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# Effect of elevated atmospheric CO<sub>2</sub> on growth, photosynthesis and water relations of salt marsh grass species

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## ABSTRACT

Rozema, J., Dorel, F., Janissen, R., Lenssen, G., Broekman, R., Arp, W. and Drake, B.G., 1991. Effect of elevated atmospheric CO<sub>2</sub> on growth, photosynthesis and water relations of salt marsh grass species. *Aquat. Bot.*, 39: 45–55.

The C<sub>3</sub> grass species *Scirpus maritimus* L. and *Puccinellia maritima* (Huds.) Parl., and the C<sub>4</sub> grass species *Spartina anglica* C.E. Hubbard and *Spartina patens* (Ait.) Muhl. were grown at ambient (340 p.p.m. CO<sub>2</sub>) and elevated (580 p.p.m. CO<sub>2</sub>) atmospheric CO<sub>2</sub> concentration, at low (10 mM NaCl) and high salinity (250 mM NaCl) under aerated and anaerobic conditions in the culture solution. The relative growth rate of both the C<sub>3</sub> grass species was enhanced with atmospheric CO<sub>2</sub> enrichment, no such increase was found in the C<sub>4</sub> grass species. High salinity reduced growth of the C<sub>3</sub> species tested, but this relative growth reduction was not prevented by elevated CO<sub>2</sub> concentration. The growth increase at elevated CO<sub>2</sub> of *Scirpus maritimus* and *Puccinellia maritima* is greater under aerated than under anaerobic solution conditions. Water-use efficiency of all species was increased by elevated CO<sub>2</sub>. In the case of *Scirpus* (C<sub>3</sub>), this increase was caused by increased net photosynthesis, for *Spartina patens* (C<sub>4</sub>) photosynthesis was not increased, but transpiration was reduced. The water potential of the shoot was less negative under conditions of CO<sub>2</sub> enrichment, in particular at increased salinity (250 mM NaCl).

## INTRODUCTION

Atmospheric CO<sub>2</sub> is expected to double its present value of ~340 p.p.m. within the next century. In experiments with elevated CO<sub>2</sub>, most C<sub>3</sub> plants demonstrate an increase in relative growth rate and a stimulation of the rate of photosynthesis, in contrast to C<sub>4</sub> plant species which show much less if any stimulation of any of these processes (Carter and Peterson, 1983; Gates et al., 1983; Kimball, 1985; Oechel and Strain, 1985; Reynolds and Acock, 1985).

Most studies on the effect of atmospheric CO<sub>2</sub> enrichment have used crop plants because of agricultural interest or horticultural species. Recently, it has

become clear that the effects of elevated  $\text{CO}_2$  are modified by environmental factors that limit plant growth and crop production. For example, growth is enhanced by increased atmospheric  $\text{CO}_2$  when the temperature is above  $\sim 20^\circ\text{C}$  (Idso et al., 1987) and it has been suggested that this temperature interaction may be due to a further interaction with phosphate metabolism (Goudriaan and de Ruiter, 1983; Sage and Sharkey, 1987).

In the salt-marsh environment, growth of halophytes is limited by direct and secondary effects of the flooding of the vegetation and soil with seawater (van Diggelen, 1988). Plant species respond to gradients of soil salinity and redox status of the soil. In the root system of several salt-marsh halophytes, an aerenchyma system is present or induced by flooding conditions, possibly allowing the exchange of  $\text{CO}_2$  and  $\text{O}_2$  between root and shoot (cf. Keeley et al., 1984). The Dutch group (Free University, Amsterdam) and the U.S. group (Smithsonian Environmental Research Center, Edgewater) have a cooperative research programme with field experiments in a Chesapeake Bay salt marsh (Curtis et al., 1989) and growth chamber and greenhouse experimental work in Amsterdam (Rozema et al., 1990a,b).

