Tasks for vegetation science 41

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Plants and Climate Change

Edited by

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Preface

Special issue – *Plants and Climate Change*

April 23, 2004 a symposium was held at the Vrije Universiteit, Amsterdam, The Netherlands, entitled Plants and (Present and Past) Climate Change on the occasion of the new Chair on Climate–Biosphere Interactions for Jelte Rozema. The aim of that Chair is to promote research on how climate affects or affected the biosphere and *vice versa* both in the present and past.

Contributors were invited to write review-like papers providing the State-of-the-Art of topics relating to plant–climate interactions, but also new research data are presented here.

This Special Issue of the International Journal Plant Ecology on Plants and Climate Change covers 14 peer-reviewed papers highlighting plant responses to atmospheric CO_2 increase, to global warming and to increased ultraviolet-B radiation as a result of stratospheric ozone depletion.

Dependent on how and how well plant responses to increased temperature, atmospheric CO_2 and ultraviolet-B have been preserved in the (sub)-fossil record, past climates and past atmospheric chemistry may be reconstructed. Pollen and tree-ring data reflect plant species composition and variation of temperature and precipitation over long or shorter time intervals. In addition to well preserved morphological and chemical plant properties, new analytical techniques such as stable isotopes are becoming increasingly important in this respect. The development and validation of such biotic climate and environment proxies builds a bridge between biological and geological research. This highlights that Plant–Climate Change research is becoming a multi- and transdisciplinary field of relevant research.

The guest editors acknowledge the opportunity provided by Springer Publishers and the Editor-in-Chief of Plant Ecology, Prof. Arnold van der Valk, to prepare and edit this Special Issue. We are also indebted to the many referees who helped to review the submitted papers.

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Photo. Geothermally influenced ground, such as illustrated here from Bellingshausen Island in the South Sandwich Islands, provides protection from some of the most extreme conditions of the Antarctic, and is often colonised by exceptional plant communities otherwise only known from lower latitudes, illustrating the separate controls on processes involved in long distance transport to (colonisation) and subsequent establishment at an Antarctic location.

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Responses of terrestrial Antarctic ecosystems to climate change

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Key words: Alien species, Antarctic, Bryophyte, Climate change, Colonisation, Microbiota, Phanerogam, Terrestrial ecosystem, UV radiation

Abstract

Antarctic terrestrial biota are generally limited by the inexorably linked environmental factors of low summer temperature and lack of available water. However, in parts of the Antarctic, both these factors are changing rapidly on contemporary timescales. Terrestrial biota have concurrently been faced with changes in the timing of UV-B maxima associated with spring ozone depletion. The region of the Antarctic Peninsula and Scotia Arc has experienced one of the most rapid rates of environmental warming seen worldwide over the last 30–50 years. Together with local changes in precipitation, this has resulted in a rapid reduction in extent and thinning of many ice-fields and glaciers, exposing new terrain for colonisation while, at the same time, altering patterns of water availability in terrestrial habitats. The rapid development of communities on newly-exposed ground is also facilitated by the existence of soil propagule banks, which contain propagules of both local and exotic origin. In this paper we collate and review evidence from a range of observational and manipulative studies that investigate the effect of climate change, especially increased temperature, on the processes of colonisation and subsequent community development by plants in the Antarctic. Biological changes that have been associated with climate change are visible in the form of expansions in range and local population numbers amongst elements of the flora. Environmental manipulation experiments further demonstrate the possibility of large and rapid species and community responses to climate amelioration, with many resident biota responding positively, at least in the absence of increased competition from exotic colonists. Manipulation studies are also starting to elucidate more subtle responses to climate changes, at levels ranging from cell biochemistry to habitat and food web structure. Integrating such subtle responses is vital to improving our ability to understand the consequences of climate change, as these may lead to much greater consequential impacts on communities and ecosystems.

Introduction

Antarctic terrestrial ecosystems

This paper focuses on two of the three biogeographical zones that are conventionally recognised in Antarctica, the sub- and maritime Antarctic (Smith 1984), which include the west coast of the Antarctic Peninsula northwards from Alexander Island, through the island archipelagos of the Scotia Arc (South Shetland, South Orkney and South Sandwich Is.), to South Georgia.

The maritime Antarctic climate is markedly seasonal, with a strong maritime influence especially during summer that becomes reduced during winter through seasonal sea ice formation. The maritime influence on sub-Antarctic climates is present year-round, resulting in a damping of seasonal temperature variation relative to other polar regions (Convey 1996a; Danks 1999). Faunal and floral diversity are very restricted in comparison with lower latitude locations (Block 1984; Smith 1984; Convey 2001a), generally regarded as a consequence of low summer temperatures, geographical isolation from neighbouring temperate landmasses, and the relatively short period available for colonisation since the commencement of the most recent phase of glacial retreat. For instance, only two higher insects and two flowering plants are present in the maritime Antarctic, where the fauna otherwise comprises simple communities of soil arthropods (Acari, Collembola) and other invertebrates (Nematoda, Tardigrada, Rotifera), and the flora is cryptogamic (bryophytes, lichens). Contemporary communities typically have low species richness and complexity, with few trophic links and interactions. Communities of the most extreme Antarctic environments appear to be at the first stages of colonisation or succession, and are limited purely by the extreme conditions rather than biotic interactions. They are expected to be very sensitive to changes in climate or consequential processes (Callaghan and Jonasson 1995; Freckman and Virginia 1997; Frenot et al. 2005).

Antarctic climate change

In the context of climate change, three elements are fundamental to the biology of Antarctic terrestrial organisms, temperature, water and solar irradiance. Low thermal energy input is a key defining characteristic of Antarctic terrestrial habitats, even when compared with the Arctic. Mean air temperatures even during the warmest summer months are low (below 0 °C in the continental, 0–2 °C in the maritime and 5–10 °C in the sub-Antarctic; Walton 1984; Convey 1996a; regional definitions after Smith 1984), a factor that is particularly significant in the context of climate change, being near to lower threshold temperatures for many biological functions. In this situation, a small temperature increment has a potentially greater biological impact than one of similar scale in a less extreme environment.

Recent air temperature increases are well documented along the Antarctic Peninsula and islands of the Scotia Arc (Smith 1990; Fowbert and Smith 1994; King and Harangozo 1998; Skvarca et al. 1998; King et al. 2003), with those along the west coast of the Antarctic Peninsula being the most rapid in the Southern Hemisphere. At several locations, increases in annual air temperatures of more than 1 °C have occurred over the last 30–50 years, with rates of warming during the winter months being even greater, up to 0.1 °C per year. A feature of Antarctic Peninsula warming is that much stronger trends are seen in the winter months (King and Harangozo 1998; King et al. 2003), which has a potentially important biological impact, by effectively shortening the winter season. Even greater rates of warming have been reported in some Antarctic freshwater ecosystems (Quayle et al. 2002, 2003), which appear to magnify the signal seen in air temperatures.

