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Effects of Elevated Atmospheric CO_2 on Wetland Plants: A Review

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Last 20 years have witnessed many studies dealing with effects of elevated CO_2 on terrestrial ecosystems. However, fewer efforts have been made to elucidate effects on wetland ecosystems, although they play a key role in global biogeochemical cycles. This review synthesizes published data to reveal effects of elevated CO_2 on wetland plants. In particular, we focused on the changes in primary production, community structures, evapotranspiration, and nutrients in plants. Many studies have reported increases in primary production in individual plants, but we could not conclude that this will lead to increases in carbon sequestration in wetland ecosystems. The reasons include transport of photosynthates into belowground parts, species-specific responses, interaction among different species, and limitation of other nutrients. However, elevated CO_2 increased transpiration rates in many wetland plants, suggesting substantial influences on water budgets of wetlands. In addition, similar to terrestrial ecosystems, elevated CO_2 increased C/N ratio of many plants, which may impede organic matter decomposition in the long term. However, further information on dynamics of belowground carbon supplied from wetland plants is warranted to assess effects of elevated CO_2 on wetland carbon cycle accurately.

Key words : wetland, elevated CO_2, Vegetation, photosynthesis, peatland

INTRODUCTION

Anthropogenic activities have increased the concentration of atmospheric CO_2 continuously from about 280 parts per million (ppm) at the beginning of the industrial revolution to 369 ppm at the present time. Future estimations on the atmospheric CO_2 concentration range between 450 ppm and 600 ppm by the year of 2150 (IPCC, 2001). More than two decades of study on the effects of CO_2 enrichment has provided a rich suite of data and understandings about a wide variety of plant response such as net primary productivity, species abundance, community composition and soil respiration (root plus microbial respiration) in terrestrial ecosystems (Poorter, 1993; Curtis & Wang, 1998; Ball & Drake, 1998; Mooney *et al*., 1999; Edwards & Norby, 1999; Zak *et al*., 2000). For example, Curtis & Wang (1998) documented increased net primary production in terrestrial ecosystems under elevated CO_2 conditions (Figure 1), although longer-term impacts have yet been identified. In addition, the chemical and physical composition of plant material and decomposability of plant litter have drawn much attention (Cotrufo *et al*., 1994; Cotrufo & Ineson, 1995; King *et al*., 1997). Mathematical models have also been employed to assess effects of elevated CO_2 on vegetation. For example, Levis *et al*. (2000) have reported large scale vegetation feedbacks on doubled CO_2 climate by a modeling approach.

Unlike the terrestrial ecosystem studies, how-

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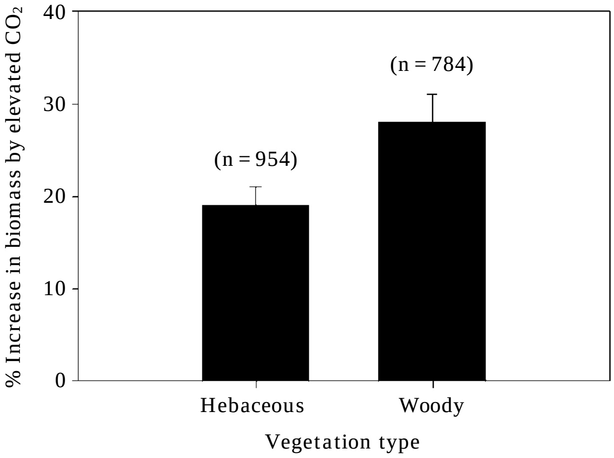

Fig. 1. Effects of elevated CO_2 concentration on the changes in shoot biomass of terrestrial plants. Terrestrial vegetation was classified into woody plants and herbaceous plants. The number (n) represents data points considered. Modified from Curtis and Wang (1998).

ever, relatively less efforts have been made to elucidate possible effects of elevated CO_2 on wetland ecosystems. Although wetland ecosystems including peat-forming wetland cover only 2-6% of global land surface (Gorham, 1991), they play a pivotal role in global biogeochemical cycles. Firstly, peat accumulation in peatland ecosystems over thousands of years has resulted in a vast store of carbon of 455 Pg C (Gorham, 1991; Van Breemen, 1995; Adams & Faure, 1998). This represents 20-30% of the world's pool of soil organic carbon and is comparable to the total carbon in the atmosphere as CO_2 (IPCC, 2001). Secondly, wetlands are substantial sources of the radiatively active trace gases such as CH_4 and N_2O (Freeman *et al*., 1993). For example, natural wetlands and rice paddies release about 40-50% of global emissions of CH_4, which is 25 times more radiatively active than CO_2 on a molar basis (Cicerone & Oremland, 1988). As such, even small changes in net primary productivity or decomposition of soil organic matter by elevated CO_2 could significantly influence the balance of greenhouse gas flux between the atmosphere and biosphere. This would be of great importance in future trajectory of global warming scenario (Mitchell *et al*., 2002).

