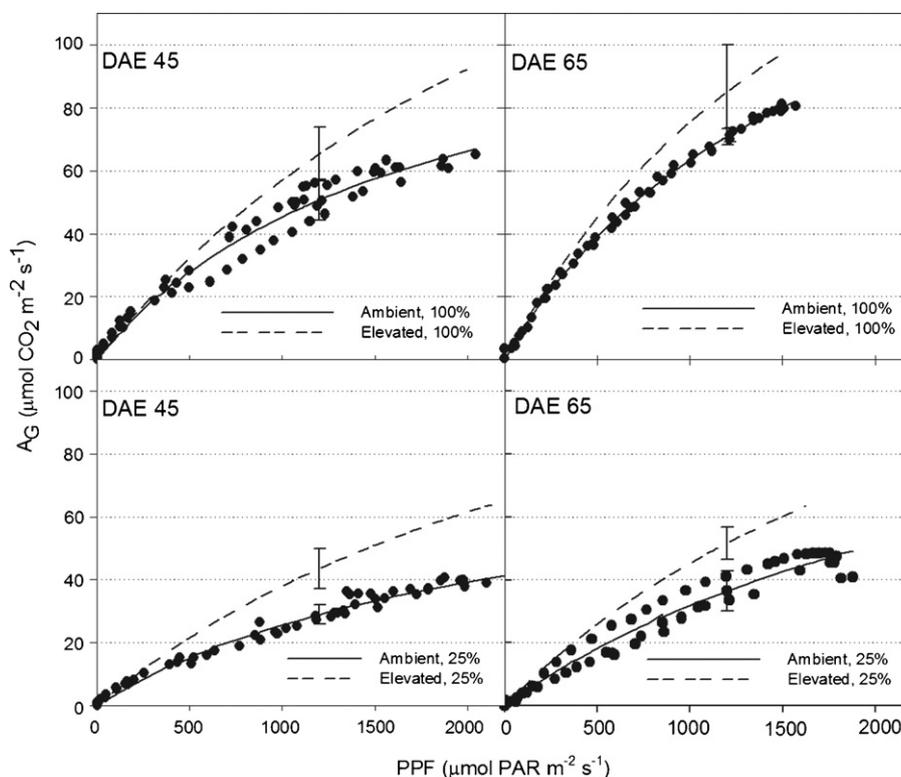


Fig. 2 – Gross photosynthetic rate versus photosynthetic photon flux (PPF) at 45 and 65 days after emergence (DAE) for selected irrigation treatments at ambient and elevated $[\text{CO}_2]$. Curve parameters are from Table 2 and 95% confidence limits are shown at $1200 \mu\text{mol PAR m}^{-2} \text{ s}^{-1}$. Measured data shown for ambient treatments only for clarity.

Table 2 – Canopy light utilization efficiency (α) and canopy conductance to $[\text{CO}_2]$ transfer (τ) for potato canopies grown at 370 and 740 $\mu\text{mol mol}^{-1} [\text{CO}_2]$ at different water stress treatments

DAE	Irrigation (% control)	α ($\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$)		τ (mm s^{-1})	
		370	740	370	740
29	100	0.070 \pm 0.004	0.061 \pm 0.003	5.9 \pm 0.35	4.2 \pm 0.33
	90	0.088 \pm 0.005	0.062 \pm 0.003	5.3 \pm 0.27	3.7 \pm 0.3
	75	0.057 \pm 0.005	0.052 \pm 0.002	5.7 \pm 0.51	2.9 \pm 0.18
	50	0.053 \pm 0.006	0.051 \pm 0.003	4.2 \pm 0.49	2.9 \pm 0.2
	25	0.042 \pm 0.003	0.069 \pm 0.005	2.6 \pm 0.15	1.4 \pm 0.07
	10	0.057 \pm 0.004	0.048 \pm 0.007	2.3 \pm 0.1	1.6 \pm 0.18
45	100	0.072 \pm 0.004	0.074 \pm 0.004	8.2 \pm 0.68	8.1 \pm 1.1
	90	0.081 \pm 0.004	0.059 \pm 0.002	9.5 \pm 0.83	8.5 \pm 1.1
	75	0.062 \pm 0.004	0.065 \pm 0.004	8.5 \pm 0.78	9.0 \pm 1.62
	50	0.057 \pm 0.003	0.053 \pm 0.003	10.1 \pm 1.20	6.8 \pm 1.0
	25	0.037 \pm 0.002	0.05 \pm 0.003	5.6 \pm 0.35	5.3 \pm 0.74
	10	0.045 \pm 0.002	0.034 \pm 0.003	3.3 \pm 0.16	1.4 \pm 0.13
65	100	0.10 \pm 0.001	0.11 \pm 0.008	11.4 \pm 0.21	7.7 \pm 1.1
	90	0.11 \pm 0.001	0.088 \pm 0.001	11.5 \pm 0.23	8.7 \pm 0.27
	75	0.10 \pm 0.004	0.094 \pm 0.002	11.5 \pm 0.62	10.0 \pm 0.45
	50	0.11 \pm 0.003	0.067 \pm 0.001	15.0 \pm 0.73	6.4 \pm 0.3
	25	0.042 \pm 0.003	0.061 \pm 0.002	8.6 \pm 1.26	5.8 \pm 0.54
	10	0.041 \pm 0.002	0.033 \pm 0.001	2.2 \pm 0.09	1.1 \pm 0.04

Parameters are shown at three different days after emergence (DAE). Standard errors of the estimate are provided.

estimated by approximately 30%; thus, respiration was most likely over-predicted for this chamber. Regression lines were not significant for seasonal specific respiration when this treatment was removed from analysis (Fig. 4B). Therefore, respiration rates were not affected by irrigation amount on a unit dry mass basis. Specific respiration was significantly higher ($\alpha = 0.05$) for ambient versus elevated $[\text{CO}_2]$ when averaged across remaining irrigation treatments ($7.5 \pm 0.68 \text{ mol } [\text{CO}_2] \times 10^{-3} \text{ g dry mass}^{-1}$ versus $5.2 \pm 0.46 \text{ mol } [\text{CO}_2] \times 10^{-3} \text{ g dry mass}^{-1}$)

Results of the fit of Eq. (3) to cumulative net assimilation versus DAE are shown in Table 4. Fig. 5A depicts the fit for the 100% irrigation treatment. Maximum assimilation rate was nonlinearly correlated with decreasing irrigation amount and was significantly larger for elevated $[\text{CO}_2]$ treatments at a given level of irrigation (Fig. 5B). Maximum assimilation rate also nonlinearly increased with

irrigation amount, likely due to increased period of leaf development and appearance in the canopy, resulting in a distribution of younger leaves in the canopy of the well-watered treatments (van Loon, 1981). The duration of the maximum assimilation rate throughout the growth season was linearly correlated with irrigation but was not influenced by $[\text{CO}_2]$ as regression lines were not significantly different (Fig. 5C).