The availability of liquid water may be even more important than temperature to biological activity in Antarctic terrestrial habitats (Kennedy 1993; Sømme 1995; Block 1996). Water availability is influenced directly by precipitation events (especially in summer), and also by release from seasonal snow cover and glaciers (i.e. the timing can be separated from the original precipitation event). Increased precipitation is predicted in this region (Budd and Simmonds 1991), with some documentary evidence published (Turner et al. 1997). There are also reports of decreasing trends in precipitation, more particularly in the sub-Antarctic (Frenot et al. 1997; Bergstrom and Chown 1999), but also from the maritime Antarctic South Orkney Is. (Noon et al. 2001), highlighting the importance of understanding trends at the appropriate (local) scale. Rapid decreases in glacial extent, and loss of smaller 'permanent' snow banks, may both in the short-term release increased quantities of liquid water into terrestrial habitats. Such decreases are documented along the Antarctic Peninsula and Scotia Arc (Smith 1990; Gordon and Timmis 1992; Fowbert and Smith 1994; Pugh and Davenport 1997; Fox and Cooper 1998; Vaughan et al. 2001; Quayle et al. 2003). In the longer term, loss or seasonal exhaustion of previously permanent sources of water supply may

itself provide another limitation to terrestrial habitats (see Convey et al. 2003).

Finally changes in radiation climate have been predicted to impact terrestrial biota. The 'ozone hole' that forms annually in the austral spring over Antarctica has occurred, at least in the recent era, only since the early 1980s (Farman et al. 1985). When present, increased penetration of biologically damaging shorter wavelength UV-B radiation is possible. While maximum intensities of radiation received under the ozone are similar to normal summer maxima, they differ in two important features in that maxima now occur earlier in the season (in particular, when biota may not be fully physiologically active and able to respond) and that lower wavelengths penetrate to ground level than is normal at this time of year.

Predictions

It has been recognised since the late 1980s that the climate changes being experienced in parts of Antarctica are likely to lead to clear responses in these simple terrestrial ecosystems (Roberts 1989; Smith and Steenkamp 1990; Voytek 1990). As has happened globally, this recognition has encouraged the development of a predictive literature (e.g. Adamson and Adamson 1992; Wynn-Williams 1994, 1996; Kennedy 1995a; Convey 1997; Walton et al. 1997; Bergstrom and Chown 1999; Smith 2003; Frenot et al. 2005), addressing potential consequences for microbial groups, invertebrate fauna, flora, colonisation and ecosystem level processes. As a very broad generalisation, changes in two of the three major environmental variables (temperature, water) lead to predictions of positive responses in indigenous Antarctic biota, essentially through relaxation of current abiotic constraints on biological activity (Kennedy 1995a; Convey 2003). However, they are also predicted to lead to an increase in colonisation by exotic species (Kennedy 1995a; Smith 1996; Convey 1997, 2003; Frenot et al. 2005), generating increased diversity and trophic complexity and altering the physical structure of habitats. In the longer term, the latter process may lead to the loss of Antarctic species and communities through increased competition, as defining features of contemporary Antarctic biota and ecosystems include poor competitive abilities and general insignificance of competition (Convey 1996b). In contrast, changes in the radiation environment experienced as a result of exposure to increased UV-B under the ozone hole are likely to result in negative consequences for biota, as the costs of mitigation strategies are increased.

Over the last decade, a range of Antarctic terrestrial biological studies have been designed to test predictions associated with climate change, and there is now a literature pertaining to the real consequences of change in the Antarctic [see reviews by Convey (2001b, 2003) and Smith (2001); Walther et al. (2002) provide a global review of such evidence]. These can be separated into (i) descriptive and observational studies, and (ii) manipulative studies applied to more or less realistic natural habitats. In the remainder of this paper, we aim to summarise and collate the evidence obtained from such studies relating to the consequences of climate change for botanical elements of Antarctic terrestrial ecosystems.

Evidence from field observations

While the recent period of rapid regional climate change in the Antarctic is, justifiably, receiving much attention, it is also the case that the region has experienced change on a scale of 100s–1000s of years, during and subsequent to the cycles of Pleistocene glacial advance and recession (Convey 2003). During the early 1960s, within the first two decades of the current warming phase, rapid ice recession was already apparent at a number of maritime Antarctic locations, such as Signy I. and the Argentine Is. (R.I.L. Smith, personal observations). At this time, lichen trim-lines visible adjacent to glaciers, and the re-exposure of vegetation buried under ice, indicated that a previous cold period (possibly equating to the 'mini Ice Age' of Europe) had allowed greater extent of glaciers and icefields (Smith 1972, 1990; Corner and Smith 1973; Fenton 1982).

The most frequently quoted and striking proposed consequence of regional warming in the maritime Antarctic are the recent increases (1–2 orders of magnitude; Table 1) in populations of the two native Antarctic flowering plants (*Deschampsia antarctica* and *Colobanthus quitensis*) (Fowbert and Smith 1994; Smith 1994, 2001, 2003; Grobe et al. 1997). These increases do not include

Table 1. Increase in numbers of plants of *Deschampsia antarctica* and *Colobanthus quitensis* recorded between 1964 and 1990 at three sites in the Argentine Islands, western Antarctic Peninsula (extracted from Fowbert and Smith 1994).

Year	*Deschampsia antarctica*	*Colobanthus quitensis*
1964	610	62
1990	c. 17,000	377

any southwards extension of the species' geographical ranges, which remain defined by a lack of suitable ice free habitat south of the current limit in the Terra Firma Islands of southern Marguerite Bay. The most important factor behind the expansions is likely to be through more frequent success in the maturation of seeds (cf. Edwards 1974; Convey 1996c), which may have a further impact through their being able to remain dormant in soil propagule banks (McGraw and Day 1997).

Rapid population increases have been seen amongst bryophytes and microbiota in the maritime Antarctic (Smith 1993, 2001; Wynn-Williams 1996). These are again assisted by the characteristic of many of these groups of having propagules which are capable of remaining dormant in the soil propagule bank for many years (Table 2) (Smith and Coupar 1987; Smith, 1987, 1993). Antarctic soils have been manipulated *in situ* and subjected to laboratory culture in order to examine the diversity of (culturable) propagules present, with results indicating that propagule banks contain locally-occurring and, rarely, exotic species (Smith 1987, 1993, 2000; Smith and Coupar 1987). Aerobiological and palynological studies further demonstrate infrequent transfer of exotic biological material into the region, primarily from southern South America (Barrow 1978; Marshall 1996). While pollen of South American origin is frequently a component of such sampling studies, to date no spores of bryophyte or lichen species of confirmed non-Antarctic origin have been found (Marshall and Convey 1997). However, the presence of lower latitude bryophytes at ephemeral geothermally active sites in the maritime and continental Antarctic (Smith 1991; Bargagli et al.