The aim of this review is to organize existing knowledge about effects of elevated CO_2 on wetland plants.

RESPONSE OF GROWTH, PHOTOSYNTHESIS AND RESPIRATION

Elevated CO_2 stimulates growth of individual plants in the terrestrial ecosystem in general (Curtis & Wang, 1998; Delucia *et al*., 1999; Norby *et al*., 1999), but net primary production of a whole plant community did not necessarily increase (Körner, 1996; Koch & Mooney, 1996). This indicates that the CO_2 response is species specific, with some species declining and other species gaining in abundance (Warwick *et al*., 1998; Leadley *et al*., 1999).

Effects of elevated CO_2 on wetland plant community, however, are largely unknown, as measurements have only been done on individual species (Table 1, 2 and 3). Especially boreal and subarctic peatlands represent an important long-term carbon sink by *Sphagnum* species and thus play a key role in the global carbon cycle. Many studies have focused on the effects of increased atmospheric CO_2 levels on the growth of *Sphagnum* species. But previous studies on the effects of elevated CO_2 on *Sphagnum* biomass production are still controversial, because of a species-dependent response and variable effects on parameters of growth (Jauhiainen *et al*., 1993, 1994, 1997; Jauhiainen & Silvola, 1996; Van der Heijden *et al*., 1998; Heijmen *et al*., 2000, 2002; Berendse *et al*., 2001; Hoosbeek *et al*., 2001; Mitchell *et al*., 2002). The positive effects of CO_2 on *Sphagnum* growth have been reported both in the laboratory (Jauhiainen *et al*., 1994, 1998a, b; Van der Heijden *et al*., 2000; Heijmans *et al*., 2000), and in the field (Heijman *et al*., 2002). However, Hoosbeek *et al*. (2001) and Berendse *et al*. (2001) reported that an increased CO_2 concentration had no significant effects on *Sphagnum* or vascular plant biomass at four sites in four countries (Netherlands, Finland, Sweden and Switzerland) using free-air carbon dioxide enrichment (FACE) field experiments. Smolders *et al*. (2001) also found that atmospheric CO_2 is not sufficient to enable *Sphagnum* to develop its normal vertical growth pattern. Heijmans *et al*. (2001a) showed that elevated atmospheric CO_2 resulted in a 17% higher biomass production in *Sphagnum*-dominated bog ecosystem but this effect was not significant. More recently Heijmans *et al*. (2002) have reported that the height and green biomass increment of *S. magellanicum*

Table 1. Effects of elevated CO_2 on the growth of bog plants. Changes in biomass by elevated CO_2 are presented as (elevated–ambient)/ambient × 100. No significant differences between ambient CO_2 and elevated CO_2 treatments are indicated by the letter, NS.