It is the aim of the present paper: (a) to assess the effect of elevated atmospheric  $\text{CO}_2$  on the growth, photosynthesis and water relations of *Scirpus maritimus* L. ( $\text{C}_3$ ), *Puccinellia maritima* (Huds.) Parl. ( $\text{C}_3$ ), *Spartina anglica* C.E. Hubbard\* ( $\text{C}_4$ ) and *Spartina patens* (Ait.) Muhl. ( $\text{C}_4$ ) and to compare the responses; (b) to measure the effect of increased salinity and anaerobic conditions on growth, water relations and photosynthesis, and the interaction of these treatments with  $\text{CO}_2$  enrichment.

## MATERIALS AND METHODS

Plants of *Spartina anglica*, *Puccinellia maritima* and *Scirpus maritimus* were grown from tillers collected in March 1986 in the salt marsh of Den Oever (North Holland, The Netherlands). Plants were grown for 3 weeks in the greenhouse in commercial Calceolaria garden soil and with a 12-h photoperiod ( $20^\circ\text{C}$ , 70% relative humidity (RH),  $300 \mu\text{mol m}^{-2} \text{s}^{-1}$  photosynthetically active radiation (PAR) (400–700 nm), from 400-W HPI/T lamps, measured with a Licor-Quantum sensor Li-185B) and a 12-h dark period,  $15^\circ\text{C}$ .

*Spartina patens* was grown from tillers originating from a Chesapeake Bay salt marsh near Edgewater (MD, U.S.A.; collected in autumn 1986) under the same conditions as above.

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\*Nomenclature follows Heukels and van der Meyden (1983).

*Growth chambers and cultivation of plants (580 p.p.m. CO<sub>2</sub>)*

Elevated CO<sub>2</sub> concentration in growth chambers was controlled by mixing CO<sub>2</sub> from an AGA-gas cylinder (200 atmospheres, AGA, Amsterdam) with ambient air (340 p.p.m. CO<sub>2</sub>) using mass flow controllers (5851 series for air flow and 5850 TR series for CO<sub>2</sub> mixing, Brooks Instruments). Growth chambers, made from stainless steel, were coated white and illuminated with 400-W Philips HPI/T lamps with 315  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (PAR) at the plant level, 60% RH and 21 °C during the 12-h light period and 15 °C in the dark period. The flow rate of the air stream was 100 l min<sup>-1</sup>. Plants in the CO<sub>2</sub> growth chambers (0.45 m<sup>3</sup>) were cultivated in 0.5-l pots with half-strength Hoagland's solution at pH 6.0 (three plants per pot, nutrient solution renewed every week). The final salinity of 250 mM NaCl was reached by a weekly increase of 40 mM NaCl of the salt level of the nutrient solution. The control solution contained 10 mM NaCl. Hydrocultures were flushed with oxygen (aerated) or nitrogen (anaerobic) supplied from gas cylinders. Nine replications per plant species (three pots) were used in the growth chambers. The growth period was 6 weeks. The mean relative growth rate (RGR) was calculated on the basis of plant dry weight at the end and start of the growth experiment according to Hunt (1978). The leaf elongation rate of *Scirpus maritimus* was measured using a Duncan 2201 servo rotation potentiometer in a set up described by Rozema et al. (1987) and expressed as micrometers.

*Photosynthesis and transpiration measurements*

Photosynthesis and transpiration were measured with a climatized (20 °C, 70% RH) Infra Red Gas Absorption system, as described by Lange and Redon (1983) from Walz, Effeltrich, F.R.G., with a BINOS CO<sub>2</sub> analyzer (Leybold Heraeus, Hanau, F.R.G.). With this system, transpiration was continuously monitored as the increase in the humidity of the air stream passing the plant leaf, recorded as the change in the condensation temperature of a gold mirror. Photosynthetic photon flux (PPF) at the leaf surface within the gas exchange chamber was 1400  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (2000 W HPI/T lamp). Measurement of the photosynthetic rate of plant leaves using this equipment implied removal of plants from the CO<sub>2</sub> growth chambers.