Table 2. The contribution of soil propagule banks to the establishment of plants on Antarctic soils under simulated warming conditions.

	Age (years exposure) of moraine				
	5	15	25	35	45
(a)					
Total plant cover (%)	11	26	43	53	75
Number of species	2	5	8	8	10
Location	Biogeographical zone	Number of species			
(b)					
Husdal, South Georgia, 54 °S	Sub-Antarctic	18			
Signy Island, South Orkney Islands, 60 °S	Maritime Antarctic (north)	8			
		15 (calcareous ground)			
Cierva Point, northern Antarctic Peninsula, 64 °S	Maritime Antarctic (central)	6			
Rothera Point, Adelaide Island, 67 °S	Maritime Antarctic (central)	5			
Clarke Peninsula, Wilkes Land, 67 °S	Continental Antarctic (coast)	2			
Mars Oasis, Alexander Island, 72 °S	Maritime Antarctic (southern)	5			
Edmondson Point, Victoria Land, 74 °S	Continental Antarctic (coast)	4			

(a) Plant species diversity present after three years under screens placed on a moraine chronosequence on sub-Antarctic South Georgia. (b) Numbers of bryophyte species cultured from unvegetated surface soil collected at recently deglaciated sites along a latitudinal gradient from sub-Antarctic South Georgia to continental Antarctic Victoria Land. Data extracted from Smith (2001).

1996; Convey et al. 2000) demonstrates that such transfer must occur.

It is clear from transplant experiments carried out during the 1960s (Edwards and Greene 1973; Edwards 1980), and from the many accidental introductions to sub-Antarctic islands (Frenot et al. 2005) that many non-Antarctic flowering plants are capable of establishment if the problems of dispersal can be overcome. Some of these species, such as *Poa annua* on South Georgia are invasive, and have rapidly occupied areas where indigenous plant communities have been removed by vertebrate activity, particularly grazing by introduced reindeer. Human activity is already particularly important in this context – more than 50% of the vascular flora of South Georgia is accounted for by persistent anthropogenically-introduced species (Smith 1996) – with successful introductions expected to increase, and extend to more southerly locations as climate amelioration continues (Frenot et al. 2005).

There have been few attempts at the biochemical or ecophysiological level to quantify responses of Antarctic plants *in situ* to changing climatic conditions. In the Antarctic, the studies of Newsham et al. (2002) and Newsham (2003) provide the only examples of measurement of a direct biochemical response to increased UV-B radiation during episodes of ozone depletion in non-manipulated field populations of three bryophyte taxa (*Andreaea*, *Cephaloziella*, *Sanionia*). These show patterns of protective pigment synthesis and loss that are most strongly correlated with their recent (natural) radiation exposure history, indicating a rapid and dynamic biochemical response to this environmental stress. Rousseaux et al. (1999) provide data linking foliar DNA damage with ozone depletion in a southern South American herb.

Evidence from field manipulations

The use of simple field manipulation techniques is widespread in Antarctic studies. Most are based around the use of some form of chamber or screen (greenhouse methodologies), which is placed over an area of habitat in order to alter aspects of the thermal and radiation climates. In their simplest form, these can be left in place in remote locations year-round. With more regular access for researchers, and availability of a power source, methodolologies can be adopted which include water or nutrient addition, and the use of lamps to alter light and UV radiation climates. However, in detail, the environmental changes achieved are often more complex and inter-related than is widely appreciated (Caldwell and Flint 1994; Kennedy 1995b, c), and care is required in both experimental design and interpretation of the data obtained.

Greenhouse methodologies have generated very rapid population responses in studies of Antarctic microbes (Wynn-Williams 1993, 1996), and bryophytes and phanerogams (Smith 1990, 1993, 1994, 1999), with these responses also linked with changes in invertebrate populations (Kennedy 1994; Convey and Wynn-Williams 2002; Convey et al. 2002). The most rapid or largest responses appear to be obtained in manipulations of more extreme habitats, for instance at higher altitude (Kennedy 1994) or latitude (Convey and Wynn-Williams 2002). Plant species typically achieve greater coverage, success in establishment, lusher growth, and increased population densities, reproductive output, enhanced sexual reproduction and juvenile survival rates. These types of manipulation are known to cause changes in vegetation growth form (Smith 1990, 2001; Day et al. 1999, 2001; Sullivan and Rozema 1999; Ruhland and Day 2000) and, it is hypothesised, subtle alterations in habitat structure and microclimate. Such changes, possibly linked with changes in diet quality (see below), are thought to underlie or facilitate some of the responses seen in faunal communities (Convey et al. 2002). The synthesis across trophic levels of responses to climate change is a complex but important task as, while subtle and apparently insignificant at one level, they may combine to create much greater effects elsewhere in the ecosystem (Day 2001; Searles et al. 2001; Johnson et al. 2002).

Studies of the effects of environmental change on plant physiology and biochemistry in the Antarctic have focused on the consequences of radiative changes experienced as a result of ozone hole formation. The potential negative effects of UV-B radiation on cell function are well-known, as are the responses available to plants and other organisms to mitigate the damage (e.g. Vincent and Quesada 1994; Wynn-Williams 1994; Cockell and Knowland 1999; Rozema 1999). In laboratory experiments the confirmation of damage predictions is relatively

straightforward (e.g. Quesada et al. 1995). However, effects seen in the field (through natural exposure or manipulation) are far smaller in magnitude or even apparently non-existent (Fiscus and Booker 1995; Allen et al. 1998), which may suggest that many experimental results are in reality artefacts of the manipulation technique used. Where identified, the biochemical impacts of exposure to UV-B follow the predicted changes in reaction pathways, particularly those involved in protective pigment synthesis (e.g. Rozema 1999; Paul 2001). One major ecological implication of these lies in the requirement for changes in resource allocation strategies, while consequences, through changes in diet quality, may again be felt much more widely through the ecosystem.

Different research groups have used both amendment (supplementary lamps) and screening (selective absorbtion of incoming wavelengths) techniques to identify the effects of changes in UV radiation exposure on Antarctic autotrophs (Wynn-Williams 1996; Quesada et al. 1998; Huiskes et al. 1999; Montiel et al. 1999; Smith 1999; George et al. 2001; Lud et al. 2003), although note the caution (above) that all these techniques introduce potentially confounding artefacts. The groups targeted include algae, cyanobacteria, bryophytes, phanerogams and lichens, while the processes studied range through photosynthetic performance and mitigation strategies (protective pigments) to DNA damage.