A comparison of cumulative intercepted PAR at the end of the growth season, expressed as a percentage of incident radiation, is shown in Fig. 6 (top). There was little difference in intercepted PAR during the course of the growth season between $[\text{CO}_2]$ treatments at a given level of irrigation. However, RUE was larger for elevated versus ambient $[\text{CO}_2]$ plants at most water stress treatments (Fig. 6). RUE was linearly correlated with irrigation amount (Fig. 6) with a minimum differential of 0.4 g MJ^{-1} intercepted

Table 3 – Regression parameters for weekly averages of A_G at 1600 $\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$ for selected irrigation treatments in Fig. 3 at elevated and ambient $[\text{CO}_2]$, where $y = b_0 + b_1x + b_2x^2$

$[\text{CO}_2]$ ($\mu\text{mol mol}^{-1}$)	Irrigation (% of control)	Regression parameters			
		b0	b1	b2	r^2
370	100	-9.3 (5.42) a	14.8 (1.31) a	-0.7 (0.07) a	0.89
	50	-22.7 (4.4) b	19.0 (1.44) b	-1.0 (0.10) b	0.97
	25	-9.4 (5.3) a	10.3 (1.88) c	-0.6 (0.14) a	0.89
	10	-11.5 (4.56) a	12.5 (1.74) a,c	-1.0 (0.14) b	0.87
740	100	-26.3 (7.50) a	21.7 (1.73) a	-1.0 (0.08) a	0.91
	50	-14.1 (5.94) a,b	16.7 (1.95) b	-0.8 (0.14) a,b	0.94
	25	-18.3 (4.96) a	17.0 (1.75) b	-1.0 (0.13) a	0.94
	10	-7.9 (3.46) b	9.8 (1.33) c	-0.7 (0.11) b	0.89

Different letters indicate whether regression terms were significantly different between irrigations within a given $[\text{CO}_2]$ treatment. Regression equations were also significantly different between $[\text{CO}_2]$ treatments within a given level of irrigation.

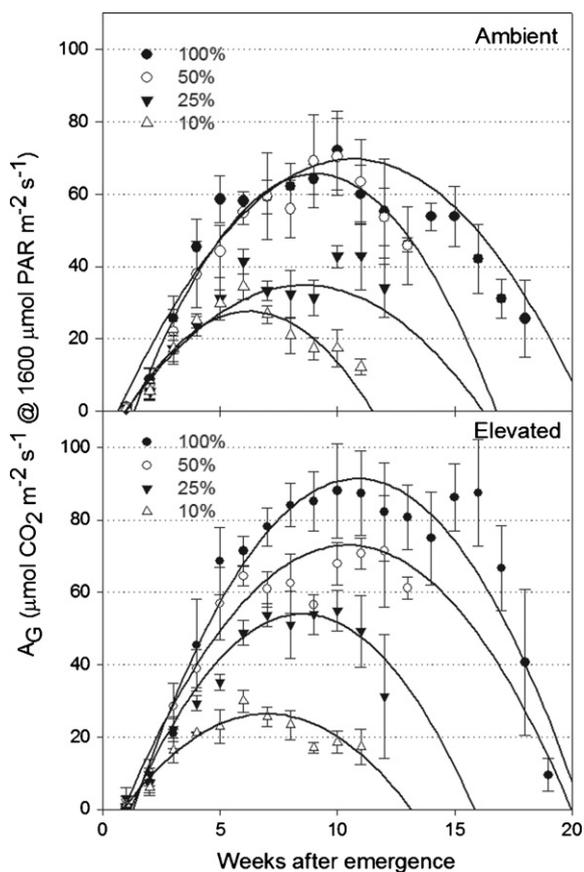


Fig. 3 – Average weekly canopy gross photosynthetic rate (A_G) at $1600 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$ from emergence through harvest for four selected percent irrigation treatments at 370 and $740 \mu\text{mol mol}^{-1} \text{CO}_2$. Standard deviations are indicated with error bars. Regression lines were significantly different between irrigation treatments at a given $[\text{CO}_2]$ and between $[\text{CO}_2]$ within a given irrigation treatment.

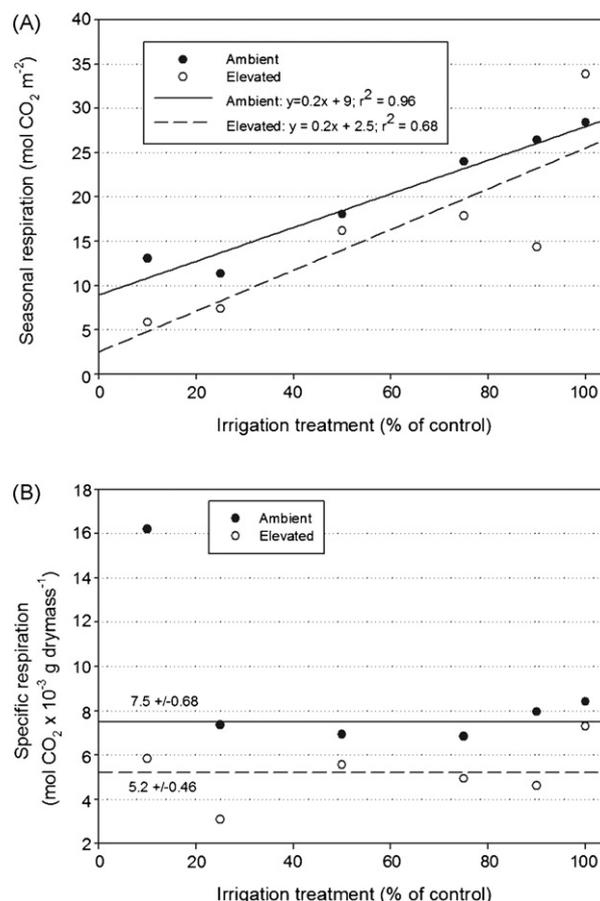


Fig. 4 – (A) Total respiration versus irrigation treatment at ambient and elevated $[\text{CO}_2]$. Regression lines were not significantly different. (B) End of season-specific respiration versus irrigation treatment. Regressions were not significant. Lines indicate significantly different treatment means averaged across irrigation level by $[\text{CO}_2]$ treatment without the 10% ambient treatment.

PAR between $[\text{CO}_2]$ treatments. RUE decreased by over 30% for both $[\text{CO}_2]$ treatments between the 100 and 10% irrigation levels. These results support the findings for increases in net assimilation rate with elevated $[\text{CO}_2]$ in Fig. 5B.