Bog	Species	CO_2 level (μL /L) Ambient /elevated CO_2	Duration of study	Change of biomass (%) A = Aboveground B = Belowground G = Green biomass		Facility	References
Moss	*Sphagnum recurvum*	360/700	6 month	+17 ($P < 0.01$)	A	Growth chamber	Heijmen *et al.* (2000)
Moss	*S. fallax* *Polytrichum strictum*	360/560	Three growing seasons	+6 NS +5 NS	A	Mini-FACE	Mitchell *et al.* (2002)
Moss	*S. balticum* *S. papillosum* *S. magellanicum* *S. fallax*	360/560	Three growing seasons	NS NS	A B	Mini-FACE	Berendse *et al.* (2001)
Moss	*S. magellanicum*	350/560	Two growing seasons	+4.7 (P<0.05) −31.6 (P<0.01)	A G	Green house	Heijman *et al.* (2002)
Moss	*S. magellanicum* (95)*	350/560	Three growing seasons	+17 NS	A	Mini-FACE	Heijman *et al.* (2001a)
Moss	*S. balticum* (61) *S. papillosum* (33) *S. magellanicum* (4)	360/560	3 years	+6.6 NS	A	Mini-FACE	Hoosbeek *et al.* (2001) Berendse *et al.* (2001)
Moss	*S. magellanicum* (69) *S. papillosum* (13) *S. balticum* (7) *S. rubellum* (7)	360/560	3 years	−11.4 NS	A	Mini-FACE	Hoosbeek *et al.* (2001) Berendse *et al.* (2001)
Moss	*S. magellanicum* (97) *S. papillosum* (1)	360/560	3 years	+21.6 NS	A	Mini-FACE	Hoosbeek *et al.* (2001) Berendse *et al.* (2001)
Moss	*S. fallax* (62) *Polytrichum strictum* (37)	360/560	3 years	−14.7 NS	A	Mini-FACE	Hoosbeek *et al.* (2001) Berendse *et al.* (2001)
Vascular species	*Rhynchospora alba* *Vaccinium oxycoccus* *Erica tetralix* *Eriophorum angustifolium* *Drosera rotundifolia*	350/560	Two growing season	−16.5 NS −22.5 NS −76.2 NS −65.0 NS +200 NS	A	Green house	Heijman *et al.* (2002)
Vascular species	*V. oxycoccus* *E. tetralix* *E. angustifolium*	350/560	Three growing season	+17.3 NS +3.2 NS +39.5 NS	B	Mini-FACE	Heijmans *et al.* (2001a)
Vascular species	*Eriophorum vaginatum* (14) *V. oxycoccus* (4) *Andromeda polifolia* (2) *Scheuchzeria palustris* (2)	360/560	3 years	+16.4 NS +10.3 NS	A B	Mini-FACE	Hoosbeek *et al.* (2001)
Vascular species	*E. angustifolium* (8) *V. oxycoccus* (3) *D. rotundifolia* (3) *Calluna vulgaris* (2) *A. polifolia* (2)	360/560	3 years	−22.4 NS +29.0 NS	A B	Mini-FACE	Hoosbeek *et al.* (2001)
Vascular species	*V. oxycoccus* (19) *E. tetralix* (9) *E. angustifolium* (4) *D. rotundifolia* (2) *C. vulgaris* (1)	360/560	3 years	+26.0 NS +18.0 NS	A B	Mini-FACE	Hoosbeek *et al.* (2001)
Vascular species	*Carex nigra* (3) *V. oxycoccus* (3) *E. vaginatum* (2)	360/560	3 years	+1.6 NS +25.4 NS	A B	Mini-FACE	Hoosbeek *et al.* (2001)

*: % cover

Table 2. Effects of elevated CO_2 on the growth of marsh plants. Changes in biomass by elevated CO_2 are presented as (elevated−ambient)/ambient × 100. No significant differences between ambient CO_2 and elevated CO_2 treatments are indicated by the letter, NS.

Marsh	Species	CO_2 level (μL /L) Ambient / elevated CO_2	Duration of study	Change of biomass (%) A = Aboveground B = Belowground S = Stem, L = Leaves		Facility	Reference
Sedge	*Scirpus olneyi* (C_3)	343/681	2 years	+83 ($P < 0.05$)	B	Open-top chamber	Curtis *et al.* (1990)
		360/700	7 years	−11.1 NS	S		Azcón-Bieto *et al.* (1994)
		360/700	7 year	+14.7 NS	A		Matamala & Drake (1999)
		360/700	8 year	+26.5 NS	A		
		364/660	4 month	NS	A		Dakora & Drake (2000
				(−) $P < 0.05$	B		
Grass	*Spartina patens* (C_4)	343/681	2 years	NS	B	Open-top chamber	Curtis *et al.* (1990)
		360/700	7 years	−4.5 NS	L		Azcón-Bieto *et al.* (1994)
		360/700	7 year	−15.3 NS	A		Matamala & Drake (1999)
		364/660	4 month	(+) $P < 0.05$	A		Dakora & Drake (2000)
		364/660	4 month	NS	B		
Shrub	*Lindera benzoin* (C_3)	360/700	7 years	+4.0 NS	L	Open-top chamber	Azcón-Bieto *et al.* (1994)