Organisms that are fully physiologically active may be able to use a range of mitigation mechanisms whenever they are exposed to damage from UV-B. However, the effectiveness of some repair mechanisms depends on the UV-B:PAR ratio, which is much higher during spring ozone depletion than in midsummer. It is also possible that sensitivity to damage may also be influenced by other environmental factors or change through developmental processes.

Photosynthetic performance in some species appears to be remarkably robust under exposure to UV-B. The two phanerogams, *Deschampsia antarctica* and *Colobanthus quitensis*, have been studied by several groups and show no reduction of photosynthetic parameters when exposed to a range of realistic irradiance stresses (Montiel et al. 1999; Lud et al. 2001), although UV screening causes changes in concentrations of UV-B absorbing pigments, growth and production (Day et al. 1999; Ruhland and Day 2000; Xiong and Day 2001). Similarly, the field measurements of Newsham et al. (2002) on two Antarctic bryophytes (*Cephaloziella varians*, *Sanionia uncinata*) showed no change in photosynthetic yield at the same time as increased concentrations of UV-B screening pigments and carotenoids correlated with the level of recent exposure to natural levels of UV-B. Lud et al. (2001) also reported no change in yield in a lichen (*Usnea antarctica*) at different levels of UV-B exposure. Other experimental studies of bryophytes and cyanobacteria produce equivocal results, with exposure to increased levels of UV-B leading to increases in protective pigments in some, but not all, species (Quesada et al. 1998; Huiskes et al. 1999; Montiel et al. 1999; George et al. 2001).

Taken together, these studies broadly indicate that many Antarctic autotrophs already possess considerable abilities to resist or mitigate the consequences of irradiance stress on their photosynthetic apparatus, and that the recent advent of the Antarctic ozone hole does not directly compromise these abilities. In a related study of resistance to DNA damage in Antarctic terrestrial microbiota, George et al. (2002) found that levels of damage were very low relative to than those reported in microbiota from the shallow marine environment, proposing this to relate to much greater development of screening systems in terrestrial organisms over evolutionary time. Lud et al. (2002) found no increase in DNA damage (measured by cyclobutyl pyrimidine dimer formation) in the moss *Sanionia uncinata* under natural levels of UV-B radiation in the Antarctic and, although damage was caused by experimental UV-B enhancement, concluded that repair processes were sufficient on a daily timescale. As mentioned above, dynamic switches in utilisation of biochemical pathways relating to pigment production and metabolism, and repair processes, may carry both direct resource costs to the organism concerned and indirect costs elsewhere in the food web (ecosystem) through consequential changes in trophic linkages.

Conclusions

Rapid changes in three major environmental variables are being experienced in the region of the

Antarctic Peninsula and Scotia Arc, these being temperature, liquid water availability and radiation climate.

In the short term, many Antarctic terrestrial biota are likely to benefit from generally reduced environmental stresses, as they are already well-adapted to cope with the existing, rapidly fluctuating, stresses of their highly variable environment. The direct consequences of increases in UV-B exposure are likely to be negative, though subtle, as well as being expressed through consequential impacts elsewhere in the foodweb. In the longer term, colonisation of the region by lower latitude species with greater competitive ability, most likely with inadvertent human assistance, will become increasingly important, and could lead to large-scale change in the biological composition and possibly trophic complexity in some existing Antarctic terrestrial ecosystems.

Botanical responses to recent climate amelioration are already visible in the maritime and sub-Antarctic, in the form of rapid local expansion of populations of flowering plants, comparable changes in bryophytes, and rapid colonisation of ground recently exposed by snow and ice recession. These changes facilitate and are rapidly followed by the development of typical terrestrial invertebrate communities. The results of field manipulations mimicking predicted levels of thermal amelioration generally confirm these patterns of response, as well as highlighting the importance of propagule banks in the soil in accelerating the processes of establishment and community development.

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Photo. Point-intercept abundance measurements of vascular plant species in the Guisveld lowland *Sphagnum-Phragmites* reedland.

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Vascular plant responses to elevated CO_2 in a temperate lowland *Sphagnum* peatland

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Abstract

Vascular plant responses to experimental enrichment with atmospheric carbon dioxide (CO_2), using MINIFACE technology, were studied in a Dutch lowland peatland dominated by *Sphagnum* and *Phragmites* for 3 years. We hypothesized that vascular plant carbon would accumulate in this peatland in response to CO_2 enrichment owing to increased productivity of the predominant species and poorer quality (higher C/N ratios) and consequently lower decomposability of the leaf litter of these species. Carbon isotope signatures demonstrated that the extra 180 ppmv CO_2 in enriched plots had been incorporated into vegetation biomass accordingly. However, on the CO_2 sequestration side of the ecosystem carbon budget, there were neither any significant responses of total aboveground abundance of vascular plants, nor of any of the individual species. On the CO_2 release side of the carbon budget (decomposition pathway), litter quantity did not differ between ambient and CO_2 treatments, while the changes in litter quality (N and P concentration, C/N and C/P ratio) were marginal and inconsistent. It appeared therefore that the afterlife effects of significant CO_2-induced changes in green-leaf chemistry (lower N and P concentrations, higher C/N and C/P) were partly offset by greater resorption of mobile carbohydrates from green leaves during senescence in CO_2-enriched plants. The decomposability of leaf litters of three predominant species from ambient and CO_2-enriched plots, as measured in a laboratory litter respiration assay, showed no differences. The relatively short time period, environmental spatial heterogeneity and small plot sizes might explain part of the lack of CO_2 response. When our results are combined with those from other *Sphagnum* peatland studies, the common pattern emerges that the vascular vegetation in these ecosystems is genuinely resistant to CO_2-induced change. On decadal time-scales, water management and its effects on peatland hydrology, N deposition from anthropogenic sources and land management regimes that arrest the early successional phase (mowing, tree and shrub removal), may have a greater impact on the vascular plant species composition, carbon balance and functioning of lowland *Sphagnum–Phragmites* reedlands than increasing CO_2 concentrations in the atmosphere.