3.2. Transpiration and water use efficiency

Diurnal trends for canopy transpiration rates for several irrigation treatments are shown in Fig. 7 for a sunny day. Transpiration rates closely tracked the patterns in PAR during

Table 4 – Gompertz parameters (final cumulative net assimilation at harvest (X_f) and decay in cumulative net assimilation rate (D)) for the fit between cumulative net assimilation versus days after emergence (DAE) from emergence to harvest for potato plants grown at 370 and $740 \mu\text{mol mol}^{-1} [\text{CO}_2]$ at different water stress treatments

Irrigation (% of control)	X_f (mol $\text{CO}_2 \text{ m}^{-2}$)		D (days^{-1})	
	370	740	370	740
100	118.5 ± 1.14	171.3 ± 1.60	0.039 ± 0.0004	0.035 ± 0.0003
90	124.0 ± 1.20	122.2 ± 0.68	0.037 ± 0.0004	0.044 ± 0.0002
75	125.6 ± 2.57	136.5 ± 0.63	0.038 ± 0.0004	0.039 ± 0.0002
50	106.3 ± 1.13	107.3 ± 1.45	0.039 ± 0.0003	0.044 ± 0.0005
25	60.7 ± 0.80	95.5 ± 1.34	0.045 ± 0.0005	0.046 ± 0.0005
10	31.7 ± 0.29	39.5 ± 0.29	0.054 ± 0.0005	0.051 ± 0.0003

Standard errors are shown.

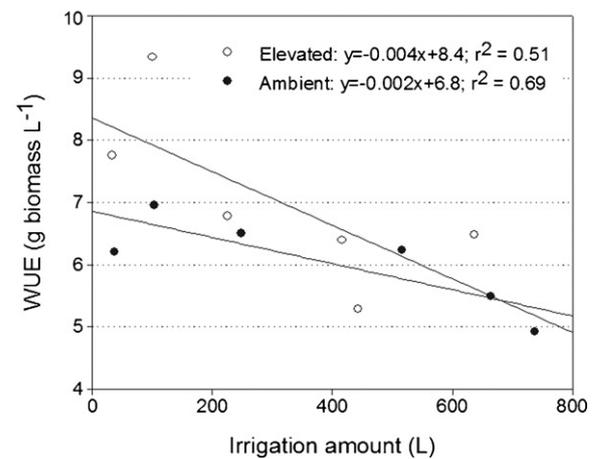
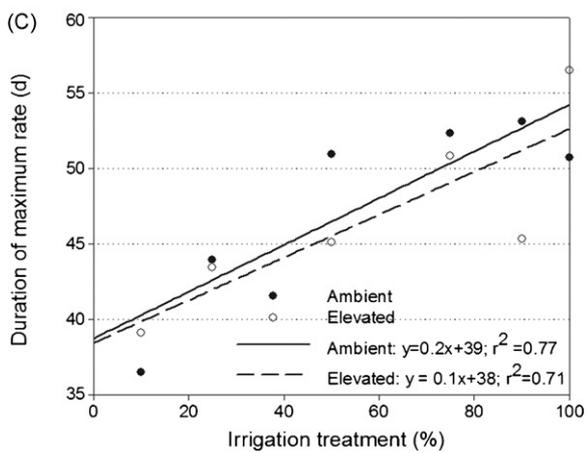
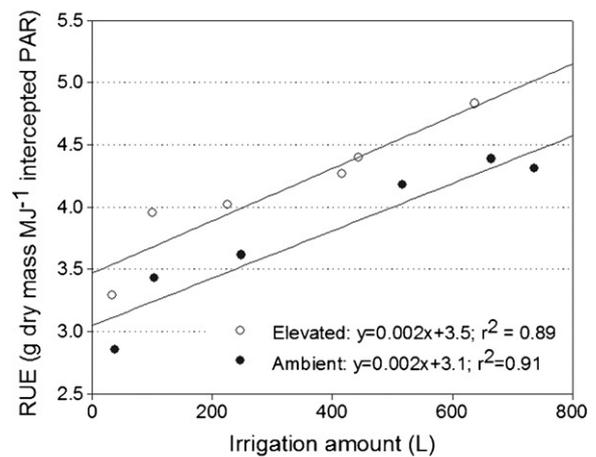
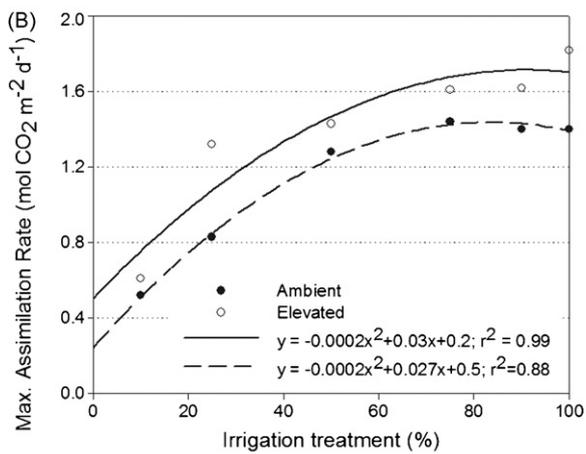
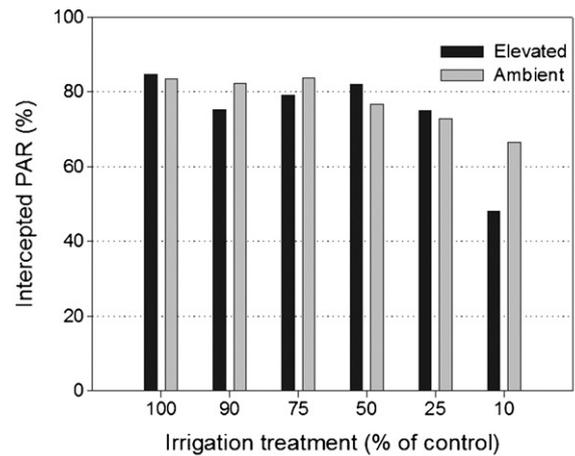
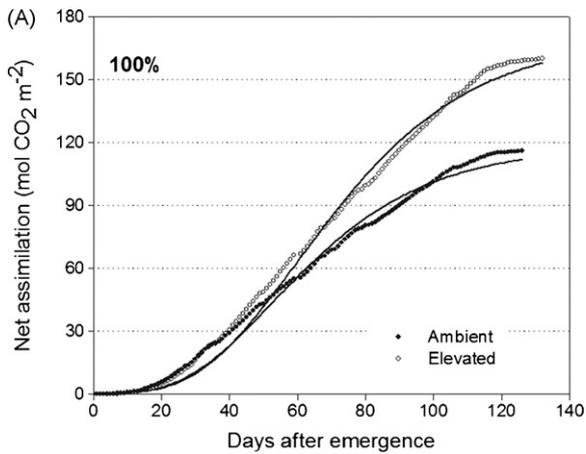


Fig. 5 – Analysis of Gompertz fit to cumulative net assimilation rate per chamber. (A) Example of Gompertz fit to data from 100% irrigation treatment. (B) Maximum daily assimilation rate during the season versus irrigation treatment. Regression lines were significantly different. (C) Duration of the maximum assimilation rate versus irrigation treatment. Regression lines were not significantly different.