were significantly reduced at elevated CO_2. Mitchell *et al.* (2002) also have showed that elevated CO_2 reduced the growth in length of both *Polytrichum strichum* (−27%) and *S. fallax* (−19%) as compared to the control. Jauhiainen *et al.* (1997) suggested that the intra-specific variability in the growth response of *Sphagnum* exposed to high atmospheric CO_2 might be due to genetic variation in the sampled material. Thus, the effects of CO_2 on the growth of *Sphagnum* are species-specific responses. The lack of CO_2 response to individual plant species was attributed to nutrient limitation (Tissue & Oechel, 1987; Oechel & Vourlitis, 1996; Arp *et al.*, 1998), nitrogen deposition rate and plant nitrogen content (Van der Heijden *et al.*, 2000). In addition, vascular plant biomass in the bog was not significantly affected by elevated CO_2 (Heijman *et al.* 2001a, 2002; Hoosbeek *et al.*, 2001).

Several studies have reported that leaf photosynthesis is stimulated by CO_2 enrichment (Silvola, 1990; Jauhiainen and Silvola, 1996; Drake *et al.*, 1996; Jauhiainen *et al.*, 1994, 1997; Van der Heijden *et al.*, 1996). For instance, Silvola (1990) showed that photosynthesis in *Sphagnum* rose linearly with increasing atmospheric CO_2. Jauhiainen and Silvola (1996) also observed that photosynthesis of *S. fuscum* was stimulated by elevated CO_2. Drake *et al.* (1996) reported the rates of photosynthesis in excised shoot and canopies of salt marsh plant were stimulated by 53% and 30%, respectively. In other reports, when CO_2 concentration was raised, the net photosynthesis of *sphagnum* increased, but dry mass production remained surprisingly low (Jauhiainen *et al.*, 1994, 1996, 1997; Van der Heijden *et al.*, 1996). A similar result was reported in another wetland plant *S. olneyi* stands grown under elevated CO_2, which showed enhanced ecosystem photosynthesis rates since the beginning of the project in 1987 (Arp & Drake, 1991; Long & Drake, 1992; Drake *et al.*, 1996, 1997). However, elevated CO_2 did not affect aboveground biomass in a brackish marsh plant community. Megonigal & Schlesinger (1997) performed experiments with *Orontium aquaticum*, a common emergent aquatic macrophyte in temperature and sub-tropical wetlands. They reported that photosynthetic

Table 3. Effects of elevated CO_2 on the growth of other types of wetland plants. Changes in biomass by elevated CO_2 are presented as (elevated−ambient)/ambient × 100. No significant differences between ambient CO_2 and elevated CO_2 treatments are indicated by the letter, NS.

Plant	Species	CO_2 leve (μL /L) Ambient /elevated CO_2	Duration of study	Change of biomass (%) T = Total plant A = Aboveground B = Belowground		Facility	Reference
Fen plant	*Juncus Festuca* spp.	350/700	4 month	+135.2 NS	A	Open−top chamber	Kang *et al.* (2001)
				+225.4 NS	B		
				+208.1 ($P<0.05$)	T		
Emergent aquatic macrophyte	*Orontium aquaticum*	350/700	3 month	+17 NS	T	Glasshouse	Megonigal & Schlesinger (1997)
				+10 NS	B		
		350/720	6 month	+16 NS	T	Growth chamber	
				+18 NS	B		
Wetland tree	*Acer rubrum*	422/722	17 week	NS	T	Growth chamber	Vann & Megonigal (2002)
	Taxodium distichum	350/700	12 week	NS	T	Glasshouse	
Rice	*Oryza sativa*	350/700	40 days	+63.9 ($P<0.005$)	B	Temperature Gradient Greenhouse Tunnels	Schrope *et al.* (1999)
			68 days	+38.5 ($P<0.005$)	B		
			138 days	+16.3 ($P<0.005$)	B		
			40 days	+10.8 NS	A		
			68 days	+12.6 ($P<0.05$)	A		
			130 days	+8.0 ($P<0.054$)	A		

rates of the plant were 54 to 71% higher under elevated CO_2 than ambient CO_2, but plant biomass was not significantly different at the end of the experiments. Vann and Megonigal (2002) determined the growth responses of wetland tree seedlings, *Toxodium districhum* and *Acer rubrum*, to elevated CO_2 and water table depth. Elevated CO_2 increased leaf−level photosynthesis, whole−plant photosynthesis, and trunk diameter of *T. districhum* regardless of water treatment, but it did not increase biomass of *T. districhum* or *A. rubrum*. It is suspected that the photosynthetically fixed carbon was transferred into the belowground parts of plants rather than build up as shoots of plants (Helal & Sauerbeck, 1984; Lambers, 1987).