Introduction

Global atmospheric CO_2 concentrations have steadily risen from 280 ppm before the Industrial Revolution to 370 ppm currently and 560 ppm will be reached by the end of the 21st century according to most predictions (IPCC 2001). Peatlands store a substantial proportion of the global organic carbon pool (Gorham 1991), which is a consequence of a long-term greater productivity compared to decomposition rates. Higher atmospheric CO_2 concentrations could potentially change the balance between productivity and decomposition of peatlands, which could have major repercussions for large-scale carbon budgets. In this paper, we investigate how elevated CO_2 affects the vascular plant contributions to this balance (see Toet et al. In press, for moss contributions to this balance). So far responses in terms of productivity or plant growth have been found to be very limited in realistic *in situ* experiments with CO_2 enrichment in temperate northern ombrotrophic peatlands, both for the dominant peatland moss *Sphagnum* and vascular plants (Berendse et al. 2001; Hoosbeek et al. 2001; Heijmans et al. 2002). However, to our knowledge there is no information on productivity related responses of vascular plants in partly minerotrophic temperate lowland *Sphagnum–Phragmites* reedlands. In such peatlands, a relatively thin mostly rain-fed and nutrient-poor *Sphagnum* layer sits on top of a muddy, more nutrient-rich layer fed mostly by the groundwater, which is in contact with surrounding canals and ditches. While lowland peatlands in general are widespread throughout the temperate northern hemisphere, *Sphagnum–Phragmites* reedlands, which were once more widespread in the western Netherlands and other coastal parts of NW Europe, are now restricted to some nature reserves, mainly in The Netherlands. These peatlands have great conservation value as rare ecosystems with unique compositions of species, several of which are themselves rare or under threat internationally. In these ecosystems, the roots of the predominant vascular plants, including *Phragmites australis* reed, penetrate into this deeper, richer soil horizon. In ombrotrophic peatlands, the lack of CO_2 growth responses may be explained partly by the strong constraint imposed by low nutrient availability, as has been reported from various plants and ecosystems (cf. Curtis and Wang 1998; Stitt and Krapp 1999; Poorter and Pérez-Soba 2001; Hoosbeek et al. 2002). In contrast with these findings, Hoorens et al. (2003a) found significantly increased growth in response to CO_2 enrichment in two graminoids from mesotrophic peatland when grown at corresponding ('mesotrophic') nutrient availability. Therefore, our first hypothesis is that the predominant vascular species in lowland *Sphagnum–Phragmites* reedlands, which can penetrate into deeper, more nutrient-rich soil layers, will show a significant increase in productivity (as represented by abundance) in response to CO_2 enrichment. Increasing dominance of such plants could decrease the conservation value of these rare ecosystems, if they were to outcompete other vascular plants rooting in the *Sphagnum* peat layer (e.g. orchid spp., *Drosera rotundifolia*).

On the other side of the carbon balance, i.e. the organic matter breakdown side, CO_2-induced increases in productivity might result in greater litter amounts entering the soil surface, which may be an important contributor to changing soil carbon dynamics (Norby and Cotrufo 1998). CO_2 enrichment may have indirect effects on the abiotics of peatlands (and thereby on the soil decomposer communities), for instance CO_2 induced plant species replacements or increased water efficiency of extant species could change the hydrology of the peatland (e.g. Heijmans et al. 2001). In lowland *Sphagnum–Phragmites* reedlands, of which the hydrology is tightly controlled by human management, we expect that litter decomposition responses to CO_2 enrichment, if any, would be related mostly to the quantity and quality of the litter produced by plants growing at ambient vs. elevated CO_2 concentrations. Firstly, CO_2 enrichment may change litter quality via changes in species abundances, given the knowledge that vascular peatland species may vary greatly in litter quality and decomposability (Hoorens et al. 2003b; Quested et al. 2003). Second, leaf litter decomposability of a given species at elevated CO_2 may differ from that at ambient CO_2 mostly because of: (1) dilution of nutrient concentrations of green leaves due to increased storage of (mostly mobile, non-structural) organic carbon (Poorter et al. 1997; Curtis and Wang 1998; Saxe et al. 1998; Cornelissen et al. 1999); (2) a different pattern of

resorption of mineral nutrients (N, P) or carbon compounds from senescing leaves. In a large meta-analysis of CO_2 responses in terms of nutrient resorption efficiency and litter quality and decomposability no consistent overall response patterns emerged, although a slight decline in litter N concentrations was seen in the less realistic experimental set-ups (Norby et al. 2001a, see also van Heerwaarden 2004). However, peatland species were hardly represented in these datasets. Hoorens et al. (2003a) did find significantly reduced litter N concentrations and litter respiration in the peatland sedge *Carex rostrata* grown at elevated CO_2 (but not in two other vascular peatland species), while Robinson et al. (1997) found either faster or slower decomposition of shoot litter from the subarctic peatland grass *Festuca vivipara* grown at elevated CO_2, depending on the incubation environment. Here, in addition to our first hypothesis outlined above, we predict that the predominant vascular plants in lowland *Sphagnum* reedland respond to CO_2 enrichment by (a) higher C/N and C/P ratios of green leaves; (b) similar N and P resorption efficiencies resulting in higher leaf litter C/N and C/P ratios and correspondingly lower leaf litter decomposability.

We tested our hypotheses in a Dutch lowland *Sphagnum–Phragmites* peatland using a relatively non-intrusive *in situ* MINIFACE (Free air CO_2 enrichment) system (Miglietta et al. 2001; Norby et al. 2001b). In terms of uspscaling of our study to CO_2 responses of peatlands, these two-teer ecosystems can provide insights into the general responses of both oligotrophic (upland) and minerotrophic (lowland) peatlands.

Methods

Study area

We conducted our experiment in a lowland *Sphagnum–Phragmites* reedland in the nature reserve Het Guisveld, Westzaan, The Netherlands (52°29′ N, 4°47′ E. at sea level). These ecosystems used to cover large areas in the northwestern Netherlands, but only small pockets have remained to date. The climate in this region is temperate-maritime, with annual precipitation at 780 mm distributed over all seasons. Mean temperature is 17 °C in the warmest and 3 °C in the coldest month (1971–2000, KNMI weather station at nearby Schiphol airport). The upper soil profile of our experimental site hosts an approx. 50 cm thick *Sphagnum* peat layer, of which the live part consists mostly of *Sphagnum palustre* L., *S. recurvum* var. *mucronatum* (Russ.) Warnst. (= *S. phallax* Klingr.) and *Polytrichum commune* Hedw. (the latter species expanding in recent decades and during the course of our experiment). This layer is probably largely ombrotrophic. The predominant vascular plant is reed *Phragmites australis*, which has its roots and rhizomes mostly in the deeper layer below the peat layer, which is muddy, more nutrient-rich and fed at least partly by groundwater that is in contact with canals and ditches draining the area. Below the 50–120 cm tall reed canopy other predominant vascular species include the woody species *Rubus* cf. *fruticosus* and *Lonicera periclymenum*; the grasses *Calamagrostis canescens* and *Anthoxanthum odoratum*; the forb *Hydrocotyle vulgaris*; and the ferns *Dryopteris carthusiana* and *D. cristata* (for nomenclature of vascular plants see van der Meijden 1996). Other common vascular species include *Cirsium palustre*, *Angelica sylvestris*, *Scirpus lacustris* ssp. *tabernaemontani*, *Dactylorrhiza praetermissa* and *Thelypteris palustris*, with occasional *Drosera rotundifolia*, *Platanthera macrantha* and *Osmunda regalis*. The vegetation is mown once a year in winter at 15 cm above the *Sphagnum* surface, both in common regional reedland management and in our experiment. This management also partly halts strong potential encroachment by shrubs and trees, although they do persist in the system (e.g. *Salix* spp., *Aronia* × *prunifolia*, *Betula pubescens*, *Sorbus aucuparia*). The water table is on average at 20 cm below the *Sphagnum* surface (23 cm during autumn–winter, 18 cm during spring–summer) but there is strong spatial variation within the site. There are visible gradients of productivity (judging from plant heights and densities) from the (more productive) northern edge of the site near the main drainage canal to the (lower productive) more central parts. Slightly elevated, drier parts dominated by *Empetrum nigrum* were excluded from the experiment.