Fig. 6 – Seasonal light interception, radiation use efficiency (RUE) and water use efficiency (WUE) at end of season for potatoes grown at 370 and 740 $\mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ versus actual irrigation amount. Regression lines were significantly different between $[\text{CO}_2]$ treatments and included non-common intercepts for RUE and non-common intercepts and slopes for WUE.

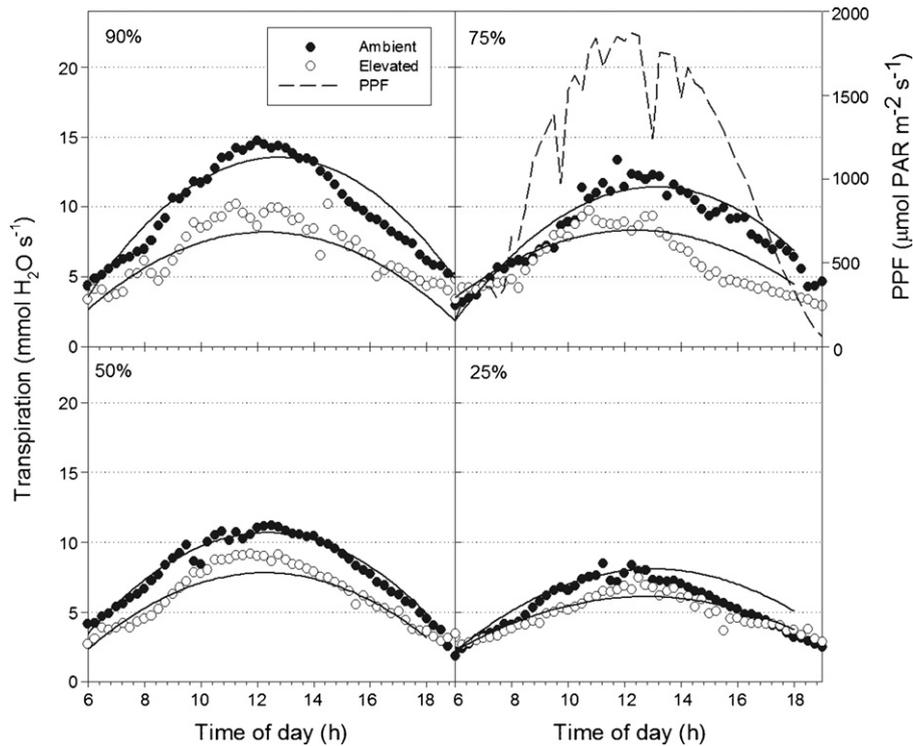


Fig. 7 – Diurnal canopy transpiration values and PAR for potatoes grown at 370 and 740 $\mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ at 90, 75, 50, and 25% irrigation treatments at 45 days after emergence.

the day at both $[\text{CO}_2]$ levels and all irrigation levels. Transpiration rates were significantly higher with increased irrigation amount at all levels of irrigation, and were also significantly higher for ambient versus elevated $[\text{CO}_2]$ within a given irrigation treatment (Table 5). At most irrigation treatments, the intercepts and linear terms in the regression equation (b1) were significantly higher for ambient $[\text{CO}_2]$ as compared with elevated $[\text{CO}_2]$. This increase explains the sharper rise in ambient $[\text{CO}_2]$ transpiration with time of day (and increasing radiation) in Fig. 7. A similar pattern was

observed for most days during the course of the growth season.

The larger photosynthetic rates and reduced transpiration of elevated $[\text{CO}_2]$ plants resulted in an increase in water use efficiency (WUE) for most days throughout the growth season (Fig. 6). End of growth season WUE increased by more than 20% between the 100 and 10% irrigation treatments for both $[\text{CO}_2]$ treatments. WUE was also larger for elevated $[\text{CO}_2]$ at most irrigation treatments, with a 26% increase over ambient $[\text{CO}_2]$ at the 10% irrigation treatment.

Table 5 – Regression coefficients for diurnal patterns of transpiration for selected irrigation treatments at 45 days after emergence corresponding to Fig. 7 where $y = b_0 + b_1x + b_2x^2$

Irrigation (% of control)	$[\text{CO}_2]$ (ppm)	Regression parameters			r^2
		b0	b1	b2	
90	370	-22.1 a	5.6 a	-0.22 a	0.92
	740	-12.9 b	3.4 b	-0.14 a	0.82
75	370	-21.2 a	4.98 a	-0.19 a	0.92
	740	-9.93 b	2.96 b	-0.12 b	0.79
50	370	-16.7 a	4.44 a	-0.18 a	0.97
	740	-13.2 b	3.43 b	-0.14 b	0.89
25	370	-12.2 a	3.12 a	-0.12 a	0.93
	740	-7.75 b	2.17 a	-0.085 a	0.84

Different letters (a and b) indicate whether regression terms were significantly different between $[\text{CO}_2]$ treatments within a given irrigation treatment. Regression equations were also significantly different between irrigation treatments within a given level of $[\text{CO}_2]$.

