Winter carbon losses from a boreal mire succession sequence follow summertime patterns in carbon dynamics

Talviaikainen hiilivuo boreaaliselta suosukkessiogradientilta seuraa kesäaikaisen hiilidynamiikan vaihtelua

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Although carbon (C) gas exchange during the summer largely determines the annual C balance of mires, the wintertime fluxes cannot be ignored. Decomposition continues as long as the soil is not frozen and a proportion of the gases produced during summer are also released during winter. We measured carbon dioxide (CO_2) and methane (CH₄) fluxes along a successional mire sequence during two winters following growing seasons with divergent weather conditions. We studied the successional trends in wintertime C release in boreal mires, and quantified the contribution of wintertime C fluxes to annual fluxes. Wintertime CO₂ and CH₄ fluxes from the successional mire sequence were related to the flux rates during the previous summer. Average winter CO₂ release along the successional sequence varied between 19.5 and 44.9 g CO₂-C m⁻² winter⁻¹(6-months), and accounted for 8–14% of the annual CO₂ release. There was no clear successional trend in CO₂ fluxes. Average winter CH₄ release along the successional sequence varied between 0.20 and 7.29 CH_4 -C g m⁻² winter⁻¹ (6-months). The winter CH₄ fluxes accounted for up to 38% of the annual CH₄ emissions. Occasional CH₄ uptake was detected at the younger successional stages during winter following the dry summer, while after the wet summer all sites emitted CH₄. In general, most of the winter C losses were composed of CO₂.

Keywords: mire succession, mire development, primary paludification, carbon dioxide, methane, snow pack, land uplift coast, Siikajoki

Introduction

Mire succession can be seen as a change from a groundwater-fed fen stage towards an ombrotrophic bog stage, which is rainwater-fed and dominated by *Sphagnum* mosses (Klinger et al. 1990, Hughes & Dumayne-Peaty 2002). During mire succession, changes occur in the peat layer thickness, vegetation, hydrology and nutrient status (Laine & Vasander 1996, Rydin & Jeglum 2006). These changes in ecosystem attributes result in accompanied changes in ecosystem functions, such as primary production and carbon (C) gas exchange between the ecosystem and atmosphere.

Boreal mires are generally sinks of atmospheric C (Gorham 1991, Clymo et al. 1998; Turunen et al. 2002; Nilsson et al. 2008). Most of the C gas exchange occurs during the growing season when atmospheric carbon dioxide (CO_2) is bound by plants during photosynthesis. Additional inputs of organic C to the ecosystem occur through water flow from surrounding areas (Gorham 1991). C is regularly lost from the ecosystem through respiration, methane (CH₄) emissions and water runoff (Gorham, 1991 Roulet et al.,2007), while fires may cause rapid periodic losses (Turetsky & Wieder 2001).

Despite the low temperatures, snowpack and soil frost, the C gas exchange of boreal mires has been shown to continue during the winter months (Dise 1992; Nilsson et al. 2008). The wintertime C release may be substantial and therefore, have an important impact on the annual C gas balance (Melloh & Crill 1996; Alm et al. 1999a; Lafleur et al. 2003). Part of the produced CH_4 and CO_2 is stored in the peat during the growing season and released through diffusion during winter. However, despite the cold air temperatures decomposition may also continue throughout the winter as the soil is rarely too cold for decomposition (Kelly et al. 1968; Dise et al. 1993, Mariko et al. 2000, Roehm & Roulet 2003). The winter C release occurs as a direct flux from the soil to the atmosphere during snow-free periods or as an indirect flux through the snowpack. A snowpack of less than one meter promotes emissions by acting as a thermal insulator that keeps the soil warmer than the air and, therefore, enhances decomposition. When the snowpack is more than two meters deep, it strongly slows down or interrupts gas diffusion (Mariko et al. 1994).

During the last two decades, several studies have investigated the wintertime C exchange of boreal mires (Dise 1992, Melloh & Crill 1995, 1996, Alm et al. 1999a, Panikov & Dedysh 2000, Aurela et al. 2002). To our knowledge, this is the first study exploring the role of wintertime C release along a mire succession gradient. Our previous studies (Leppälä et al. 2008, 2011a, 2011b) revealed successional changes in the rates and dynamics of growing season CO2 and CH4 fluxes. The early successional stages appeared to have negligible CH₄ release during a dry growing season, after which the emissions increased under moister conditions, while the older stages acted as a constant CH₄ source (Leppälä et al. 2011b). The net C sink function appeared to peak in the middle of mire sequence, i.e. the intermediate successional phase had the highest net ecosystem CO₂ exchange (NEE), but only small differences were observed in the ecosystem respiration (R_{ECO}) between the successional phases (Leppälä et al. 2008).

