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Carbon dynamics and changing winter conditions: a review of current understanding and future research directions

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Abstract

Despite the important role of winters for northern ecosystems, it remains the least understood of all the seasons. Here, we summarize existing empirical studies on winter climate and carbon dynamics and highlight some important future research directions. The existing studies include field-scale snow-cover manipulation experiments representing extreme soil climate conditions, laboratory soil incubations studying the influential factors, and time-series of climate and carbon data showing long-term natural variations and existing trends. Most of the field and laboratory experiments indicate an increased soil organic carbon loss due to soil frost. Long-term data demonstrate temporal changes in winter CO_2 efflux and its important contribution to the annual fluxes. A number of research priorities to improve our understanding of winter conditions include (i) ecosystem processes in the fall-winter and winter-spring shoulder seasons, (ii) extreme events, (iii) partitioning into organic- and inorganic carbon, (iv) carry-over effects of winter and growing season on each other, (v) long-term cumulative impacts, and (vi) improved winter process modelling. These areas of research would enable an improved understanding of the role of the snow covered period for carbon cycling, and provide a basis for more realistic models that include winter processes.

1 Introduction

Long winters, including seasonal snow-cover and variable soil frost conditions, are defining features over large areas of the Northern Hemisphere. Approximately 57 % of the terrestrial land surface experiences long periods of freezing, at least occasionally (Duguay et al., 2005). In the arctic and boreal biomes, as well as in large parts of the northern temperate region, winters constitute a major part of the year. These northern ecosystems are particularly vulnerable to anticipated climate change (IPCC, 2007) at the same time as they store more than half of the terrestrial organic carbon pool and therefore play a major role in the global carbon cycle (Hobbie et al., 2000). Litter production, root exudates and microbial biomass are the major sources of organic carbon in soils. Carbon in the high latitude systems is sequestered through photosynthesis and lost mainly as autotrophic and heterotrophic CO_2 respiration, release of methane (CH_4) and volatile organic compounds, or through surface water export of dissolved and particulate carbon. Dissolved organic carbon (DOC) plays a fundamental role in biogeochemical processes as it acts as a source of energy and nutrients (Berggren et al., 2010) and a strong complexing agent for metals and micropollutants (e.g. Bergknut et al., 2010). DOC has also impacts on the depth of the photic zone in surface waters (Weishaar et al., 2003; Karlsson et al., 2009), pH (Hruska et al., 2003) and food web structure (Jansson et al., 2007), and is overall important for landscape carbon balance (Cole et al., 2007).

Climate observations during the 20th century have shown a more pronounced increase in air temperature of the northern regions as compared to the global mean (Zhang et al., 2008; Campbell et al., 2010), with a more rapid temperature increase during winter and spring in the last few decades (Cayan et al., 2001; Parida and Buermann, 2014). Global climate projections predict a continued increasing trend for air temperature in the coming decades, again with more warming occurring in the winter season (IPCC, 2001; Christensen and Christensen, 2007; Zhang et al., 2008). Records of winter precipitation have shown a range of responses, from no clear trend (Hayhoe et al., 2008; Campbell et al., 2010) to an increase in rain-to-snow ratio in the last few decades (Huntington et al., 2004; Knowles et al., 2006). There is more uncertainty in the projections of future precipitation compared to temperature, but increases of up to 30 % in winter precipitation have been suggested (Hamburg et al., 2013), with more arriving as rain than snow in the future (Anandhi et al., 2013; Casson et al., 2012). In high-latitude regions, a major carbon cycle feedback to warming is melting of permafrost followed by the release of substantial amounts of carbon into atmosphere (Schuur et al., 2015). Snow-cover protects the soil from temperature fluctuations, regulates soil frost regime, provides water upon melting and controls winter biogeochemical processes (Arnold et al., 2014; Brooks et al., 2011; Campbell et al., 2010; Groffman et al., 2001). Therefore any change in snow-cover arrival, duration and/or extent may have implications on the soil structure, root mortality, runoff generation, spring snowmelt, nutrient fluxes and carbon dynamics (Anandhi et al., 2013; Casson et al., 2012; Edwards et al., 2007). The insulating effect of snow-cover is a function of the depth and density, and snow depth of 20–40 cm is suggested to insulate the soil environment enough to decouple the air- and soil temperatures (Edwards et al., 2007; Hayashi, 2013). Due to the insulating effect of snow-cover, changes in air temperature cannot directly be translated into an alteration in the soil temperature in snow-covered regions (Jungqvist et al., 2014; Zhang et al., 2008). Therefore, it is important to consider the interacting effects of changes in air temperature, precipitation patterns and snow-cover in order to understand and predict how soil temperature will be affected by a changing climate (Lawrence and Slater, 2010). In addition to alterations in soil temperature, changes in the patterns of snow-cover may have implications for the soil frost regime and freeze–thaw events throughout the winter (Stieglitz et al., 2003). Groffman et al. (2001) introduced the concept of "colder soils in a warmer world" highlighting the development of soil frost in response to later/lesser formation of snow-cover, and its implications for ecosystem functioning, carbon and nutrients. Although colder soil temperatures generally promote the soil frost formation, soil type, organic content and moisture control the formation of different types of soil frost (concrete, granular, prismatic), occurrence of frost heaving and therefore the impacts on soil structure, root injuries and carbon dynamics.