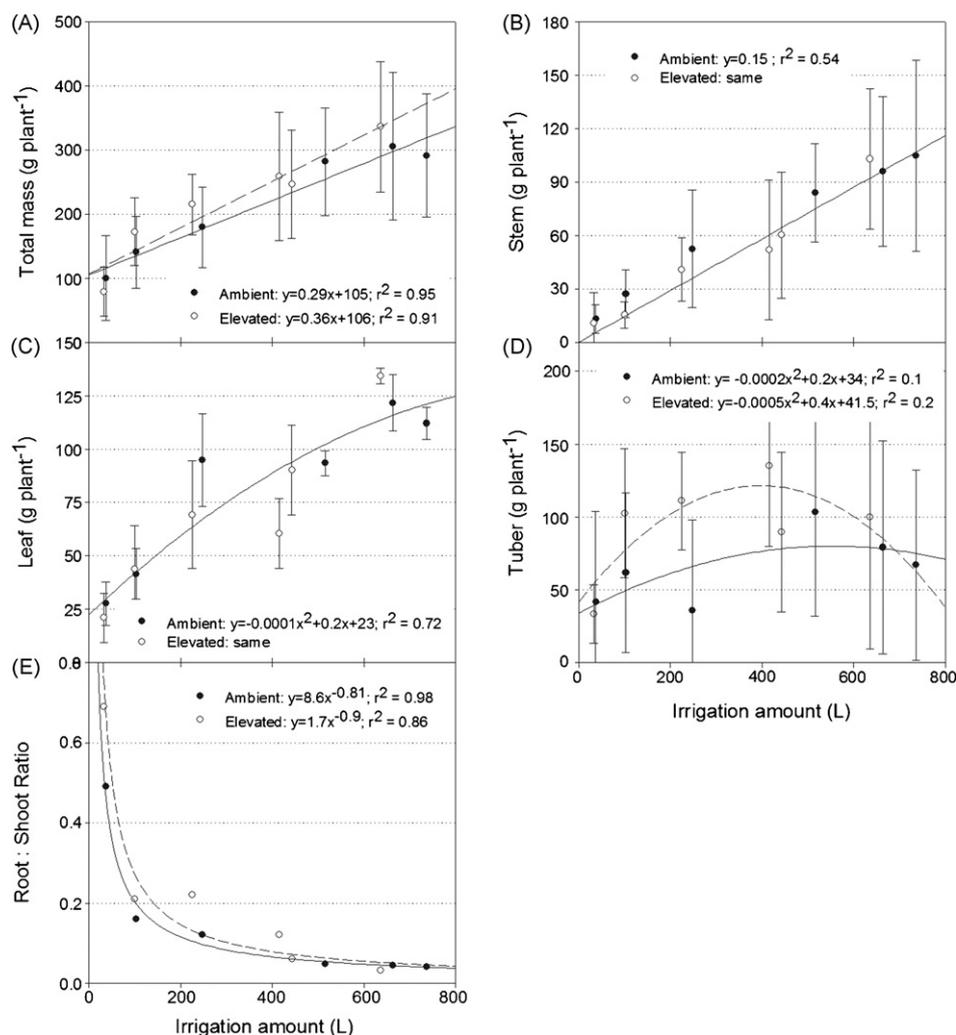


Fig. 8 – End-of-season dry mass production for potatoes grown at 370 and 740 $\mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ versus irrigation amount. (A) Total biomass, (B) stem mass, (C) green and dead leaf mass, (D) tuber mass, (E) root/shoot ratio. Regression lines are significantly different in panels where two lines are plotted and regression parameters provided.

3.3. Dry matter production

Dry matter production reflected the differences in photosynthetic rate and respiration between $[\text{CO}_2]$ and irrigation treatments (Fig. 8). Total biomass and stem mass were linearly correlated with irrigation (Fig. 8A and B). Elevated $[\text{CO}_2]$ treatments produced significantly more total biomass than ambient $[\text{CO}_2]$, particularly as irrigation increased. Leaf mass continued to increase with irrigation (Fig. 8C), while tuber mass peaked at 396 L of irrigation (between 50 and 75% irrigation treatments) at elevated $[\text{CO}_2]$ and 554 L at ambient $[\text{CO}_2]$ (between 75 and 90% irrigation treatments) (Fig. 8D). Root to shoot ratios were highest at lower levels of irrigation and rapidly decreased with irrigation amount (Fig. 8E). There was a small, but significant $[\text{CO}_2]$ effect. Dead leaf and root mass were not significantly different between $[\text{CO}_2]$ treatments (data not shown), but were correlated with irrigation (dead leaf: $y = 2.0x$; $r^2 = 0.9$; roots: $y = -0.01x + 14.5$; $r^2 = 0.5$).

4. Discussion

4.1. Canopy photosynthesis, respiration, and RUE

The increase in maximum net assimilation rate between $[\text{CO}_2]$ treatments (Fig. 5B) is attributable to the higher A_G and lower specific respiration rates at a given irrigation treatment. The increase in canopy A_G with PAR with elevated $[\text{CO}_2]$ was observed for other C3 crops (e.g. Reddy et al., 1989, 1995; Jones et al., 1985). The decrease in A_G -1600 and the duration of maximum assimilation rate with irrigation is largely a response of decreased production of leaf mass (Fig. 8C) and a shorter growing season (Table 1). The shortened growing season due to water stress has been observed previously with potato (Onder et al., 2005; Trebejo and Midmore, 1990; Susnoschi and Shimshi, 1985).

Specific respiration rates of plants grown in enriched $[\text{CO}_2]$ have been reported to decrease (Bunce, 2005; Idso and Kimball,

1993; Wullschleger et al., 1992). One possible reason for the decreased respiration rate per unit mass is a lowered protein content in tissue with elevated $[\text{CO}_2]$ (e.g. Bunce, 2005). In this case, we measured an average 1 and 0.5% increase in leaf and stem N content for ambient versus elevated $[\text{CO}_2]$ plant tissue taken at several points during the growth season (data not shown). In addition, the majority of the additional photosynthate fixed by the elevated $[\text{CO}_2]$ potato plants was partitioned to tubers and roots (Fig. 8D and E). The relatively low respiratory requirements for these organs may also explain the lower specific respiration rates observed in this study (Fig. 4B).

Various researchers have observed that leaves of C3 plants rapidly acclimate to $[\text{CO}_2]$ enrichment, with the result being that initial increases in leaf level net assimilation rate decline to that of ambient $[\text{CO}_2]$ after several days of exposure (Lawson et al., 2001; Sicher and Bunce, 1999). Thus, observed increases in productivity due to increased $[\text{CO}_2]$ would primarily depend on more rapid establishment of leaf area than in ambient $[\text{CO}_2]$. In the present study, differences in the quantity of intercepted PAR throughout the growth season were not detected (Fig. 6, daily patterns not shown). Although leaf area index was not measured in-season, individual leaf expansion rates were slightly higher at ambient $[\text{CO}_2]$ and leaf appearance rates were not significantly different between $[\text{CO}_2]$ treatments (data not shown). Significant differences in leaf dry matter production or senesced leaf were also not observed between $[\text{CO}_2]$ treatments within a given irrigation treatment (Fig. 8C). The specific leaf area of green leaves at harvest ranged between 123 and 232 $\text{cm}^2 \text{g}^{-1}$ dry mass; however, not enough samples were taken to evaluate if statistical differences were present between $[\text{CO}_2]$ treatments. These results indicate that the total leaf area produced per treatment throughout the growth season was similar at each irrigation level. Thus, the dynamics of canopy leaf area expansion and intercepted PAR were not significantly different between $[\text{CO}_2]$ treatments for a given irrigation treatment over the course of the growth season. Similar results were reported by Schapendonk et al. (2000) and Miglietta et al. (1998). The increased productivity with the elevated $[\text{CO}_2]$ treatment must be due to increased rate of assimilation at the elevated $[\text{CO}_2]$, a result which is indicated by the elevated RUE (Fig. 6).