In here we aim to study whether successional patterns, similar to those detected during the growing seasons, may also occur during the following winters. We studied the successional trends in wintertime CO_2 and CH_4 fluxes and quantified the contribution of wintertime release to the annual fluxes.

Material and methods

Study area and experimental design

The study was conducted at the land-uplift coast of Bothnia Bay in Siikajoki (64°45′N, 24°42′E), western Finland. The long-term average air temperature in the area for the period November to April is -5.3°C (Drebs et al. 2002). The study sites constituted a sequence that contains five differently aged mires. All sites had developed via primary paludification (Merilä et al. 2006) and exemplify a change from the first stages of mire succession towards a bog-phase. The mires were 0.5 to 1.5 ha in size and their ages from youngest to oldest are: 178, 205, 700, 1000 ± 70 and $2520\pm$ 50 BP yrs. The age estimation of the three youngest sites SJ1, SJ2, and SJ3 is based on the equation by Ekman (2001) and the bottom ages of the two oldest sites (SJ4 and SJ5) were ¹⁴C dated.

Along the 8 km successional mire sequence from the coast to inland, the vegetation changed from sedge and herb dominated to shrub and *Sphagnum* dominated. At the youngest site (SJ1), neither the vascular plant nor moss cover was fully closed. Along the successional sequence, the vegetation cover increased and at the oldest site (SJ5) the moss cover was already very dense. At the two youngest sites, SJ1 and SJ2 (wet meadows), the peat depth was less than 0.1m, while at sites SJ3 (mesotrophic fen), SJ4 (oligotrophic fen) and SJ5 (fen-bog transition), the peat depths were 0.4, 0.9 and 1.9m, respectively. More site details are given in Leppälä et al. (2008, 2011b).

In order to measure CO_2 and CH_4 fluxes, we located five permanent sample plots at each site. The sample plots (0.56 x 0.56m) were located to cover the site-specific variation in vegetation, topography and water level. Water table well (a perforated tube with a diameter of ~2cm), was inserted into the soil beside each sample plot. Sample plots were surrounded by boardwalks to minimize disturbance.

Measurements of CH₄ and CO₂ fluxes and environmental parameters

CH₄ and CO₂ flux measurements were made monthly (November-April) during the winters 2003-2004 and 2004-2005 (in total 12 times per site). The measurements were conducted using either the chamber or the snowpack method depending on the thickness of the snowpack. In both methods, the C gas concentration of the air samples was determined within 24 hours in the laboratory. CO₂ concentration was determined in the Department of Chemistry, University of Oulu by an EGM-2 gas analyzer (PP Systems, UK) and the CH₄ concentration was determined using a Perkin-Elmer 8420 gas chromatograph (Perkin-Elmer Co., Beaconsfield, Buckinghamshire, UK) equipped with a flame ionisation detector (temperature 200 °C). Gas samples were injected

through a syringe filled with calcium carbonate to the external six port gas sample injector (Vici Ag, Schenkon, Switzerland) equipped with 1 ml loop. Before injection the loop was flushed with 15 ml of sample. From the loop sample was injected with carrier gas (He, 22 psig) to the column (HayeSep Q, mesh: 80/100, length: 6 ft, OD: 1/8" (Alltech, Deerfield, IL, USA)). Two standard samples were measured before the four actual samples and the average of the standards was compared to the samples.

The chamber method was used during snowfree periods (mostly November-December) and if the snowpack was less than 20 cm thick. The opaque aluminium chamber (size 60x60x30 cm) equipped with a battery-operated fan was placed in the water groove of the collar located around the sample plot to keep the chamber air tight during the measurement. In addition chamber sides were packed with snow to keep the temperature similar inside of the collar at the level of untouched snow pack. Only in few cases of deeper snow pack (nearly but less than 20 cm) insulation was done with moist snow. Gas samples were taken from the headspace into 30ml syringes after 5, 15, 25 and 35 minutes from the closure. Simultaneously with gas measurements, air temperature inside the measurement chamber and the water table level (WT) were measured. The fluxes were calculated from the linear change in the gas concentration in relation to time, area, volume, and air temperature.