Raised concentration of CO_2 is known to increase photosynthesis and biomass accumulation in terrestrial ecosystems, especially in the roots (Chu *et al.*, 1992; Cotrufo & Gorissen, 1997; Ginkel *et al.*, 1997; Silvola & Ahlholm, 1993; Dacey *et al.*, 1994). Belowground carbon allocation is a major component of a plant's carbon budget, yet relatively little is known about the response to roots of wetland plant under elevated atmospheric CO_2. Curtis *et al.* (1990) showed that growth under elevated CO_2 resulted in an 83% increase in root dry mass for the C3 sedge *S. olneyi*. Schrope *et al.* (1999), who studied methane emissions from rice grown under doubled CO_2 concentrations, reported that root and aboveground biomass were higher in the CO_2 enriched treatment by 83% and 35%, respectively. In contrast to these results, Matamala and Drake (1999) showed that elevated CO_2 did not affect belowground biomass of *S. olneyi* and *S. patens* responded to eight years of elevated CO_2 exposure. Dakora and Drake (2000) also reported that shoot dry mass of *S. olneyi* was the same for plants grown under either ambient or elevated CO_2, but the dry mass of root plus rhizome was significantly reduced by elevated CO_2. Heijmans *et al.* (2001a) reported that elevated CO_2 did not change allocation to belowground of vascular plant in a *Sphagnum*−dominated bog ecosystem. In addition, other studies have reported that the root biomass of wetland plants was not affected by elevated CO_2 (Berendse *et al.*, 2001; Hoosbeek *et al.*, 2001; Curtis *et al.*, 1990; Kang *et al.*, 2001; Megonigal & Schlesinger, 1997). Thus, we suspect much of total fixed carbon was released from roots into the rhizosphere, rather than increasing the biomass of plants (Whipps & Lynch, 1983; Helal & Sauerbeck, 1984).

CO_2 enrichment may impact on CO_2 fluxes by causing acclimation of the growth and photosynthesis. Many short-term experiments have revealed changes in plant development in response to changes in CO_2 concentration (Heijmen *et al.*, 2000; Dakora & drake, 2000; Kang *et al.*, 2001; Schrope *et al.*, 1999), but these results appear to be less significant in the longer-term experiments (Heijman *et al.*, 2001a; Hoosbeek *et al.*, 2001; Mitchell *et al.*, 2002; Berendse *et al.*, 2001; Niklaus *et al.*, 2001; Curtis & Wang, 1998). To date, the longest observation under elevated CO_2 conditions in relation to wetland was made in a brackish marsh on along Chesapeake Bay for over 8 years (Matamala & Drake, 1999). Drake *et al.* (1992, 1996) reported that the stimulation of photosynthesis (+30%) and inhibition of plant respiration (−19 to −40%) by elevated CO_2 concentration increased net ecosystem production (NEP) 59% in 1993 and 50% in 1994. However, after eight years of CO_2 enrichment, these high rates of growth were not sustained (Matamala & Drake, 1999). Studies in a tussock tundra ecosystem in northern Alaska, USA, reported that initial increases in net carbon assimilation were no longer apparent after 3 years of *in situ* CO_2 fertilization (Grulke *et al.*, 1990, Oechel *et al.*, 1994). Van der Heijden *et al.* (2000) reported that after three days of exposure to elevated CO_2, net photosynthesis was down-regulated to control levels. Acclimation of photosynthesis over prolonged exposure at raised CO_2 concentrations seems to be associated with decreased Rubisco (ribulose-1, 5-biphosphate carboxylase/oxygenase) activity (Ziska *et al.*, 1991; Tissue *et al.*, 1993; Hymns *et al.*, 2001), a low soluble carbon sink potential (Arp, 1991; Tissue, 2001), and changes in nitrogen uptake, assimilation, and allocation (Van der Heijden *et al.*, 2000; Hobbie *et al.*, 2001; Walch-Liu *et al.*, 2001).