The values for canopy light use efficiency and canopy conductance to $[\text{CO}_2]$ were within reported values for other C3 plants (e.g. Acock et al., 1985; Reddy et al., 1989, 1995). Neither α or τ declined with time (Table 2), indicating photosynthetic acclimation to $[\text{CO}_2]$ was not detected at the canopy level. It has been speculated that photosynthetic acclimation to elevated $[\text{CO}_2]$ may be somewhat reduced by potato due to its capacity to form large storage sinks for carbohydrate (Schapendonk et al., 2000; Miglietta et al., 1998). Some of the largest differences in A_G-1600 between $[\text{CO}_2]$ treatments at a given irrigation level were observed during the middle portion of the growing season. For example, maximum A_G-1600 at week 10 was approximately 72 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ for ambient and 83 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ for elevated $[\text{CO}_2]$ at the 100% irrigation treatment (Fig. 3). Net assimilation rates were also linear during this time for most irrigation treatments (Fig. 5A). This time corresponded

to approximately 2 weeks after mainstem flowering and tuber initiation. These results support this hypothesis that tuber sink strength may play a role in mediating certain aspects of photosynthetic acclimation in potato leaves (Basu et al., 1999).

4.2. Transpiration, water uptake, and WUE

Transpiration rates were lower for plants grown under elevated $[\text{CO}_2]$ at most water stress treatments (Fig. 7). Whole growth season water uptake values were also smaller for elevated $[\text{CO}_2]$ plants (Table 1). As noted above, the dynamics of leaf area production and light interception were similar throughout the growth season at both $[\text{CO}_2]$ treatments at a given level of water stress. Thus, the lower transpiration rates at elevated $[\text{CO}_2]$ were likely the result of reduced stomatal conductance in the canopy as has been reported in other studies of potato under elevated $[\text{CO}_2]$ (Sicher and Bunce, 1999; Wheeler et al., 1999).

Seasonal water uptake (Table 1) was linearly proportional to irrigation for all treatments and fell within the typical range of 400–700 mm cumulative evapotranspiration for field-grown potato (Wright and Stark, 1990), particularly for the well-watered treatments. At both $[\text{CO}_2]$ treatments, WUE increased with decreasing irrigation amount (Fig. 6), consistent with observations from other potato studies (Onder et al., 2005; Trebejo and Midmore, 1990; Vos and Groenwold, 1989). Increased WUE with $[\text{CO}_2]$ enrichment has been reported for other C3 species (Baker and Allen, 1994; Eamus, 1991). Wheeler et al. (1999) observed an increase in WUE when $[\text{CO}_2]$ was increased from 400 to 1000 $\mu\text{mol mol}^{-1}$ for hydroponically grown potato and Ku et al. (1977) measured increased leaf-level WUE; however, few other studies on water use and $[\text{CO}_2]$ interactions have been conducted for potato. When expressed on a tuber fresh weight basis, WUE values ranged from 5 to 14 and 11 to 30 kg yield m^{-3} for ambient and elevated $[\text{CO}_2]$, respectively. Typical values for field grown potato range from 5 to 11.7 kg m^{-3} (Trebejo and Midmore, 1990). Thus, WUE is nearly doubled when expressed on a tuber yield basis for the elevated $[\text{CO}_2]$ treatments.

Although general C3 crop responses to $[\text{CO}_2]$ enrichment include improved WUE, seasonal water use can actually be larger for plants grown at elevated $[\text{CO}_2]$ because of increased leaf area (Baker and Allen, 1994; Eamus, 1991). Wheeler et al. (1999) observed slightly more water use for hydroponically grown potato at elevated $[\text{CO}_2]$. However, only a 50-day growth cycle was used in the analysis. We did not observe this response due to the majority of the increase in biomass at elevated $[\text{CO}_2]$ partitioned to below ground organs.

4.3. Dry matter production

Typical responses of well-watered potato to $[\text{CO}_2]$ enrichment include increased total biomass and yield (Schapendonk et al., 2000; Sicher and Bunce, 1999; Miglietta et al., 1998; Wheeler et al., 1991, 1999). Our results indicate that this increase in productivity between $[\text{CO}_2]$ levels is also maintained at most levels of water stress (Fig. 8A). The increase in biomass was accompanied by a decrease in water uptake and irrigation

requirements as compared to the well-watered control treatment, resulting in larger WUE for the elevated $[\text{CO}_2]$ treatments (Table 1; Fig. 6). The additional biomass produced with elevated $[\text{CO}_2]$ was primarily partitioned to tubers and roots as leaf and stem production were not significantly different between $[\text{CO}_2]$ treatments at a given irrigation level (Fig. 8). Reduced water use and increased productivity indicate that elevated $[\text{CO}_2]$ will result in more efficient potato production given similar environmental conditions for non-droughted and droughted plants.

A similar nonlinear tuber yield response to irrigation was observed for both $[\text{CO}_2]$ treatments (Fig. 8D). A decline in tuber production has been observed with drought in other research (e.g. Walworth and Carling, 2002; Deblonde and Ledent, 2001; Costa et al., 1997; Trebejo and Midmore, 1990). The maximum tuber yield occurred at irrigation amounts between the 50 and 75% irrigation treatments at elevated $[\text{CO}_2]$ and the 75 and 90% treatments at ambient $[\text{CO}_2]$. Harvest indices were highest at the 10 or 25% irrigation treatments; however, as irrigation increased, more biomass is partitioned to leaves and stems (Fig. 8C), resulting in a drop in harvest index to below 0.3 for both $[\text{CO}_2]$ treatments. This decrease in harvest index with increased irrigation has been reported by Onder et al. (2005) and Susnoschi and Shimshi (1985).

One reason for the curvilinear response is likely due to increased respiratory demand by the higher biomass of the well-irrigated treatments (Fig. 8A) resulting in less carbon available for tuber growth.

Kennebec is classified as a cultivar with a high degree of drought resistance (Vos and Groenwold, 1988). Thus, extrapolation of the measured effects of $[\text{CO}_2]$ and water stress on its productivity and canopy gas exchange responses to other potato cultivars should be conservative. Care must also be taken when extrapolating these results directly from a controlled environment study to field production. Nonetheless, the relative responses observed in the study are applicable for crop modeling and evaluating climate change scenarios. The general responses described in this paper indicate $[\text{CO}_2]$ enrichment increased WUE and partitioning to tubers in response to season long water stress as compared with ambient $[\text{CO}_2]$ production. This increase in tuber sink in the elevated $[\text{CO}_2]$ plants may help play a role in drought induced substrate feedback inhibition of photosynthesis (Basu et al., 1999) by serving as a large sink for photosynthate (Farrar and Williams, 1991). Overall, the results indicate that increases in potato gas exchange, dry matter production and yield with elevated $[\text{CO}_2]$ are consistent at various levels of water stress as compared with ambient $[\text{CO}_2]$. These data and findings can be used to support studies and decision support tools for evaluating potato production under various climate change scenarios.