The snowpack diffusion method was used during the snow-covered season (more than 20cm of snow) (mostly January–April). The gas samples were taken into syringes from the top and bottom of the snowpack using a 2mm diameter metal pipe. In addition, the snow porosity and the snow temperature were determined. The flux rate was calculated from the difference in concentrations between the bottom and top samples with respect to snowpack depth, porosity and snow temperature using Fick's Law of diffusion (Sommerfeld et al., 1993). The chamber and snowpack diffusion methods are described in more detail by Alm et al. (1999a, 2007).



Figure 1. A) Air temperature (7-day moving average) and daily soil temperatures, and B) linearly interpolated average snow depth at the sites during winter 1 (2003–2004) and winter 2 (2004–2005).

Kuva 1. A) Ilman lämpötila (seitsemän päivän liukuva keskiarvo) ja päivittäiset maalämpötilat, B) lineaarisesti interpoloidut lumikerroksen paksuudet tutkimusaloilla talvena 1 (2003–2004) ja talvena 2 (2004–2005).

Data analysis

We used linear interpolation between the measurements to reconstruct the fluxes over the two winters (from November to April) in 2003–2004 (winter 1) and 2004–2005 (winter 2). To estimate the proportion of winter fluxes from the annual flux we utilised growing season CO_2 and CH_4 flux data from Leppälä et al. (2011a, 2011b). In the present study we used the CO_2 exchange models from Leppälä et al. (2011a) to reconstruct average fluxes for each study site.

Air temperature and precipitation data were obtained from a nearby weather station (64°41'N, 25°05'E). Hobo data loggers (H08-008-04, Onset Computer Corporation, USA) were used to obtain continuous soil temperature data at a 30cm depth in each site. The thickness of snowpack was linearly interpolated to cover the whole wintertime for both winters.

We applied repeated measures ANOVA to test differences in the cumulative CO_2 and CH_4 fluxes, and in the thickness of snowpack. Winter

was used as the within-subjects factor and site as between-subjects factor. The tests were performed with SPSS 19.0 for Windows (SPSS, Inc.).

Results

Environmental conditions during the winters

The winter 2004–2005 (winter 2) was colder than the winter 2003–2004 (winter 1), with average air temperatures of -4.7° C and -4° C during November–April, respectively. Both winters were slightly warmer than the long-term average for the same period, i.e., $-5.3 \,^{\circ}$ C (Drebs et al. 2002). The snowpack was at its thickest in the middle of February in both winters, and it was thicker during winter 1 at all sites (p < 0.001) (Fig. 1). In both years, the second youngest mire site SJ2 had the thickest snowpack (p < 0.001). In winter 1 the snowpack remained low until mid-February after which it rapidly gained thickness



Sites

Figure 2. The mean \pm SE of cumulative A) CH₄-C and B) CO₂-C emissions during winter 1 (2003–2004) and winter 2 (2004–2005). Statistically significant differences (P<0.05) are marked with *.

Kuva 2. Keskiarvo \pm SE kumulatiiviselle A) CH₄-C ja B) CO₂-C emissioille talvena 1 (2003–2004) ja talvena 2 (2004–2005. Tilastollisesti merkitsevät erot (P<0.05) on merkitty tähdellä (*).

(Fig. 1). Soil temperature followed the changes in air temperature with a time lag, declining from November to April and thereafter increasing. The temperature at 30cm soil depth remained mostly above 0°C during the winters (Fig. 1). When the soil was not frozen, the water table was mostly near the soil surface and varied from -15cm below to 10cm above the peat surface (data not shown). The water table was lowest at the site SJ3.

Variation in winter C emissions between the sites

On average, the sites emitted 0.09–0.27 g CO_2 -C m⁻² d⁻¹ during the two winters, and the cumulative CO_2 emissions over the 6-month winter

period varied from 18.6 to 43.7g CO_2 -C m⁻² (Fig. 2). There were no statistically significant differences in the CO_2 fluxes between the sites (Table 1). However, the site SJ3, a mesotrophic fen, had slightly higher fluxes than the other sites (Fig. 2a).