In terrestrial ecosystem respiration rates have been observed to decline (Hamilton *et al.*, 2001; Griffin *et al.*, 2001) or remain unchanged (Hamilton *et al.*, 2001) with CO_2 enrichment, depending on the species. A similar response was found in a wetland by Van der Heijden *et al.* (2000) who found doubling CO_2 inhibits respiration in *Sphagnum*, resulting in an accumulation of soluble sugars in capitula. Drake *et al.* (1996) also reported that elevated CO_2 reduced dark respiration in excised shoots and canopies of salt marsh plant *S. olneyi*. Azcón-Bieto *et al.* (1994) found that respiration of *Spartina patens* (C4) leaves was unaffected by CO_2, but respiration decreased in the C_3 salt marsh plants (*S. olneyi* & *Lindera benzoin*) grown at high CO_2. Reduction of the rate of respiration in *S. olneyi* and *L. benzoin* was shown to be due largely to reduction in some enzymatic complexes of the mitochondrial electron transport chain, resulting in the reduction in the activity of the Cyt pathway (Azcón-Bieto *et al.*, 1994).

RESPONSES OF COMMUNITY STRUCTURE

Changes in plant species composition may have important effects on the balance of productivity and decomposability in wetland ecosystems. In particular, the changes in the competitive balance between *Sphagnum* and vascular plants under elevated CO_2 are potentially important. Firstly, the relative dominance of the plants will change the amount of carbon sequestered in bogs by photosynthesis, and hence affect the global carbon cycle. Secondly, changes in relative contribution of both species groups will have consequences for the exchange of green house gases between bog and atmosphere (Joabsson *et al.*, 1999).

Heijmans *et al.* (2001a) reported the elevated CO_2 increased height growth of *Sphagnum*, but vascular plant biomass was not significantly affected by elevated CO_2. Thus, elevated CO_2 gives a competitive advantage to *Sphagnum* in *Sphagnum*-dominated mire (bog) vegetations. More recently, they also studied in a glasshouse by exposing peat monoliths with monocultures and mixtures of *S. magellanicum* and *Eriophorum angustifolium* to elevated CO_2. *Sphagnum* had a negative effect on *E. angustifolium* biomass, particularly on the number of flowering stems under raised CO_2 (Heijmans *et al.*, 2002). Mitchell *et al.* (2002) also suggested that elevated CO_2 might have some positive effects on bog regeneration processes through a positive influence on *Sphagnum* re-growth and negative influence on initial colonizer *Polytrichum strichum*. Therefore, elevated CO_2 may give a competitive advantage to *Sphagnum*, resulting in increased peat accumulation (thus carbon sequestration) in the long term. However, such conclusion should be taken with care because of the absence of information on effects of elevated CO_2 on decomposition rates, which are an important component of the carbon balance.

EVAPOTRANSPIRATION

Evapotranspiration is one of the most important responses that should be considered in wetlands, because water balance determines many aspects of wetland characteristics. Several studies have shown a reduction of evapotranspiration in terrestrial ecosystems exposed to elevated CO_2 (Arp *et al.*, 1998; Owensby *et al.*, 1997; Field *et al.*, 1997). The reduction in evapotranspiration can be explained by reduced vascular plant transpiration through increased stomatal closure (Bettarini *et al.*, 1998) and increased water use efficiency (Arp *et al.*, 1998) under elevated CO_2 conditions. Similar effects of elevated CO_2 were reported in wetland ecosystems. Heijmans *et al.* (2001b) found that elevated CO_2 significantly reduced evapotranspiration by 9−10% in an ombrotrophic bog, which is composed of peat monoliths with vascular plant. In addition, the changes in evapotranspiration by elevated CO_2 were influenced by vascular plant biomass and the area of exposed moss surface. Reduced evapotranspiration is expected to favor *Sphagnum* growth in ombrotrophic bog vegetation. However, evapotranspiration at elevated CO_2 may be increased by the denser growth form of *Sphagnum*, which helps water transporting through capillary rise between pendant branches and stems (Hayward & Clymo, 1982). Megonigal & Schlesinger (1997) also observed a significant decrease in transpiration rates under elevated CO_2 in a growth chamber study with *Orontium aquatium*.