In addition, photosynthesis and transpiration were measured on plant leaves in the CO<sub>2</sub> growth chambers using a portable ADC/LCA instrument (Analytical Development Co., Hoddesdon, Herts., U.K.), equipped with an Epson datalogger and Epson HX20 microprocessor. The flow rate through the ADC assimilation unit was 325 ml min<sup>-1</sup>.

Photosynthesis, transpiration and related measurements with the ADC equipment were conducted within the growth chambers at 315  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at 340 p.p.m. (ambient) or 580 p.p.m. (elevated) CO<sub>2</sub>.

Plants grown in the controlled-environment chambers (340 p.p.m. CO<sub>2</sub> ambient and 580 p.p.m. CO<sub>2</sub> elevated) were harvested after 6 weeks of growth. At harvest, the total water potential of the shoot was estimated by day using a Scholander Pressure bomb and leaf area was measured with a Licor-3000 leaf area meter. The fresh weight of root and shoot tissue was determined at harvest and dry weight after drying for 48 h at 80°C in an oven. Statistical analysis was carried out according to procedures described by Sokal and Rohlf (1969).

## RESULTS

Elevated CO<sub>2</sub> enhanced growth of the C<sub>3</sub> species *Scirpus maritimus* and *Puccinellia maritima*, but not of the C<sub>4</sub> species *Spartina patens*. The relative growth rate of *Spartina patens* was very low compared with the other species, even under control conditions. Growth of *Spartina anglica* was poor and only at low salinity (10 mM) did growth occur (RGR 10.9 mg g<sup>-1</sup> day<sup>-1</sup>). At 250 mM NaCl, no growth occurred and leaves started to die off. Therefore, data for *Spartina anglica* are not presented in Table 1.

Apparently, the C<sub>3</sub> grass species *Puccinellia maritima* is relatively sensitive to 250 mM NaCl. The relative increase in the RGR, expressed as the percentage RGR increase when values for elevated and ambient CO<sub>2</sub> conditions are compared, were higher for *Puccinellia* than for *Scirpus* (Table 2). Elevated CO<sub>2</sub> had less effect on growth rate under anaerobic than aerobic conditions in *Scirpus* and *Puccinellia*.

TABLE 1

Relative growth rate (mg g<sup>-1</sup> day<sup>-1</sup>) on a dry weight basis of C<sub>3</sub> and C<sub>4</sub> salt-marsh species grown in culture solution for 6 weeks with variation of CO<sub>2</sub>, salinity and aeration. Values are the average of four replicates. LSD calculated at  $\alpha=0.05$

CO <sub>2</sub> (p.p.m.)	Salinity (mM NaCl)	Aeration	<i>Scirpus maritimus</i>	<i>Puccinellia maritima</i>	<i>Spartina patens</i>
Ambient	10	Aerated	42.0	27.1	2.3
		Anaerobic	47.2	36.8	8.2
	250	Aerated	34.8	4.1	9.3
		Anaerobic	34.9	8.2	8.7
Elevated	10	Aerated	56.1	46.3	3.6
		Anaerobic	54.5	35.0	2.8
	250	Aerated	49.2	8.0	4.9
		Anaerobic	40.0	11.9	2.1
LSD ( $\alpha=0.05$ )			5.0	3.9	3.2

TABLE 2

Percentage increase in the relative growth rate when values of elevated CO<sub>2</sub> and ambient CO<sub>2</sub> conditions are compared

Salinity (mM NaCl)	Aeration	<i>Scirpus maritimus</i>	<i>Puccinellia maritima</i>	<i>Spartina patens</i>
10	Aerated	33.6	70.8	56.5
	Anaerobic	15.5	-4.9	-76.9
250	Aerated	43.9	95.1	-48.3
	Anaerobic	14.6	45.1	-75.9

TABLE 3

Percentage decrease in the relative growth rate when values from 250 and 10 mM NaCl are compared

CO <sub>2</sub> (p.p.m.)	Aeration	<i>Scirpus maritimus</i>	<i>Puccinellia maritima</i>
340	Aerated	17.2	84.9
	Anaerobic	26.1	77.8
580	Aerated	12.3	82.8
	Anaerobic	26.3	66.0