The 6-month cumulative winter CH₄ flux varied between 0.20 and 7.29 CH₄-C g m⁻², with a daily average varying between 0.64 and 37.65 CH₄-C mg m⁻² d⁻¹ (Table 2). During winter 2, which followed a rainy summer, CH₄ fluxes peaked in the middle of the successional mire sequence, i.e. in the mesotrophic fen site (SJ3).

Interannual variation, and contribution to annual C gas fluxes

The seasonal pattern in CO_2 and CH_4 release was rather similar in all sites and for both winters: the fluxes were lowest during the midwinter when the snowpack was at its thickest, and the highest emissions were detected either during the early or late winter (Fig. 3). CH_4 uptake was observed at some individual sample plots at the two youngest sites, SJ1 and SJ2, from November to January during winter 1, but on average these sites acted as CH_4 sources to atmosphere (Table 2). SJ3 acted as a small CH_4 sink from November to March during winter 1, with an average uptake of -0.27 mg CH_4 -C m⁻² d⁻¹.

Table 1. Repeated measures ANOVA of the cumulative winter CO_2 and CH_4 fluxes of sites SJ1–SJ5 (n = 5) with winter as within-subjects factor and with site as between-subjects factor.

Taulukko 1. Alojen SJ1–SJ5 (n=5) kumulatiivisten talviaikaisten CO₂- ja CH₄-virtojen vertailu toistettujen mittausten varianssianalyysillä.

Parameter	DF	F	р	
CO ₂				
site	4	5.484	0.004	
winter	1	0.955	0.340	
winter*site	4	0.407	0.801	
CH ₄				
site	4	3.104	0.039	
winter	1	37.689	0.000	
winter*site	4	4.753	0.007	



Figure 3. Measured wintertime CO_2 and CH_4 emissions during winter 1 (2003–2004, black dots) and winter 2 (2004–2005, white dots). Data are mean \pm SE of five measurement points at each site.

Kuva 3. Mitattu talviaikainen CO_2 ja CH_4 emissio talvena 1 (2003–2004, mustat pisteet) ja talvena 2 (2004–2005, valkoiset pisteet). Kukin piste on yhden alan viiden mittauspisteen keskiarvoa \pm SE.

The CO₂ flux rate varied little between the two winters and no significant differences were found (Table 1). The wintertime CO₂ release accounted for 8–14% of the annual CO₂ ecosystem respiration (Table 2). The proportion was slightly higher at the two oldest sites, especially during the second year.

There was a clear difference in the CH_4 emissions between the two winters in most sites. At sites SJ1 to SJ4, the CH_4 fluxes differed significantly between the two winters, with higher emissions during winter 2 (Table 1) (Fig. 3). At the oldest site SJ5, the CH_4 fluxes did not differ between the winters (p = 0.267) (Table 1). The winter CH_4 fluxes accounted for up to 38% of the annual CH_4 emissions. These proportions remained similar at the oldest site between years, while at the other sites the winter CH_4 flux accounted for more of the annual CH_4 emissions during the second year. Despite higher CH_4 emissions following the wet summer most of the total annual C gas efflux was contributed by CO_2 (Table 2).

Discussion

Winter fluxes in relation to the previous summer

The patterns in wintertime CO_2 and CH_4 emissions along the succession gradient were similar to those detected during the growing seasons (Leppälä et al. 2008, 2011a, 2011b). In our previous study (Leppälä et al. 2008) the rates of ecosystem

Table 2. Daily average CO_2 and CH_4 emissions (n=5) and annual ecosystem respiration CO_2 and CH_4 emissions along the sequence (for the sites SJ1–SJ5) during winter 1 (2003–2004) (left in the column) and winter 2 (2004–2005) (right in the column). The integrated annual emissions cover the periods of 1 July 2003 – 30 June 2004 and 1 July 2004 –30 June 2005. The values in parenthesis indicated the proportion of winter emissions to the total annual release of CO_2 and CH_4 .