NUTRIENTS IN PLANT

Elevated CO_2 atmosphere have decreased in nitrogen content in the tissues of wetland vascular plants (Curtis *et al.*, 1989; Jacob *et al.*, 1995; Drake *et al.*, 1997; Curtis *et al.*, 1990; Matamala & Drake, 1999; Dakora & Drake, 2000) and non−vascular plants (Cotrufo *et al.*, 1998; Niklaus *et al.*, 2001; Stulen *et al.*, 1994; Van der Kooij & De Kok, 1996; Van der Heijden *et al.*, 2000; Heijmans *et al.*, 2001a; Jauhiainen *et al.*, 1998a). Such results were due to changes in 1) protein concentration at the level of Rubisco (Van Oosteen & Besford, 1995; Jacob *et al.*, 1995; Drake *et al.*, 1996) or respiratory proteins (Azcón−Bieto *et al.*, 1994), and 2) greater accumulation of non−structural carbohydrates (Drake *et al.*, 1996; Kuehny *et al.*, 1991; Hertog *et al.*, 1996; Van der Heijden *et al.*, 2000a) resulting in dilution of nitrogen. However, Heijmans *et al.* (2002) have recently reported that the nitrogen concentrations in *Sphagnum* and some of vascular plants were higher under elevated CO_2. Curtis *et al.* (1989, 1990) found that elevated CO_2 had no effects on the nitrogen or carbon content of roots for the C_4 grass *Spartina patens*. However, N% in root was significantly lower for the C_3 sedge *Scirpus olneyi* community. As a result, elevated CO_2 increased the C/N ratio of *S. olneyi* root tissue by 22% (C/N = 75). Matamala and Drake (1999) also showed the effects of continuous CO_2 enrichment for eight years on nitrogen contents of salt marsh plant and soils. Nitrogen concentration in the elevated CO_2 treatments was reduced 15% in stems of *S. olneyi* and 29% in the upper 10 cm of the soil profile. However, C_4 grass *S. patens* and soils underneath displayed none of such effects. These results suggested the level of nitrogen concentration in the plant tissue exposed to CO_2 enrichment was species dependent. As C/N ratio is known to represent decomposability of organic matter, any changes in C/N ratio of wetland plants would modify decomposition rates of organic matter in the long−term.

CONCLUSION

Elevated CO_2 induces various responses of wetland plants. However, some changes are species−specific, and hence future trajectories at the large scale are still unclear. Decreases in transpiration as well as increases of C/N ratio in certain wetland plants by elevated CO_2 imply that the rates of organic matter decomposition may be hindered in the long−term. However, further information on dynamics of belowground carbon supplied from wetland plants is warranted to assess effects of elevated CO_2 on wetland carbon cycle accurately.

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<국문적요>

대기중 이산화탄소 농도 증가가 습지 식물에 미치는 영향

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지난 20여년간 대기 중 이산화탄소 농도의 증가가 육상 생태계에 미칠 영향에 대한 많은 연구가 진행되었다. 그러나 전지구적 물질 순환에 중요한 역할을 담당하는 습지 생태계에서 일어나는 반응에 대한 연구는 미흡하다. 본 종설에서는 대기 중 이산화탄소 농도가 증가했을 때 습지의 식생들이 어떠한 반응을 보일 것인지에 대해 알아보고자, 이와 연관하여 발표된 논문들의 결과를 모아 정리하였다. 특히, 습지 식생의 일차생산성, 군집 구조, 증발산량, 식물체의 영양소 등에 미치는 영향을 살펴 보았다. 이산화탄소 증가가 개개 식물의 광합성량을 증가 시키는 것은 많이 관찰 되었으나, 이러한 현상이 바로 습지식생의 탄소보유를 증가시키는 것으로 결론 내릴 수 없었다. 그 이유는 고정된 탄소의 지하부로의 전달, 개개 종의 상이한 반응, 종간의 상호작용, 영양소의 부족 등 다른 요인들의 작용 때문이다. 그러나 이산화탄소 농도의 증가는 전반적으로 습지 식물의 증발산량을 감소 시키는 경향을 보였다. 한편, 육상 식물의 반응과 유사하게 많은 습지에서 이산화탄소의 증가가 식생의 C/N 비를 증가 시키는 것이 일부 종에서 관찰 되었으며, 이러한 종에서는 장기적인 유기물 분해의 속도가 감소될 수 있음을 암시한다. 그러나 지하부로 유입되는 새로운 광합성 산물들의 동태에 대한 더 많은 정보가 모아져야 정확한 예측이 가능할 것이다.