TABLE 4

Photosynthetic rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), transpiration rate ( $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) and water-use efficiency of *Scirpus maritimus*, *Puccinellia maritima* and *Spartina anglica* under elevated and ambient CO<sub>2</sub> conditions with  $1400 \mu\text{mol m}^{-2} \text{ s}^{-1}$  PAR, 20°C and 70% RH. Values are the average of three replications with the standard deviation

CO <sub>2</sub> (p.p.m.)	Salinity (mM NaCl)		<i>Scirpus maritimus</i>	<i>Puccinellia maritima</i>	<i>Spartina anglica</i>
340	10	Photosynthesis	7.1±2.3	20.0±3.1	8.0±1.5
		Transpiration	2.4±1.0	2.7±1.2	1.8±1.0
		Water-use efficiency	2.9±1.3	7.4±1.8	5.3±0.2
580	10	Photosynthesis	10.2±2.8	25.7±1.8	10.1±3.9
		Transpiration	2.0±0.8	3.2±1.7	1.2±0.5
		Water-use efficiency	5.1±2.1	8.0±2.5	8.3±2.1

Salinity and CO<sub>2</sub> enrichment have marked effects on the growth rate of two C<sub>3</sub> salt-marsh grass species, in contrast with the C<sub>4</sub> species (Table 3). Elevated CO<sub>2</sub> increased photosynthesis in *Scirpus maritimus* and *Puccinellia maritima*, but not in *Spartina patens* (Tables 4 and 5). Water-use efficiency

TABLE 5

Photosynthesis, transpiration and water-use efficiency of *Spartina patens* cultivated under various conditions of CO<sub>2</sub>, salinity and aeration, with 315  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PAR, 21°C, and 60% RH. Values are the average of four replications and the standard deviation

CO <sub>2</sub> (p.p.m.)	Salinity (mM NaCl)		Photosynthesis ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	Transpiration ( $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ )	Water-use efficiency
340	10	Aerated	2.06 ± 0.82	2.82 ± 1.88	0.73
		Anaerobic	4.54 ± 3.73	5.94 ± 0.12	0.76
340	250	Aerated	6.49 ± 5.89	3.93 ± 1.44	1.65
		Anaerobic	3.19 ± 5.20	5.21 ± 0.05	0.61
580	10	Aerated	3.27 ± 1.93	1.16 ± 0.06	2.81
		Anaerobic	4.71 ± 2.98	2.28 ± 0.93	2.06
580	250	Aerated	6.86 ± 2.67	3.24 ± 1.37	2.12
		Anaerobic	2.19 ± 2.10	0.90 ± 0.23	2.43
LSD	( $\alpha=0.05$ )		3.5	2.8	

TABLE 6

Water potential of the shoot of three salt-marsh grass species (MPa). Values are the average of three replications

CO <sub>2</sub> (p.p.m.)	Salinity (mM NaCl)	Aeration	<i>Scirpus maritimus</i>	<i>Puccinellia maritima</i>	<i>Spartina patens</i>
340	10	Aerated	-1.83	-1.90	-2.03
		Anaerobic	-1.75	-1.93	-2.38
340	250	Aerated	-4.00	-3.31	-2.98
		Anaerobic	-3.04	-3.50	-2.10
580	10	Aerated	-1.80	-2.38	-1.90
		Anaerobic	-2.01	-2.24	-1.67
580	250	Aerated	-2.81	-2.53	-2.72
		Anaerobic	-2.93	-2.61	-2.26
LSD	( $\alpha=0.05$ )		0.29	0.31	0.23

increased in *Spartina patens*, mainly as a result of reduced transpiration, while in *Scirpus maritimus* increased photosynthetic rate may be the cause of increased water-use efficiency. Salinity and aeration did not seem to influence the photosynthesis and transpiration of *Spartina patens* leaves.