Compared to numerous studies on the role of the growing season, little work has been carried out on and during winter conditions despite its fundamental role for ecosystem processes. In fact, winter ecosystem processes are likely the least understood of all seasons. The objective of this work is therefore to summarize the empirical studies on winter climate and its role for the fate and behavior of carbon, in mid to high latitude regions. The paper also points at major research gaps in our general understanding. The studies we review include field-scale experiments representing extreme soil climate conditions, laboratory experiments providing more details on the contributing factors and processes, and time-series of climate and carbon data showing the long-term natural variations and changes. In addition to the literature compilation of existing studies, we highlight some research directions which deserve more attention in order to move our understanding of the role of winter climatic conditions forward.

2 Methods

2.1 Field and laboratory experiments

The studies included in this paper have been carried out in mid to high latitude regions including the arctic, boreal and temperate biomes. In the field studies, the snow-cover was primarily manipulated using snow removal treatments (Table 1). By taking away the snow the insulating effect of the snow-cover was removed. This, in turn, promoted deeper soil frost development. Exiting laboratory experiments consisted mainly of soil incubations (soil cores/columns) at different low temperatures, different durations and with/without freeze–thaw events (Table 2). In most of the field and lab experiments, dissolved organic carbon (DOC) has been studied as the response variable. In a few studies, carbon in gaseous inorganic forms (CO_2/CH_4) was explored. Among the existing experiments (Tables 1 and 2), there were several studies which explicitly explored the effects of cold temperatures and frost on carbon compounds, and in some cases on roots and soil microbial biomass and activity, combining both laboratory and field-scale experiments in the same systems.

2.2 Time-series and literature search

The time-series datasets mainly included climate variables, total organic carbon (TOC) and DOC in streams, and soil CO_2 efflux (Table 3). In a large majority of the studies on organic carbon, changes were primarily explored during the following season.

Literature search was initially performed in Web of Science^{TM} (Thomson Reuters) using keywords such as “carbon”, “soil”, “stream”, “winter climate”, “climate change”, “soil frost” and “snow-cover” in different combinations. The search was then expanded using citations in the relevant papers and known exiting literature. Studies which indirectly dealt with carbon production or allocation (e.g. vegetation and microbial community) were also included.

3 Results

3.1 Empirical experiments versus time-series

Both field and laboratory studies focused primarily on soil solution DOC (and TOC) leachates and extracts, while the time-series were primarily related to stream and riverine DOC and soil CO_2 efflux. While field and lab studies focused on the treatment effects of changes in snow-cover and soil frost regime, the time-series focused mainly on other aspects of winter climate such as timing of snowmelt and temperature changes. The results of field and laboratory experiments on the same types of soils and at the same areas have not been consistent in all cases. Due to different designs and methods applied, it is sometimes difficult to compare all studies and draw general conclusions (Henry, 2007).

3.2 Field and laboratory studies

Most field and laboratory studies of soil freezing effects indicate an increase in DOC, but some observations depart from this trend. In Norwegian heathland soils and boreal forests of northern Sweden (Fig. 1), soil frost increased the soil solution DOC and its lability in both field (Austnes et al., 2008; Haei et al., 2010) (Table 1) and laboratory experiments (Austnes and Vestgarden, 2008; Vestgarden and Austnes, 2009; Haei et al., 2012) (Table 2). While the length of winter (days with frozen soils) could explain the variations in both concentration and quality of DOC in the Swedish field study (Haei et al., 2010), colder temperatures (not frost duration) appeared to be more influential in the laboratory incubation of soil samples from the same area (Haei et al., 2012). In addition, in northern Sweden, Ågren et al. (2012) reported an increase in mire profile