Taulukko 2. Päivittäinen talviaikaisen vuon keskiarvo (n=5) ja vuosittaiset CO_2 ja CH_4 kumulatiiviset vuot sukkessiogradientilla (aloille SJI–SJ5) talvella 1 (2003–2004) (vasen sarake) ja talvella 2 (2004–2005) (oikea sarake). Integroimalla lasketut vuosittaiset vuot kattavat ajanjaksot 1. heinäkuuta 2003 – 30. kesäkuutta 2004 ja 1. heinäkuuta 2004 – 30. kesäkuuta 2005. Suluissa olevat arvot tarkoittavat talviaikaisten voiden osuutta vuosittaisista CO_2 ja CH_4 kokonaispäästöistä.

		C) ₂			C	H4	
	Average d winter flu (g C m ⁻² c	laily x t ⁻¹)	^a Annual ecosystem (g C m ⁻²)	respiration	Average d winter flu (mg C m ⁻	laily x ² d ⁻¹)	^a Annual emission (g C m ⁻²)	
	Päivittäin keskivuo talvella	en	Vuotuinen ekosysteen hengitys	nin	Päivittäin keskivuo talvella	en	Vuotuinen päästö	
Site	winter 1	winter 2	winter 1	winter 2	winter 1	winter 2	winter 1	winter 2
1	0.16	0.16	341.5 (9%)	370.6 (8%)	0.64	10.43	1.8 (11%)	14.1 (16%)
2	0.2	0.21	333.2 (11%)	386.4 (10%)	0.92	18.45	2.5 (12%)	14.3 (28%)
3	0.23	0.25	407.1 (10%)	394.4 (11%)	0	37.65	1.3 0 %)	18.9 (38%)
4	0.11	0.17	207.2 (9%)	227.8 (13%)	7.8	31.05	10.5 (15%)	23.6 (26%)
5	0.2	0.2	261.7 (12%)	259.5 (14%)	17.25	11.7	18 (17%)	18.5 (16%)

^aEcosystem respirations and CH_4 emissions during growing season are according to Leppälä et al. 2011a and 2011b. The periods between measurements are linearly interpolated to cover the entire year.

respiration differed only slightly between the sites during the growing season. Similarly in this study, only minor variations in CO₂ emissions were noticed between sites during wintertime. This is in accordance with large comparisons of Reichstein et al. (2007) and Lund et al. (2010) that show only little variation in the overall respiration rates between boreal mires. Furthermore, we also found a clear connection between growing season CH₄ emissions (Leppälä et al. 2011b) and CH₄ flux rates during the following winter. The three youngest sites had negligible CH₄ emissions during the dry growing season, whereas during the wet growing season the emissions clearly increased (Leppälä et al. 2011b). The same pattern was observed during the following winters. Thus, the summertime gas exchange determines at least part of the wintertime C release. This is reasonable as the CO₂ and CH₄ formed in the peat during the summer are stored in the pore water and released from peat through diffusion during winter (Dise 1992, Dise et al. 1993). Winter emission rate is a result of the diffusion of gas stored during summer and the diffusion of the gas formed during winter. Despite colder air temperatures, the soil temperature is usually adequate for soil respiration even during winter and the substrate stored during summers provides the energy needed for the decomposition processes (Kelly et al. 1968, Mariko et al. 2000, Roehm & Roulet 2003, Juottonen et al. 2008). Both CO_2 and CH_4 fluxes were highest from the mesotrophic site (SJ3). Along the sequence, this is the first site that has an adequate peat layer, vital fen vegetation dominated by sedges and a rather dense moss carpet. These conditions ensure that there are optimal conditions for substrate production during the summer, which in turn will enable the decomposition processes to continue during the winter months.

Methane emissions during winter

Measured daily CH₄-C emissions (0.64–37.65 mg m⁻²) and the cumulative winter losses of CH₄-C (0.20–7.29 mg m⁻²) were in accordance with earlier studies (Dise 1992, Alm et al., 1999b, Moore & Roulet 1995, Nilsson et al. 2001).

Along the succession gradient, CH₄ uptake was measured during winter 1 at sites SJ1, SJ2 and SJ3, where the lowest water table levels were also detected. Aerobic methanotrophs consume methane and benefit from the additional air space when water tables are low (Sundh et al. 1994). Similar to our study, winter time CH_4 uptake has also been observed from forestry drained peatlands (Martikainen et al. 1995, Alm et al. 1999b). The seasonal CH_4 dynamics often involve high episodic fluxes during spring thaw (Tokida et al. 2007; Hargreaves et al. 2001). Although we were not able to catch episodic fluxes with the resolution of monthly measurements, we noticed clearly higher emissions in April, especially at site SJ3.