5. Conclusions

Potato photosynthesis and dry matter production exhibited a positive response to $[\text{CO}_2]$ enrichment at various levels of water stress as compared with production under ambient $[\text{CO}_2]$ when studied under controlled environment conditions. Total biomass, yield, and water use efficiency (WUE)

increased under elevated $[\text{CO}_2]$, with the largest percent increases occurring at irrigation levels that induced the most water stress. WUE was nearly doubled under enriched $[\text{CO}_2]$ when expressed on a tuber fresh weight basis. In contrast with ambient $[\text{CO}_2]$ conditions, elevated $[\text{CO}_2]$ plants maintained a higher daily net assimilation rate throughout most of the growing season. At moderate and more severe levels of water stress, $[\text{CO}_2]$ enrichment appeared to encourage shifting of assimilate into tubers as opposed to additional vegetative growth. As a result, harvest indices were higher with elevated $[\text{CO}_2]$. Care must be taken when extrapolating these results directly from a controlled environment study to field production. Nonetheless, these results indicate that the enhancements to potato productivity under enriched $[\text{CO}_2]$ are consistent at various levels of water stress.

REFERENCES

- Acock, B., Reddy, V.R., Hodges, H.F., Baker, D.N., McKinion, J.M., 1985. Photosynthetic response of soybean canopies in full-season carbon dioxide enrichment. *Agron. J.* 77, 942–974.
- Acock, B., Hand, D.W., Thornley, J.D.H., Wilson, W.J., 1976. Photosynthesis in stands of green peppers. An application of empirical and mechanistic models to controlled-environment data. *Ann. Bot.* 40, 1293–1307.
- Baker, J.T., Kim, S.-H., Gitz, D.C., Timlin, D., Reddy, V.R., 2004. A method for estimating carbon dioxide leakage rates in controlled-environment chambers using nitrous oxide. *Environ. Exp. Bot.* 51, 103–110.
- Baker, J.T., Allen Jr., L.H., 1994. Assessment of the impact of rising carbon dioxide and other potential climate changes on vegetation. *Environ. Pollut.* 83, 223–235.
- Basu, P.S., Sharma, A., Garg, I.D., Sukumaran, N.P., 1999. Tuber sink modifies photosynthetic response in potato under water stress. *Environ. Exp. Bot.* 42, 25–39.
- Bélanger, G., Walsh, J.R., Richards, J.E., Milburn, P.H., Ziadi, N., 2001. Tuber growth and biomass partitioning of two potato cultivars grown under different N fertilization rates with and without irrigation. *Am. J. Potato Res.* 78, 109–117.
- Bunce, J., 2005. Response of respiration of soybean leaves grown at ambient and elevated carbon dioxide concentrations to day-to-day variation in light and temperature under field conditions. *Ann. Bot.* 95, 1059–1066.
- Costa, L.D., Vedove Delle, G., Gianquinto, G., Giovanardi, R., Peressotti, A., 1997. Yield, water use efficiency and nitrogen uptake in potato: influence of drought stress. *Potato Res.* 40, 19–34.
- Deblonde, P.M.K., Ledent, J.F., 2001. Effects of moderate drought conditions on green leaf number, stem height, leaf length and tuber yield of potato cultivars. *Eur. J. Agron.* 14, 31–41.
- Dutton, R.G., Jiao, J., Tsujita, M.J., Grodzinski, B., 1988. Whole plant CO_2 exchange measurements for nondestructive estimation of growth. *Plant Physiol.* 86, 355–358.
- Eamus, D., 1991. The interaction of rising CO_2 and temperatures with water use efficiency. *Plant Cell Environ.* 14, 843–852.
- Farrar, J.F., Williams, M.L., 1991. The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. *Plant Cell Environ.* 14, 819–830.
- Fleisher, D.H., Timlin, D.J., Reddy, V.R., 2008. Interactive effects of CO_2 and water stress on potato canopy growth and development. *Agron. J.* 100, 711–719.