DOC by an increase in soil frost depth. A one-winter snow removal in an alpine forest in Sichuan, China, also led to higher soil DOC concentrations and microbial biomass carbon (Tan et al., 2014) (Table 1). In the northern hardwood forests at Hubbard Brook Experimental Forest (HBEF) in New Hampshire, USA, no soil freezing effect was detected on the soil solution DOC after a two-year snow removal treatment (Fitzhugh et al., 2001). However, in a later study, Groffman et al. (2011) found higher DOC concentration as affected by soil frost in a two-year study at the same area, but the changes were not consistently significant (Table 1). In German temperate forests, soil DOC concentration was not affected by soil frost in the field (Hentschel et al., 2009), while in a snow-pack manipulation in a temperate deciduous forest in western Michigan, DOC concentrations decreased in both snow removal and ambient plots, compared to the snow addition, prior to spring snow-melt, and were not different between the treatments in the spring (Aanderud et al., 2013) (Table 1). However, in the latter experiment, soil temperatures reached to minima of −1 and −3 °C in the ambient and snow removal treatments, respectively. Laboratory incubations of organic soil cores from two forests at HBEF, at −15, −0.5 and +5 °C, did not have a significant effect on neither DOC nor cumulative fluxes of CO_2 and CH_4 (Reinmann et al., 2012) (Table 2), but a two-week permanent soil frost in the laboratory increased the DOC concentrations at −8 and −13 °C (but not at −3 °C) in the soils of the German temperate forest, and did not lead to higher DOC lability (Hentschel et al., 2008) (Table 2). Higher DOC concentrations have been observed after freeze–thawing cycles (Austnes and Vestgarden, 2008; Grogan et al., 2004), while no effects of freeze–thaw cycles were found on the quality of DOC (Austnes and Vestgarden, 2008; Hentschel et al., 2008).

There are fewer field studies dealing with inorganic carbon in response to changes in snow cover and soil frost. Some of the few existing experiments studied the concentrations and fluxes of inorganic carbon (mainly CO_2) during winter and some in the winter-spring transition time. At HBEF, Groffman et al. (2006) found significantly lower winter fluxes of CO_2 and CH_4 as the result of snow removal treatment, accounting for 9–15 % and 13–18 % of the annual fluxes of CO_2 and CH_4, respectively (Table 1). However,

CO_2 production was stimulated by severe freezing (−13 °C) in a laboratory experiment at the same area (Neilson et al., 2001) (Table 2). In temperate forests of Germany, (Muhr et al., 2009) found a decrease in both total- and heterotrophic soil respiration in response to soil frost, while there was no evidence for respiration sensitivity to freezing temperatures in the temperate deciduous forests of Michigan (Aanderud et al., 2013) (Table 1). Aanderud et al. (2013) also found that winter fungal and bacterial communities changed during winter and response of the bacterial community was prolonged into the spring-thaw period. Öquist and Laudon (2008) reported a negative correlation between the maximum soil frost depth in winter and the rates of CO_2 emission into atmosphere during the following growing season, in the boreal forests of northern Sweden (Table 1). In the same area, longer durations of soil frost largely explained the enhancement of soil heterotrophic respiration (Haei et al., 2013) (Table 1), and fungal to bacterial growth ratio increased as the result of intensive soil freezing (temperatures down to −12 °C) (Haei et al., 2011) (Table 2). In a one-year experiment in an alpine bog in northern Italy, no snow removal effect was observed on soil respiration and microbial biomass carbon (Bombonato and Gerdol, 2012) (Table 1). Soil carbon amendment and snow manipulation in forests of Colorado Rockies indicated a positive correlation between carbon availability and winter CO_2 fluxes in snow-covered soils (Brooks et al., 2005) (Table 3). In the same experiment, soil microbial preference to utilize the newly added carbon to the soil indicated the growth and activity of soil heterotrophic community in temperatures between 0 and −3 °C (Table 1). In a laboratory incubation of forest soils with carbon and nutrients addition, Drotz et al. (2010) found no difference between the allocation of carbon into newly synthesized biomass and respired CO_2, between frozen and unfrozen soils. However, heterotrophic respiration was identified as the main contributor to the soil CO_2 efflux during the simulated winter conditions in a chamber respiration study, accounting for 75 % of the total winter efflux (Beverly and Franklin, 2015). Studies on frost and inorganic carbon mainly indicated rising levels of CO_2 in response to continuous frost and upon thawing (e.g. Goldberg et al., 2008; Vestgarden and Austnes, 2009; Haei et al., 2011).

Although soil frost did not affect the soil microbial biomass and lignin contribution to TOC (Schmitt and Glaser, 2011), it increased the fine root mortality by 30 % and led to three times decrease in root longevity in the temperate German forest (Gaul et al., 2008) (Table 1). In contrast, Repo et al. (2014) reported longer lifetime of fine roots of their deep soil frost/snow removal plots in Finnish boreal forests (Table 1). At HBEF, mild freezing (–5 °C) at the same area led to increased overwinter fine root mortality, and was mainly attributed to the mechanical damage to roots (Tierney et al., 2001). Similar results were reported from the same experimental area at a later occasion (Cleavitt et al., 2008). In addition, in a complementary laboratory experiment, no significant effect of frost heaving was detected on root damage (Cleavitt et al., 2008). In the Swedish northern boreal forest, snow removal reduced the annual cellulose decomposition by 46 % (Kreyling et al., 2013), and led to 50 % lower fine root biomass and 50 % decline in the total vegetation cover (Kreyling et al., 2012) (Table 1).