The water potential of the shoot, as estimated using the Scholander bomb technique, becomes more negative under saline conditions (Table 6). Aeration is of no apparent importance in this respect. The lowering of the water potential due to salinity is partially compensated for under CO<sub>2</sub>-enriched

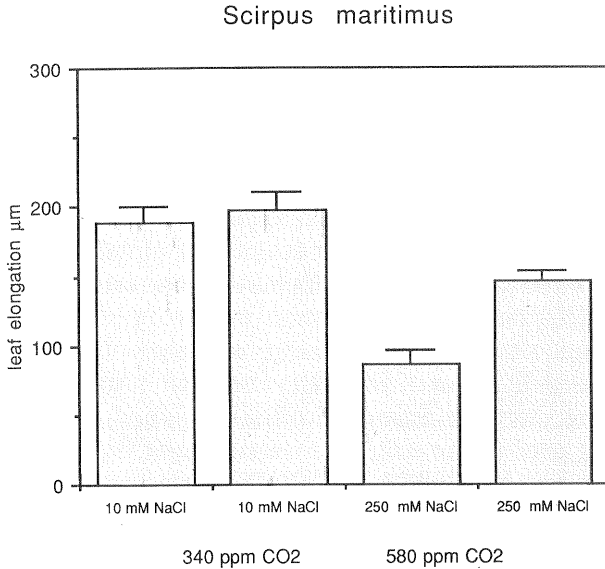


Fig. 1. Leaf elongation ( $\mu\text{m}$ ) of *Scirpus maritimus* under ambient and elevated CO<sub>2</sub> conditions at low (10 mM NaCl) and increased (250 mM NaCl) salinity. Average values of the leaf elongation measured daily over a two week period, with SD.

conditions (*Scirpus maritimus* and *Puccinellia maritima*). Shoot length growth of *Scirpus maritimus* (Fig. 1) in response to increased salinity and CO<sub>2</sub> enrichment correlates to the response of RGR to these factors and may relate to the variation of the shoot water potential ( $\psi_T$ ). There is a strong reduction of leaf length growth under saline ambient conditions, but this is restored to some extent by CO<sub>2</sub> enrichment.

## DISCUSSION

Salinity and flooding are major environmental factors in the salt-marsh environment that govern growth and competitive relationships of salt marsh species (Scholten et al., 1987; van Diggelen, 1988). It can, therefore, be expected that increased atmospheric CO<sub>2</sub> will not simply stimulate the growth of salt-marsh plants, as has been found for crop plants under optimum conditions of nutrient and water supply.

The results of the present paper demonstrate a growth increase of the C<sub>3</sub> salt-marsh plants *Scirpus maritimus* and *Puccinellia maritima*, as has been commonly found for other species (Carlson and Bazzaz, 1982; Carter and Peterson, 1983; Enoch and Kimball, 1985). The relative increase in growth due to increased CO<sub>2</sub> is even greater under saline (250 mM NaCl) than under non-saline (10 mM NaCl) conditions. This means that the growth depression



caused by increased salinity is in part alleviated under conditions of increased CO<sub>2</sub> for *Scirpus* and *Puccinellia*. This is in agreement with the findings of Schwarz and Gale (1984) who found an increase in salt tolerance with increased CO<sub>2</sub> (2500 µl l<sup>-1</sup>) in the C<sub>3</sub> species *Phaseolus vulgaris* L. and *Xanthium strumarium* L., and the C<sub>4</sub> species *Zea mays* L. and *Atriplex halimus* L. These results lead to the prediction for the field situation that there will be a shift in the competitive balance between C<sub>3</sub> and C<sub>4</sub> species towards expansion of C<sub>3</sub> species and an expansion of the distribution area of salt-marsh vegetation as a whole, since the salt tolerance of the C<sub>3</sub> halophytes tested tends to increase with atmospheric CO<sub>2</sub> enrichment.