The MINIFACE experiment

Details of the experimental technology, design, and management are in a companion paper focusing on moss responses (Toet et al. In press) and here we only give a summary description. Our CO_2 enrichment system (MINIFACE) was modified from Miglietta et al. (2001). Following a randomised spatial design, there were six control plots and six elevated CO_2 plots, at minimum distances of 7 m to avoid cross-contamination. They were accessed via a board-walk system. It was not possible to find 12 very similar plots initially, but both treatments appeared to have a similar range of variation in productivity among plots. In enrichment plots CO_2 was injected into ambient air that was vented out of two rows of 280 (1 mm diameter) holes each in a 1 m diameter ring and, through a feedback system, maintained at 560 ppmv during daytime. Concentrations stayed within 20% of this target for more than 95% of the operational time and concentrations at 25 cm from the inner edge of the rings deviated on average less than 10% from those in the centre of the plots. CO_2 concentrations in the ambient plots, which had the same rings, but venting ambient air only, ranged generally between 360 and 400 ppmv in daytime. Fumigation started on 26 April 2001 and continued throughout the study period until January 2004, except for a break between 18 December 2001 and 22 March 2002 (before the system was made frost-proof).

Plant abundance measurements

The abundance of each of the vascular plant species as well as litter in each plot was monitored using the point-intercept method (modified from Jonasson 1988), which tends to be an adequate correlate of biomass (Jonasson 1988; Hobbie 1999). We lowered a 5 mm diameter steel pin rod through each experimental plot at 121 points in a grid with 5 cm distances (Figure 1). Thus, we sampled within a 0.5 by 0.5 m square in the central part of each plot. For each species at each point we

Figure 1. Point-intercept abundance measurements of vascular plant species in the Guisveld lowland *Sphagnum–Phragmites* reedland.

recorded the total number of hits of living leaves or stems by the rod, and subsequently calculated the total number of hits per plot. For litter we only recorded the first hit, which we assumed to scale with total amount at the plot level. The initial recording was between 6 and 17 July 2000, i.e. in the summer preceding the start of the CO_2 fumigation treatment, and the second recording between 24 and 31 July 2003.

Leaf and litter chemistry and carbon isotope signatures

Green leaf samples of three abundant species (*Phragmites*, *Rubus*, *Dryopteris carthusiana*) were collected from the plots in mid August 2002 and litter samples of the same species between late October and mid-December 2002. For some ambient CO_2 plots where target species were absent, complementary leaf and litter samples were collected from plants within 1 m distance from the plots. Leaf and litter samples were finely ground and dried at 70 °C for 48 h prior to chemical analyses. For total C and N concentrations of the three most abundant species, these samples were subjected to dry combustion on a Perkin Elmer 2400 CHNS analyzer. Leaf P concentration was measured colorimetrically (Murphy and Riley 1962) after digesting ground material in a 1:4 mixture of 37% (v/v) HCl and 65% HNO_3 (as in Sneller et al. 1999). C isotope compositions of green leaf samples (of the same three species plus *Hydrocotyle* and *Lonicera*) were determined using an elemental analyser (Carlo Erba EA1110) coupled to an isotope ratio mass spectrometer (Thermo Finnigan Delta-Plus). Stable isotope compositions are reported in the δ notation: $\delta = (R_{sample}/R_{standard} - 1) \times 1000‰$ where R represents $^{13}C/^{12}C$. Isotopic results are reported relatively to VPDB. $\delta^{13}C$ of the enriched CO_2 at the source was determined on 27 May, 11 July, 28 November and 4 December 2003. We expected isotope compositions in enriched plants to change in the direction of the composition at the source.

Nutrient resorption efficiency

Nutrient resorption efficiency (RE) was defined as $100\%* ([nutrient]_{green\ leaf} - [nutrient]_{litter})/[nutrient]_{green\ leaf}$ In this formula the nutrient pool ([nutrient]) is commonly expressed on a leaf mass basis, but this may produce significant deviations from real resorption efficiency due to simultaneous mass resorption during senescence (van Heerwaarden et al. 2003). We therefore also calculated nutrient resorption efficiency with the nutrient pool expressed on a leaf area basis (Delta-T area meter, Cambridge, UK), for *Phragmites* and *Rubus*, which retained relatively stable leaf area. For *Dryopteris carthusiana*, we expressed the nutrient resorption efficiency on a (presumably stable) lignin basis because senescing leaf fronds tend to shrivel up. See Rowland (1994) for lignin analysis.

Litter respiration assay

Four to six air-dried litter samples per species (*Phragmites*, *Rubus*, *Dryopteris carthusiana*) and treatment (each coming from a different MINIFACE ring) were used to assess litter decomposability. We followed the procedure described by Aerts and De Caluwe (1997) and Hoorens et al. (2002), which estimates litter decomposability by measuring microbial respiration rates during initial decomposition under standardized, optimal laboratory conditions. The samples were remoistened for 24 h in a filtrate of a mixture of soil and litter from the study site to promote the local microbial community, and to fully hydrate the litter. Each remoistened sample was placed in a 100 ml glass jar. In order to keep jar air humidity as high as possible, 10 ml of a potassium sulphate buffer solution was added to each jar. Some glass marbles were subsequently placed in the buffer so that the top marbles emerged from the solution. A mesh (to host the litter samples) was placed on the top of the marbles, to avoid direct contact between the buffer solution and the samples. The top of the jars was left open to permit free air circulation between the jar and the incubation environment.