In summary, even if treatment effects of snow-cover (soil frost) manipulation were not observed in all field-scale studies, the results of most of the investigations showed a tendency to increased soil DOC concentrations as the result of soil freezing (Fig. 2). The few studies including investigations on the quality of frost induced organic carbon indicated higher lability of these organic compounds. Most of the laboratory experiments which found increases in the quantity and quality of carbon compounds attributed these results to continuous soil freezing, rather than repeated freeze–thaw events.

3.3 Time-series

The existing datasets on winter processes and carbon dynamics has mainly dealt with organic carbon in streams and rivers, and inorganic carbon fluxes (mainly CO_2) from soil surface and through the snowpack. In the Salsa River in boreal northern Latvia, time-series of data indicated higher winter concentrations of DOC during warmer winters with more precipitation as rain (Klavins et al., 2012). Similarly, export of DOC increased during warmer winters with higher air temperatures, leading to a decline in the relative export during following seasons, in eight mid-to-high-latitude catchments (Laudon et al., 2013). This finding was corroborated by Spence et al. (2015) in north-western Canada who observed higher loads of winter DOC associated with enhanced winter stream flow (Table 3). As indicated by 15 year records in both boreal forests and mires of northern Sweden, winter climate could be an important controlling factor for the DOC concentrations in streams, particularly during spring snowmelt. Among the winter climatic conditions that increased stream DOC, variables indicating longer winters, later ending date of antecedent winter and larger number of preceding winter's days with sub-zero air temperature, appeared to be most influential in forests (Ågren et al., 2010; Haei et al., 2010). In addition, variables representing colder winter temperatures in both air and surface soils also exhibited a significant influence on increasing spring DOC concentrations (Haei et al., 2010; Ågren et al., 2010) (Table 3). In contrast, Lepisto et al. (2014) reported a decrease in DOC concentrations after harsher winters with deeper soil frost at a river outlet in northern Finland (37 year dataset) (Table 3). In summary, the time-series datasets of stream waters mostly indicate that concentration and export of DOC are higher during warmer winters with less soil freezing, while winter seasons with longer and colder soils are followed by higher DOC concentrations during the snowmelt period.

Continuous measurements of soil CO_2 efflux have mostly been carried out for one or two winter seasons/years, but there are also several year-long records of soil CO_2 fluxes (Table 3). In a 17 month soil respiration measurement in northern China, an exponential increase was observed in soil respiration rate with soil temperature over the year in forest, shrubs and meadow grasslands. However, there was no significant difference between the winter and growing season's CO_2 efflux between different ecosystems (Wang et al., 2010) (Table 3). In a one season CO_2 efflux measurement in Austrian mountain forests, early winter CO_2 efflux was highest and the efflux decreased until the end of snow-cover (Schindlbacher et al., 2007) (Table 3). In the same area, a 5 year time-series study of the impacts of natural variation in snow-cover on soil CO_2 efflux showed that the shorter winter had the highest winter CO_2 efflux (15 %

of the annual efflux), but the variations in temperature did not have a significant effect on annual fluxes (Schindlbacher et al., 2014) (Table 3). In a one-year study in northern China, the highest soil respiration rates were reported for July or August and the lowest rates in February (Shen et al., 2014) (Table 4). The results were similar for grassland, shrub-land and plantation. CO_2 efflux measurements in three tundra types in Brooks Range in Alaska, indicated that the number of warmer days in early spring strongly regulated the switch from CO_2 source to sink, turning warmer spring to seasons with increased net CO_2 uptake (Euskirchen et al., 2012) (Table 3). In a few exceptional years, the advancement of spring onset appeared to enhance soil respiration in sub-alpine meadows of Sierra Nevada, leading to longer growing seasons and increased CO_2 fluxes (Arnold et al., 2014) (Table 3). Monson et al. (2006a) found that changes in snow depth did not substantially affect the CO_2 concentrations in sub-alpine forests of Colorado, and the beneath snow concentration was fairly constant during the winter months. However, the concentration increased during snowmelt and reached a maximum in late spring (Table 3). Based on a six-year record of CO_2 exchange in the same area, shallower snow-cover was coupled to colder soils and lower rates of soil respiration (Monson et al., 2006b) (Table 3). Similarily, a one-winter study in Summit County, Colorado, showed a strong positive correlation between subnivian CO_2 flux and soil carbon content (Brooks et al., 2005) (Table 3).