Anaerobic conditions did not markedly affect the growth rate of *Scirpus* and *Puccinellia*. Under elevated CO<sub>2</sub> conditions, the increase in growth is somewhat greater than under aerated conditions. For the salt-marsh species, interactions between the CO<sub>2</sub> pool in the soil, root respiratory CO<sub>2</sub> and atmospheric CO<sub>2</sub>, such as described by Madsen (1987) for the aquatic CAM macrophyte *Littorella uniflora* (L.) Aschers. and *Isoetes lacustris* L., may influence the plant response to elevated atmospheric CO<sub>2</sub>. There is a well-developed aerenchyma system in *Scirpus maritimus* allowing CO<sub>2</sub> transport from root to shoot, as found by Brix (1988) in *Phragmites australis* (Cav.) Trin. ex Steud. The hypothesis of uptake of CO<sub>2</sub> via the roots and transport via the aerenchyma to the leaves to be used for photosynthesis is now studied with salt-marsh plants cultivated in flooded organic soil rather than in nutrient solution.

Increased growth under elevated CO<sub>2</sub> conditions in the C<sub>3</sub> species may be related to increased photosynthesis or to improved water relations. For the two C<sub>3</sub> species studied at low salinity, there was an increase in the water-use efficiency, mainly based on an increased photosynthetic rate. For both the C<sub>4</sub> species of *Spartina* tested, the transpiration rate was depressed at elevated CO<sub>2</sub> resulting in a higher water-use efficiency. Reduced transpiration under elevated CO<sub>2</sub>, as a result of partial stomatal closure, has been reported by Wong (1979). The total water potential of the C<sub>3</sub> and C<sub>4</sub> plants measured decreased at increased salinity. Under elevated CO<sub>2</sub> conditions, significantly less negative values were found at increased salinity (250 mM NaCl). Probably, the CO<sub>2</sub> effect on the water potential will improve the turgor pressure potential, as reported by Sionit and Patterson (1985). In accordance with the higher values of the water potential, leaf elongation rate was found to be increased for *Scirpus maritimus*.

In a Chesapeake Bay estuarine salt marsh, Curtis et al. (1989) found increased densities and delayed senescence in the C<sub>3</sub> species *Scirpus olneyi* Gray, and no such an effect in the C<sub>4</sub> grasses *Spartina patens* and *Distichlis spicata* (L.) Greene. In similar studies, Carter and Peterson (1983) have provided evidence that global CO<sub>2</sub> enrichment may alter the competitive balance between C<sub>3</sub> and C<sub>4</sub> plants in favor of C<sub>3</sub> plants. On the other hand, the rise in

temperature caused by increased atmospheric CO<sub>2</sub> may help to extend the distribution of C<sub>4</sub> species to regions with a previously cooler climate. Idso et al. (1987) have indicated that there is a strong interaction between air temperature and the effects of atmospheric CO<sub>2</sub> enrichment. At temperatures > 18.5°C, mean air temperature enhances the CO<sub>2</sub> enrichment effect, but at < 18.5°C the interaction effect is negative and plant growth will be reduced. Perhaps the air temperature in the growth chamber used in our experiments (21°C day/15°C night) may have been too low for the C<sub>4</sub> species *Spartina patens* and *Spartina anglica*. On the other hand, Dunn et al. (1987) reported successful growth of *Spartina anglica* in Europe, such as in NW regions of England, where the mean temperature of the warmest month only reaches 16°C. Air temperatures in the summer period at the Chesapeake Bay salt marsh are 30–35°C. Because of a relatively high temperature optimum of photosynthesis, growth of C<sub>4</sub> plants is usually favored at increased temperature compared with C<sub>3</sub> plants (Ehleringer and Björkman, 1977; Farquhar and Sharkey, 1982). At the moment, new experiments are being prepared with the C<sub>3</sub> and C<sub>4</sub> salt-marsh grasses to test their response to CO<sub>2</sub> enrichment at a higher temperature. In further research, the interaction of CO<sub>2</sub> enrichment with increased ultraviolet-B radiation as a result of ozone depletion is also being studied (Rozema et al., 1990c).

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