Importance of winter fluxes

Measured CO₂-C values ranged between 0.11 and 0.25 g m⁻² d⁻¹ resulting in total losses of 20 to 45 CO₂-C g m⁻² during winters. The magnitude of both the daily and winter losses are similar to previous studies carried out in boreal mires (Lafleur et al. 2003, Alm et al. 1999b). Furthermore, the annual ecosystem respiration of the sites ranged from 207 to 407 g CO₂-C m⁻² (Table 2), being similar to those found earlier in boreal mires, 60-539 g C m⁻² yr⁻¹ (Silvola et al. 1996, Lund et al. 2010 and the references therein). The wintertime CO_2 release accounted for 8–14% of the annual CO₂ release, in the same range as earlier estimates for mires (Alm et al. 1999b). Alm et al. (1999a) measured higher proportions in bogs than fens. Even though the proportions were slightly higher at the older end of the sequence during winter 2, no clear difference was found. The winter CO2-C losses from the different sites along the sequence were equivalent to 14-62% of the 2004 growing season NEE detected in our previous study (Leppälä et al. 2008). Similarly Lafleur et al. (2003) found 30-70% of the net gain in summer was released during the winter months.

The cumulative annual CH₄ emissions ranged from 1.3 to 23.6 g C m⁻²; this is in accordance with earlier studies with emissions ranging from 1.4 to 17.3 g CH₄-C annually (Nilsson et al. 2001, Huttunen et al. 2003, Rinne et al. 2007). The contribution of wintertime CH₄ fluxes to annual emissions has been observed to range between 4 to 33% (Dise 1992, Melloh & Crill 1996, Alm et al. 1999b, Rinne et al. 2007). Our results fit

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into this range, as the sites released 11-38% of the annual CH₄ emissions during the respective winters.

The monthly winter time sampling in our study may underestimate the annual emissions, especially the CH_4 emissions that can sporadically be high during spring time. Therefore the presented estimates for the cumulative emissions that are based on monthly measurement are very conservative because they likely have missed the emission peaks. While accounting the low resolution in sampling, estimates were reasonable and the study showed the link between summer time C fluxes and the fluxes of the following winter.

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Tiivistelmä: Talviaikainen hiilivuo boreaaliselta suosukkessiogradientilta seuraa kesäaikaisen hiilidynamiikan vaihtelua

Vaikka kesäaikainen hiilikaasunvaihto (C) suurilta osin määrittääkin soiden vuosittaisen hiilitaseen, ei talviaikaisia hiilivirtoja voida jättää huomiotta. Orgaanisen aineen hajotusprosessit jatkuvat niin kauan kuin maa pysyy sulana sekä osa kesällä tuotetusta maahan varastoituneesta kaasusta vapautuu talven aikana ilmakehään. Mittasimme hiilidioksidi- (CO_2) ja metaanivoita (CH_4) suosukkessiogradientilla kahtena talvena, jotka seurasivat kahta sääoloiltaan eroavaa kesää. Tutkimme onko boreaalisten soiden talviaikaisessa hiilipäästössä havaittavissa soiden kehitykseen liittyviä muutoksia sekä määritimme kuinka suuri merkitys talviaikaisilla hiilivoilla on vuotuisille voille.

Talviaikaiset CO_2 ja CH_4 vuot suosukkessiogradientilta ilmakehään olivat suhteessa edellisen kesän tasoon. Keskimääräinen talviaikainen hiilipäästö sukkessiogradientilta vaihteli välillä 19.5 ja 44.9 g CO_2 -C m⁻², vastaten 8–14 % vuotuisesta hiilipäästöstä. Suon kehitykseen liittyvää trendiä CO_2 virroissa ei havaittu. Nuoremmat sukkessiovaiheet toimivat ajoittain metaanin nieluina kuivaa kesää seuranneena talvena, kun taas sateisemman kesän jälkeen kaikki suot olivat metaanin lähteitä. Pääosa talven hiilipäästöstä koostui hiilidioksidista.

Avainsanat: sukkessio, suon kehitys, primaarisoistuminen, hiilidioksidi, metaani, lumikerros, Siikajoki, maankohoamisrannikko

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