4 Discussion

4.1 Mechanisms of carbon release in frozen soils

In this work, we have compiled all available studies on carbon in both organic and inorganic forms in response to winter climatic conditions in northern ecosystems showing that cold soils and soil frost generally enhance organic carbon concentrations. In addition, the timing of the onset and end of the winter season and snow-cover showed to be important for soil CO_2 production and concentration and export of terrestrial organic carbon. Lysis of microbial cells (Soulides and Allison, 1961), damage to fine roots (Tierney et al., 2001), physical disruption of the soil aggregates (Oztas and Fayetorbay, 2003) and desorption of previously adsorbed organic material (Yurova et al., 2008) are among the potential driving mechanisms for the increase in organic carbon concentrations during the soil frost periods that commonly were observed. Fine root mortality (Tierney et al., 2001) and plant root injuries (Gaul et al., 2008; Cleavitt et al., 2008) caused by frost and low temperatures may also result in a boost of more labile organic matter in the form of simple sugars and amino acids during winter (Scott-Denton et al., 2006). The balance between frost-induced root damages and increase in nutrient availability can play an important role for frost/cold temperature impacts on the growth of above-ground plants (Wipf et al., 2009). Vegetation type is a controlling factor for carbon fluxes (Neff and Hooper, 2002; Vestgarden and Austnes, 2009), and alteration of vegetation cover and performance by frost and winter climate may change the carbon input into soil, the soil microclimate and root respiration, and therefore influence the release of carbon compounds (Kreyling, 2010; Neff and Hooper, 2002). In addition, winter soil microbial activity and composition may affect soil decomposition and microbial soil respiration and have implications for the annual carbon budget (Bolter et al., 2005; Clein and Schimel, 1995).

4.2 Field-scale snow-cover manipulations and laboratory soil incubations

Field-scale manipulation studies have mainly explored the response of soil DOC and biomass carbon to changes in snow-cover and soil frost. There have also been a few studies dealing with inorganic carbon (Table 1). The existing studies, however, provide inconclusive results. In contrast to studies in the boreal forests of northern Sweden which started in 2002 (and still continues), most of the existing field investigations have consisted of short-term manipulation studies (one to two years) (Table 1). As demonstrated by Matzner and Borken (2008), the proportion of the carbon pool which is susceptible to freeze–thaw events is limited. This is indicated by decreasing carbon loss in short-term repeated events. This was for example shown for all forms of carbon fluxes in northern hardwood forest in New Hampshire (Campbell et al., 2014), for respiration in sub-arctic heath in northern Sweden (Larsen et al., 2002), and for heterotrophic and total soil respiration in a larch forest in northeast China (Du et al., 2013). So if the freezing events become more frequent or severe, the frost effects on carbon release might be suppressed. In addition to higher potential of experimental artifacts, short-term manipulation may not allow the study of more long-term and/or cumulative effects. While short-term studies could provide valuable indications of the effect of extreme weather conditions and seasonal changes in carbon fluxes, the cumulative effects and alterations in annual carbon fluxes may be important in a carbon budget perspective. When comparing the impacts of snow removal in field studies, there are inconsistences regarding the manipulation of water balance among the treatments in the field studies, which may have implications for the responses of both organic- and inorganic carbon. Soil water content is generally important for carbon dynamics, both due to dilution effects and through the impacts on microbial community and physical disturbance (Haei et al., 2012; Heimann and Reichstein, 2008), and differences in soil moisture could also help to explain variations among the results of different studies. Furthermore, the fact that the results of some of the field studies are not supported by controlled laboratory experiments may be due to several factors. First, the field studies retain intact root-soil systems, in contrast to laboratory studies. Next, differences between the temperatures and durations applied in the two types of experiments are almost always the case. The constant exposure of soil samples to low temperatures together with generally lower temperatures applied in the lab experiments compared to the field may produce unrealistic conditions. In addition, the “frost durations” in field and laboratory experiments do not necessarily imply the same conditions. While frost duration in the field studies may include any winter soil temperature below 0 °C, the frost duration in most laboratory incubations included longer periods of constant below-zero temperatures. Other influential factors are different types of soil and their different organic content as well as different types of soil frost which can also contribute to the variations in response of carbon compounds in different studies. Studies of the impacts of winter climatic changes on carbon dynamics, particularly in the field, are generally complicated due to numerous features of winter climate and their interactions such as minimum temperature, freeze–thaw cycles, type of soil frost, duration and timing of frost, rate of temperature change, as well as carry-over effects. In addition, any field experiment is subject to particular winter conditions in the year of study.