The jars were randomly arranged in laboratory trays, and placed in a climate room at 20 °C in the dark, and relative humidity at 95%. Five additional jars without litter were also included in the trays. When necessary (any signs of the samples drying out), we remoistened the samples adding distilled water with a syringe directly to the litter. The litter was incubated for 66 days. During this period, we measured net CO_2 production rate

every 7–12 days as follows. The jars were sealed with a lid carrying a silicon septum, and one gas sample of 25 μl was taken from the jar atmosphere with a syringe penetrating the septum. In the gas sample, CO_2 concentration was measured with a Hewlett Packard 5890 gas chromatograph equipped with a thermal conductivity detector. After 4 h of CO_2 build-up in the air-tight jars, CO_2 concentration was measured again. The change in CO_2 concentration during that time period was assumed to be due to microbial respiration. CO_2 concentration was corrected for the CO_2 dissolved in the buffer solution (Stumm and Morgan 1981), for the air volume extracted with the syringe (50 μl), and for the residual CO_2 production measured in the five jars without litter. Litter respiration rates were expressed as mg CO_2 g l^{-1} h^{-1}. Total estimated CO_2 production per gram of litter in each jar throughout the 66 days period of the experiment (mg CO_2 g l^{-1}) was calculated by Newton integration, after the average CO_2 production respiration rate for each time interval between two measuring dates had been computed.

Statistical analyses

Point-intercept abundance data by species were $\log(x + 1)$ transformed before analyses in order to account for zero values and to improve homogeneity of variances. We subjected these to a three-way repeated measures analysis of variance (ANOVA) with species (the five with occurrence in a sufficient number of plots: *Phragmites*, *Calamagrostis*, *Anthoxanthum*, *Rubus*, *Hydrocotyle*) and CO_2 treatment as between-subject factors and year (2000 vs. 2003) as the within-subject factor. A combination of a CO_2 effect and a CO_2 *year interaction would be interpreted as a significant overall CO_2 response, while the combination of a CO_2 effect and a species *CO_2 *year interaction would be interpreted as a possible CO_2 response of one or more species. With a similar rationale, log-transformed data for the total number of live vascular plant hits or litter hits per plot were subjected to a two-way repeated measures ANOVA, with CO_2 as between-subjects and year as within-subjects factor.

To test for treatment effects on $\delta^{13}C$ signatures, on the chemistry of green leaves and litter, on nutrient resorption efficiency, and on litter respiration rates, two-way ANOVAs with treatment and species as fixed factors were performed for each variable. We explored the relationship between litter chemistry and litter decomposability by simple linear regressions between C:N or C:P ratios and total CO_2 production. Prior to the analyses, normality and homoscedasticity were checked. $\delta^{13}C$ signatures had to be $\log(-x)$ transformed and percentage data were arcsine [square-root(X/100)] transformed where necessary to improve variance homogeneity. All statistical analyses were carried out using SPSS 11.0.

Results

Plant abundance varied significantly among species (Table 1, $F = 21.7$, $p < 0.001$). However, the three-way repeated measures ANOVA revealed no significant effect of CO_2 ($F = 0.036$, $p = 0.85$), CO_2 *year ($F = 0.562$, $p = 0.69$) or species *CO_2 *year interaction ($F = 0.405$, $p = 0.80$). The two-way repeated measures ANOVAs for total vascular plant abundance (CO_2: $F = 0.462$, $p = 0.51$, CO_2 *year: $F = 0.482$, $p = 0.48$) or for litter abundance (CO_2: $F = 0.027$, $p = 0.87$, CO_2 *year: $F = 1.55$, $p = 0.24$) did not reveal any significant CO_2 effects on abundance either. The apparently greater total vascular plant abundance after CO_2 treatment (Table 1) could partly be attributed to the expansion of patches of *Rubus*, *Lonicera* or *Dryopteris carthusiana* in some of the plots (authors' unpublished data) and was not necessarily related to CO_2 enrichment. Thus, no obvious CO_2 enrichment effects on vascular plant or litter abundance were detected at all. Correspondingly, there were no CO_2 enrichment effects on vascular plant species richness (initial in July 2000: ambient treatment 8.3 ± 0.3, CO_2 enrichment 9.0 ± 0.5 species per plot; July 2003: ambient 8.3 ± 0.6, CO_2 8.5 ± 0.5 species per plot).

Foliar $\delta^{13}C$ values were consistently lower in CO_2 enriched plots than in ambient plots (Figure 2). While all individual species showed this pattern, the significant Species *CO_2 interaction supports the observation that one species, i.e. *Phragmites australis*, had a smaller difference in $\delta^{13}C$ values between treatments than others. This may be attributed to the elevated position of *Phragmites* leaves, which probably experienced lower CO_2 concentrations than the 560 ppmv

Table 1. Point intercept abundance (number of hits) of the main vascular plant species and total vascular plant litter in Summer 2003 and the change in abundance (difference in number of hits) between both recordings. SE, standard error of the mean; *N*, number of plots. Plots in which the species was absent were included in Summer 2000 (data not shown) and Summer 2003 (zero values), but plots in which a species was absent at both recordings were not used to calculate change in abundance. In each plot a 0.25 m^2 square was sampled.

Summer 2003	Ambient			Elevated CO_2		
	Mean	SE	*N*	Mean	SE	*N*
Phragmites australis	123	38	6	103	28	6
Anthoxanthum odoratum	4	1	6	3	2	6
Calamagrostis canescens	3	2	6	1	1	6
Hydrocotyle vulgaris	40	27	6	18	15	6
Rubus cf. *fruticosus*	8	5	6	43	28	6
Total hits vascular plants	199	48	6	297	97	6
Litter from vascular plants	46	6	6	66	13	6
Summer 2003 – Summer 2000 Change						
Phragmites australis	49	36	6	49	28	6
Anthoxanthum odoratum	−8	4	6	−9	8	5
Calamagrostis canescens	−16	30	2	3	2	2
Hydrocotyle vulgaris	13	35	4	1	15	5
Rubus cf. *fruticosus*	4	5	4	37	31	4
Total hits vascular plants	64	61	6	139	79	6
Litter from vascular plants	7	8	6	31	15	6

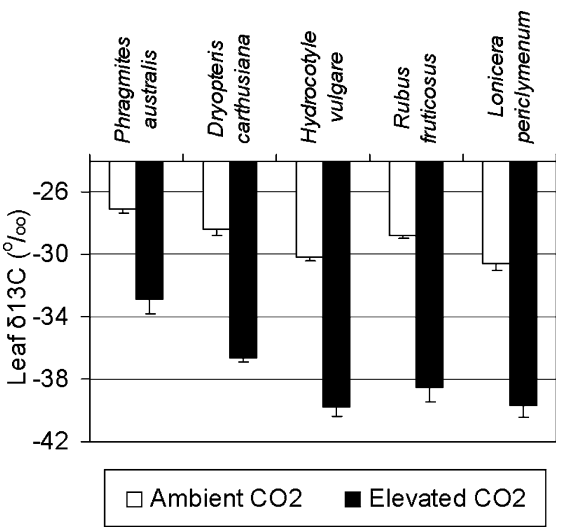

Figure 2. Response of $\delta^{13}C$ of green leaves of five vascular plant species to CO_2 enrichment. Standard errors of the means are shown one-sided only. Results of two-way ANOVA: Species: $F = 35.5$, $p < 0.001$; CO_2: $F = 539.7$, $p < 0.001$; Species * CO_2: $F = 3.28$, $p = 0.023$.