- Goudriaan, J., de Ruiter, H.E., 1983. Plant growth in response to CO₂ enrichment, at two levels of nitrogen and phosphorous supply. I. Dry matter, leaf area and development. *Neth. J. Agric. Sci.* 31, 157–169.
- Gregory, P.J., Simmonds, L.P., 1992. Water relations and growth of potatoes. In: Harris, P. (Ed.), *The Potato Crop*. Chapman & Hall, London, pp. 214–246.
- Idso, S.B., Kimball, B.A., 1993. Effects of atmospheric CO₂ enhancement on net photosynthesis and dark respiration rates of three Australian tree species. *J. Plant Phys.* 141, 166–171.
- Jefferies, R.A., 1995. Physiology of crop response to drought. In: Haverkort, A.J., MacKerron, D.K.L. (Eds.), *Potato Ecology and Modeling of Crops Under Conditions Limiting Growth*. Kluwer Academic Publishers, The Netherlands, pp. 61–74.
- Jefferies, R.A., 1993. Responses of potato genotypes to drought. I. Expansion of individual leaves and osmotic adjustment. *Ann. Appl. Biol.* 122, 93–104.
- Jefferies, R.A., Mackerron, D.K.L., 1993. Responses of potato genotypes to drought. II. Leaf area index, growth and yield. *Ann. Appl. Biol.* 122, 105–112.
- Jefferies, R.A., Mackerron, D.K.L., 1987. Aspects of the physiological basis of cultivar differences in yield of potato under droughted and irrigated conditions. *Potato Res.* 30, 201–217.
- Jones, P., Jones, J.W., Allen Jr., L.H., 1985. Seasonal carbon and water balances of soybeans grown under stress treatments in sunlit chambers. *Trans. ASAE* 28, 2021–2028.
- Ku, S.-B., Edwards, G.E., Tanner, C.B., 1977. Effects of light, carbon dioxide, and temperature on photosynthesis, oxygen inhibition of photosynthesis, and transpiration in *Solanum tuberosum*. *Plant Physiol.* 59, 868–872.
- Lawson, T., Craigan, J., Tulloch, A.-M., Black, C.R., Colls, J.J., Landon, G., 2001. Photosynthetic responses to elevated CO₂ and O₃ in field-grown potato (*Solanum tuberosum*). *J. Plant Phys.* 158, 309–323.
- Long, S.P., Osborne, C.P., Humphries, S., 1996. Photosynthesis, rising atmospheric carbon dioxide concentration and climate change. In: Breymeyer, A.L., Hall, D.O., Melillo, J.M., Agren, G.L. (Eds.), *Global Change: Effects on Coniferous Forest and Grasslands*. John Wiley and Sons Ltd., New York, pp. 121–159.
- Miglietta, F., Magliago, B., Bindi, M., Cerio, L., Vacari, F.P., Loduca, V., Peresotti, A., 1998. Free air CO₂ enrichment of potato (*Solanum tuberosum* L.): development, growth and yield. *Global Change Biol.* 4, 163–172.
- Monje, O., 1993. Effects of elevated CO₂ on crop growth rates, radiation absorption, canopy quantum yield, canopy carbon use efficiency, and root respiration of wheat. M.S. Thesis. Utah State University, USA, Logan, Utah.
- Onder, S., Caliskan, M.E., Onder, D., Caliskan, S., 2005. Different irrigation methods and water stress effects on potato yield and yield components. *Agric. Water Manage.* 73, 73–86.
- Pickering, N.B., Allen, Jr., L.H., Albrecht, S.L., Jones, P., Jones, J.W., Baker, J.T., 1994. Environmental plant chambers: control and measurement using CR-10 data loggers. In: Watson, D.G., Zazueta, F.S., Harrison, T.V. (Eds.), *Proceedings of the Fifth International Conference on Computers in Agriculture*. Orlando, Florida, February 5–9, pp. 29–35, American Society of Agricultural Engineers, St. Joseph, Michigan.
- Reddy, K.R., Baker, J.T., Reddy, V.R., McKinion, J., Tarpley, L., Read, J.J., 2001. Soil–plant–atmosphere–research (SPAR) facility: a tool for plant research and modeling. *Biotronics* 30, 27–50.
- Reddy, V.R., Reddy, K.R., Hodges, H.F., 1995. Carbon dioxide enrichment and temperature effects on cotton canopy photosynthesis, transpiration, and water-use efficiency. *Field Crops Res.* 41, 13–23.
- Reddy, V.R., Acock, B., Acock, M.C., 1989. Seasonal carbon and nitrogen accumulation in relation to net carbon dioxide exchange in a carbon dioxide-enriched soybean canopy. *Agron. J.* 81, 78–83.
- Robinson, J.M., 1984. Photosynthetic carbon metabolism in leaves and isolated chloroplasts from spinach plants grown under short and intermediate photosynthetic periods. *Plant Physiol.* 75, 397–409.
- Schapendonk, H.C.M., van Oijen, M., Dijkstra, P., Pot, C.S., Jordi, W.J.R.M., Stoopen, G.M., 2000. Effects of elevated CO₂ concentration on photosynthetic acclimation and productivity of two potato cultivars grown in open-top chambers. *Austral. J. Plant Phys.* 27, 1119–1130.
- Sicher, R.C., Bunce, J.A., 1999. Photosynthetic enhancement and conductance to water vapor of field-grown *Solanum tuberosum* (L.) in response to CO₂ enrichment. *Photosynth. Res.* 62, 155–163.
- Stitt, M., Krapp, A., 1999. The interaction between elevated carbon dioxide and nitrogen nutrition: the physiological and molecular background. *Plant Cell Environ.* 22, 583–621.
- Susnoschi, M., Shimshi, D., 1985. Growth and yield studies of potato development in a semi-arid region. 2. Effect of water stress and amounts of nitrogen top dressing on growth of several cultivars. *Potato Res.* 28, 161–176.
- Thornley, J.H.M., Johnson, I.R., 1990. *Plant and Crop Modeling: A Mathematical Approach to Plant and Crop Physiology*. Clarendon Press, Oxford, pp. 78–82.
- Timlin, D.J., Fleisher, D.H., Kim, S.-H., Reddy, V.R., Baker, J., 2007. Evapotranspiration measurement in controlled environment chambers: a comparison between time domain reflectometry and accumulation of condensate from cooling coils. *Agron. J.* 99, 166–173.
- Tingey, D.T., McVeety, B.D., Waschmann, R.S., Johnson, R.M., Phillips, D.L., Rygielwicz, R.T., Olszyk, D.M., 1996. A versatile sun-lit controlled-environment facility for studying plant and soil processes. *J. Environ. Qual.* 25, 614–625.
- Tourneux, C., Devaux, A., Camacho, M.R., Mamani, P., Ledent, J.-F., 2003. Effect of water shortage on six potato genotypes in the highlands of Bolivia (II): water relations, physiological parameters. *Agronomie* 23, 181–190.
- Trebejo, I., Midmore, D.J., 1990. Effect of water stress on potato growth, yield and water use in a hot and a cool tropical climate. *J. Agric. Sci.* 114, 321–334.
- van Iersel, M.W., Kang, J.G., 2002. Nutrient solution concentration affects whole-plant CO₂ exchange and growth of subirrigated pansy. *J. Am. Soc. Hortic. Sci.* 127, 423–429.
- van Loon, C.D., 1981. The effect of water stress on potato growth, development, and yield. *Am. Potato J.* 58, 51–69.
- Vos, J., Groenwold, J., 1989. Characteristics of photosynthesis and conductance of potato canopies and the effects of cultivar and transient drought. *Field Crops Res.* 20, 237–250.
- Vos, J., Groenwold, J., 1988. Water relations of potato leaves. I. Diurnal changes, gradients in the canopy, and effects of leaf-insertion number, cultivar and drought. *Ann. Bot.* 62, 363–371.
- Walworth, J.L., Carling, D.E., 2002. Tuber initiation and development in irrigated and non-irrigated potatoes. *Am. J. Potato Res.* 79, 387–395.
- Wheeler, R.M., Mackowiak, C.L., Yorio, N.C., Sager, J.C., 1999. Effects of CO₂ on stomatal conductance: do stomata open at very high CO₂ concentrations? *Ann. Bot.* 83, 243–251.
- Wheeler, R.M., Mackowiak, C.L., Stutte, G.W., Sager, J.C., Yorio, N.C., Ruffe, L.M., Fortson, R.E., Dreschel, T.W., Knott, W.M., Corey, K.A., 1996. NASA's biomass production chamber: a testbed for bioregenerative life support studies. *Adv. Space Res.* 18, 215–224.

Wheeler, R.M., Tibbitts, T.W., Fitzpatrick, A.H., 1991. Carbon dioxide effects on potato growth under different photoperiods and irradiance. *Crop Sci.* 31, 1209–1213.

Wright, J.L., Stark, J.C., 1990. In: Stewart, A., Nielsen, D.R. (Eds.), *Potato*. In *Irrigation of Agricultural Crops*. Agronomy

Monograph no. 30. ASA-CSSA-SSSA, Madison, WI, USA, pp. 859–888.

Wullschleger, S.D., Norby, R.J., Gunderson, C.A., 1992. Growth and maintenance respiration in leaves of *Liriodendron tulipifera* L. exposed to long-term carbon dioxide enrichment in the field. *New Phytol.* 121, 515–523.