4.3 Time-series

Time-series on organic carbon are mainly based on streams and rivers and capture the seasonal variations in both climatic and hydrological conditions. It is well known that hydrology is an important regulating mechanism for export and concentration of DOC in northern latitude streams (Laudon et al., 2012). Changes in hydrological conditions due to alterations in temperature and precipitation patterns may therefore affect the export of carbon prior to the winter season, and offset the impact of winter climate for carbon dynamics during the spring snowmelt (Haei et al., 2010; Ågren et al., 2010). In many regions, the riparian zone acts as a significant source of carbon to aquatic systems, particularly during high-flow episodes (Hinton et al., 1998; Seibert et al., 2009; Dick et al., 2015), and significantly controls stream organic carbon concentrations. Therefore, even small changes in riparian soil organic carbon production and runoff patterns can potentially have important implications for adjacent streams. Most of the existing time-series agree that longer and colder winter seasons with frozen soils are followed by higher concentrations of organic carbon in streams in the following spring. There are also indications of higher DOC export during warmer winters with higher winter stream flows (Laudon et al., 2013; Spence et al., 2015). Change in soil water flow-paths is another key effect of soil freezing on hydrology and DOC as shallower flow-paths can promote more DOC transport to streams (Dittman et al., 2007).

It has been shown that alterations in soil climatic conditions during winter can have implications for the partitioning of carbon into organic and inorganic compounds. As shown by Haei et al. (2013), frozen winter soils in northern Sweden resluted in higher DOC concentrations and lower CO_2 concentration during the following summer. While studying the carbon dynamics as a whole, this is of great importance to consider changes in both organic and inorganic species. Records of soil CO_2 flux during winter season have mainly shown the temporal patterns of CO_2 flux, accumulated winter fluxes and their contributions to the annual fluxes, and correlation between CO_2 flux and soil temperature (Table 3). However, there are a few records of soil frost and little known about how the soil frost changes correlate with fluxes of CO_2. This aspect is easier to be explored conducting snow/soil frost manipulation experiments. Based on the literature values, carbon emissions of up to ∼ 230 $\mathrm{g\,C\,m^{-2}}$ have been recorded during the snow-cover season which contributed to the annual values by up to ∼ 35 % (and 50 % in one case) (Liptzin et al., 2009). For the studies summarized in this work (Table 3), contribution of winter CO_2 efflux to the annual efflux was mostly within the range 3–12 %. Carbon uptake through photosynthesis has mainly been shown for mosses and lichens during winter-season (Tieszen, 1974; Kappen et al., 1996), but also for some higher plants during the spring when the snow-cover has not melted completely (Starr and Oberbauer, 2003). In a subarctic heath ecosystem in northern Sweden, winter-season photosynthesis (19 % of the annual gross CO_2 uptake) could somewhat balance the winter-season respiratory carbon loss which accounted for 22 % of the annual respiratory flux (Larsen et al., 2007).

Contribution of different ecosystem types to uptake and release of carbon is variable. For example winter time carbon loss in forest soils is commonly higher than for tundra. However this carbon loss can offset the higher carbon gain during the growing season (Sullivan, 2010). The variations in the existing CO_2 flux data can be due to differences in the length of winter, continuous vs. occasional measurements, different methodologies for measurements and data treatment, short-term studies, different soil types and carbon contents as well as age of the forest stands (Hubbard et al., 2005). As suggested in a conceptual model developed for sub-alpine meadows in Niwot Ridge, Colorado, different factors can control the temporal patterns of CO_2 flux from seasonally snow-covered soils. As the depth and duration of snow increases, the controlling effect of freeze–thaw cycles shifts to soil temperature to soil moisture and at last to carbon availability (Liptzin et al., 2009).

4.4 Carry-over effect

Although changes in winter climate are fundamental for ecosystem functioning and for carbon cycling in northern ecosystems, it is also important to consider the combined effects of climate warming in both winter and summer (Cornelissen and Makoto, 2014). The interactions between summer and winter warming could be due to seasonal changes in microbial communities and vegetation species, or due to carry-over effects. In boreal forests of northern Sweden, for example, winter climatic condition have been shown to play a major role in dissolution and mineralization of soil organic carbon in the following summer season (Haei et al., 2013). Prolongation of the growing season may also have implications for the input to the soil organic pool prior to onset of winter. For example, the snow-cover regime during winter has been shown to affect root turnover in the following summer. While Wipf et al. (2009) found a reduction in summer root production as the result of snow reduction, Tierney et al. (2001) suggested faster root turnover. The carry-over effect of winter climatic conditions may also be demonstrated in hydrological processes such as export of organic carbon into streams. It has been shown that higher exports of DOC during warmer winters lead to less variable DOC export during the rest of the year (Laudon et al., 2013; Spence et al., 2015).