maintained lower down. For the other four species, the differences between treatments deviated only little from the calculated expected difference of 7.7‰ based on the contribution of enriched CO_2 to the total CO_2 supply in enriched plots ((560−380)/560), where ambient CO_2 had an approximate $\delta^{13}C$ value of −8‰ and enriched CO_2 of −31.9 ± 2.1‰ (see also Toet et al. In press).

In green leaves of the three focal species (*Phragmites*, *Rubus*, *Dryopteris carthusiana*) [N] and [P] were generally lower and C/N ratios and C/P ratios generally higher in CO_2 enrichment plots than in ambient plots (Table 2), although the significant CO_2 * Species interaction for C/P could be attributed to *Phragmites* not showing a CO_2 response (data not shown). Two further species with poorer replication (*Hydrocotyle*, *Lonicera*) showed similarly reduced [N] and [P] and higher C/N and C/P ratios in green leaves of CO_2 enriched plants (data not shown). Such a chemical CO_2 response was no longer detectable in leaf litter of the same species from the same plots, except for litter C/N ratio which was still somewhat higher in elevated CO_2 plots (Table 2), mainly owing to the contribution of *Dryopteris carthusiana*. The difference in response for green leaves and litter translated into lower mass-based resorption efficiency in response to CO_2 enrichment, both for N and P, but there was no significant CO_2 effect (only a trend) on area-based N or P resorption efficiency (Table 2, Figure 3). Area-based resorption efficiencies were on average 15% higher than mass-based ones in both treatments.

Table 2. Results of two-way ANOVAs on variables relation to leaf and litter chemistry, nutrient resorption efficiency and respiration, with fixed factors CO_2 treatment and species (*Phragmites australis*, *Rubus* cf. *fruticosus*, *Dryopteris carthusiana*). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns, not significant. Codes are as follows:

	CO_2 Effect Sign	CO_2	Species	CO_2*Sp.	Error df
N_g	–	***	***	ns	17
P_g	–	**	**	*	16
N_l		ns	ns	ns	18
P_l		ns	*	ns	18
C/N_g	+	***	***	ns	17
C/P_g	+	*	**	ns	16
C/N_l	+	*	ns	ns	18
$C/P_l^{(a)}$		ns	**	ns	18
N r_m	–	*	**	ns	16
P r_m	–	**	***	ns	16
N $r_A^{(b)}$		ns	***	ns	15
P $r_A^{(a)\ (b)}$		ns	**	ns	15
$L_{respiration}$		ns	ns	ns	18

N_g, N% in green leaves; N_l,N% in litter; P_g, P% in green leaves; P_l, P% in litter; C/N_g, C/N ratio in green leaves; C/P_g, C/P ratio in green leaves; C/N_l, C/N ratio in litter; C/P_l, C/P ratio in litter; Nr_m, N resorption efficiency (mass basis); Pr_m, P resorption efficiency (mass basis); Nr_a, N resorption efficiency (area basis); Pr_a, P resorption efficiency (area basis); $L_{respiration}$, Cumulative CO_2 production over 66 days (mg CO_2/g litter).

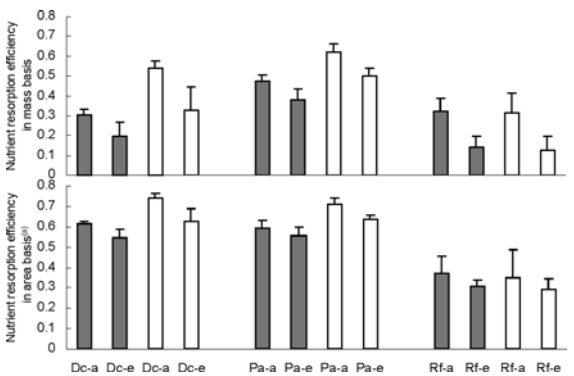

Figure 3. Mass and area based nutrient resorption efficiency. Dark bars: N resorption efficiency, white bars: P resorption efficiency. Horizontal axis: Dc, *Dryopteris carthusiana*; Pa, *Phragmites australis*; Rf, *Rubus* cf. *fruticosus*; a – ambient CO_2; e – elevated CO_2 concentration. For the bottom graph, resorption in Dc was calculated on a lignin basis, in Pa and RF on an area basis. Standard errors are shown one-sided. See Table 2 for statistical analyses.

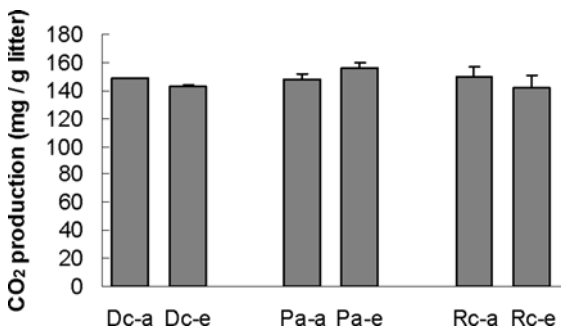

Figure 4. Cumulative CO_2 production due to initial respiration (66 days) of litter collected from ambient and elevated CO_2 plots during incubation under laboratory conditions. Horizontal axis: Dc, *Dryopteris carthusiana*; Pa, *Phragmites australis*; Rf, *Rubus* cf. *fruticosus*; a – ambient CO_2; e – elevated CO_2 concentration. Standard errors are shown one-sided. See Table 2 for statistical analyses.

There was no significant CO_2 effect on litter respiration for any of the three species investigated (Table 2), neither for patterns over time (data not shown) nor for cumulative CO_2 production (Figure 4). There was no relationship between initial litter C/N ratio and cumulative CO_2 production (negative slope, $R^2 = 0.11$, $p = 0.11$) or between initial litter C/P ratio and cumulative CO_2 production ($R^2 < 0.01$, $p = 0.88$), irrespective of the CO_2 treatment.

Discussion

The most striking finding from this 3-year experimental study in a Dutch lowland *Sphagnum*–*Phragmites* peatland was the lack of CO_2 response of the vascular vegetation component, both on the production (gains) and on the 'destruction' (losses)