4.5 Future winter climatic changes

Long-term monitoring of climatic conditions has revealed reducing trends of snow-cover in several areas in the northern region (Campbell et al., 2010; Hodgkins and Dudley, 2006), and based on different climate models, decreased snow-cover depth is predicted by the end of this century in many locations (Campbell et al., 2010; Kurylyk et al., 2013; Mellander et al., 2007). In the Northern Hemisphere above 45° N, snow disappearance has advanced 9–15 days (1972–2000) (Dye, 2002), and in a warmer future climate, length of snow-cover period has been predicted to be shortened by 70 % by the end of this century in New Hampshire, USA (Campbell et al., 2010). Furthermore Kurylyk et al. (2013) predicted 13–49 days shorter snow-cover period in east central NB, Canada, while Mellander et al. (2007) projected 73–93 days shorter duration of consistent snow-cover in boreal northern Sweden. In Germany, the decrease in snow-cover period is projected to continue so that significant parts of the country may not experience regular snow-cover in the future (Kreyling and Henry, 2011). A decreasing pattern of frost depth has also been recorded in regions with seasonally frozen ground in Russia during the period 1930–1990 (Frauenfeld et al., 2004). However, as indicated by the results of Campbell et al. (2010), the decrease in snow should be coupled with colder air temperatures in order to promote deeper soil frost. Such cold soil conditions are more valid for higher latitude regions with harsher winter conditions and particularly at the start of winter season, while in mid-latitude regions, and particularly towards south, soils will more likely turn into "warmer soils" (e.g. Jungqvist et al., 2014). The key in the North Temperate Zone is the intrusion of arctic air masses which are still cold enough to freeze soils in a warmer world. In Germany, projection of the future annual minimum soil temperature suggested a stronger increase in the southern regions compared to the currently colder northern parts (Kreyling and Henry, 2011). Shorter duration of frozen ground is suggested by several modeling approaches (Campbell et al., 2010; Helama et al., 2011). This shortening can be attributed to more frequent midwinter snowmelt, or earlier snowmelt which leads to more extensive and faster heat absorption in the ground (Lawrence and Slater, 2010). In a changing winter climate, alterations in snow-cover and soil freezing may directly affect the vegetation in different stages of their development, or indirectly change the vegetation structure via soil nitrogen availability. However, the extent and mechanisms of changes may be species-dependent (Makoto et al., 2014).

4.6 Shoulder seasons

Changes in the timing of the onset and offset of winter highlight the importance of shoulder seasons, namely the autumn-winter and winter-spring transition periods, respectively. These shoulder seasons may affect the carbon dynamics in different ways. In the fall-winter shoulder season, more precipitation falling as rain may lead to higher soil water content before frost formation which can result in more extensive and longer periods of frozen soil (Raisanen et al., 2004). In addition, such rainfalls may lead to higher winter carbon loads associated with higher winter stream flows, particularly in smaller catchments and during warmer winters (Spence et al., 2015) (Fig. 2). Soil moisture is also an influential factor for soil processes and microbial activities, and therefore important for production, accumulation and transport of carbon compounds. Soil water content influences the formation of concrete soil frost and the effects of hydrology and biology are quite distinct from other soil frost types. It has been shown that microbial communities can survive the winters and reach to a maximum biomass at the end of winter season. However, in the winter-spring transition time, before the soil temperatures rises above zero, soil microbial biomass can considerably decrease (e.g. Edwards et al., 2006). This decrease could be due to loss of cold-adapted microorganisms, limited substrate availability or changes in the physical state of soil systems caused by melt water and alterations in chemical potential (Jefferies et al., 2010). No or very low photosynthesis has been found in snow-covered higher plants during winter (e. g. Hamerlynck and Smith, 1994). However, Vermeulen et al. (2015) highlighted that winter carbon assimilation at daily average below-zero temperatures is an important factor for winter carbon fluxes, as shown for a temperate Scots pine forest. During the spring when snow-cover was still present, Starr and Oberbauer (2003) showed that carbon uptake capacity by the leaves of evergreen tundra plants was promoted in response to the favorable subnivean environment created by penetration of light, increase in temperarture and CO_2 together with available melt-water, in an Alaskan tussock-dwarf shrub ecosystem.

In the winter-spring shoulder, advances in the timing of snow-cover melt together with warmer temperatures and more light can particularly be crucial for both photosynthesis and soil respiration. Such conditions may lead to longer growing season, earlier leafing of the trees, higher rates of vegetation growth, increase in litter quality and quantity, higher decomposition rates and enhancement of surface soil CO_2 fluxes (Campbell et al., 2009; Tanja et al., 2003). It has already been shown that ecosystem productivity at latitudes 30–90° N has largely been stimulated due to spring warming (Xia et al., 2014). In addition, earlier onset of spring season increases the vulnerability of plants and soil processes to extreme weather conditions, such as late frost events (Arnold et al., 2014; Heimann and Reichstein, 2008). Frost-damages to the above- and below-ground plant organs may limit the seedling survival and plant growth (Johnson et al., 2004) and therefore supress the carbon fixation. It has further been shown that the timing of snow-melt, rather than snow depth, is important for growth, reproduction and phenology of plants (Wipf et al., 2006, 2009).

4.7 Extreme conditions

In the time-series of carbon and climate conditions (Table 3), there are only a few explicit studies on extreme winter related weather conditions. As an example, two extreme years with large variations in winter precipitation highlighted the importance of extreme conditions for variations in CO_2 fluxes in sub-alpine meadows of Sierra Nevada mountain range (Arnold et al., 2014). While time-series datasets are useful tools for studying the natural variations, short-term field-scale manipulations often represent extreme weather events. In addition, the response to mean winter climate alteration can be misleading and should be combined with seasonal variations, extreme weather and hydrological conditions in order to get clearer insights into anticipated changes in carbon dynamics in a future climate (Campbell et al., 2005; Kreyling and Henry, 2011).

4.8 Modelling

The empirical data indicate the strong relationship between winter climatic conditions and carbon dynamics, and highlight the importance of extreme weather events. This information is crusial as basis for modelling to predict how carbon production and dynamics may change in the future, as a result of changes in winter conditions. Different climate scenarios, including changes in temperature and precipitation, have been used in carbon-climate models. In addition to direct impacts of winter climatic factors on photosynthetic uptake and biological activities, alterations in CO_2 levels can play a significant role in plant performance. Such aspects have also been included in some of the carbon modelling approaches, for example in Dynamic Global Vegetation Models (DGVMs) (e. g. Sitch et al., 2008; Cramer et al., 2001). This type of approach can lead to more accurate and comprehensive future projections of carbon dynamics that also allows better understanding of winter processes. Most existing models, however, primarily focus on the long-term temporal changes in carbon exchange on global (Sitch et al., 2008; Cramer et al., 2001) and regional (e. g. Morales et al., 2007; Sitch et al., 2007; Dib et al., 2014) scales, and mainly on an annual basis. There is therefore a need to more specifically include winter variables in the models and create models which enable a better understanding of the role of winter climatic effects on carbon dynamics.

4.9 Concluding remarks and future research needs

As the existing literature indicates, winter climatic conditions, soil frost and timing of winter season are controlling factors of carbon dynamics. However, there is still a need for an improved understanding of the role of winter climatic conditions for carbon dynamics as we are just at the beginning of disentangling the mechanistic relationships associated with winter conditions. Of special interest to the scientific community would be to consider

1. the role of shoulder seasons and importance of warming in fall-winter season compared to winter-spring transition. This has mainly implications for the rates

and extent of carbon production processes, carbon accumulation and its export via streams and rivers

2. extreme events, due to their significant ecological implications, higher likelihood of occurrence in a changing future climate and large associated uncertainties
3. partitioning of carbon into organic and inorganic species, due to its substantial impacts on carbon balance on the global scale
4. carry-over effect of winter season to subsequent spring, summer and fall. The effect can result in changes in vegetation species/performance, microbial community's activity/composition and hydrological processes
5. long-term impact of warmer winters on the carbon dynamics in both soils and surface waters, as many effects potentially can be either short-term, transitional, or need cumulative changes before they can be observed
6. more realistic modelling approaches which include winter processes and enable projections of winter-season carbon exchange.

In summary, there is a need to conduct more controlled long-term field and laboratory experiments to resemble more realistic future winter climatic conditions. Field and laboratory experiments designed for reasonable and long enough durations would enable capturing more long lasting, and perhaps cumulative effects. However, natural variations should also be monitored and considered more often as they can facilitate more general conclusions about future changes and create a more reliable basis for model development. In addition, studies of climatic changes during transition times, particularly the shoulder seasons at the start and end of winter, should preferably be accompanied by research on alterations in hydrological conditions, light regime, vegetation performance and soil microbial activity, in order to make inferences of how changes in the timing and duration of growing season affect annual carbon cycling.

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Table 1. Field-scale snow-cover manipulation studies and the implications for soil organic and inorganic carbon.

Biome	Design/time	C-compound	Effect	Reference
Boreal forest in eastern Finland (62°36′ N, 29°43′ E)	Snow manipulation study in a Norway spruce stand, triplicates of three treatments (12 m × 12 m plots): control, open (snow removal) and frost (insulated) Two winters 2005–2007	C flux (fine roots as a measure of C flux)	– Longer lifetime of fine roots in deep soil frost treatment (snow removal) –> lower C flux to the soil – No effect of deep soil frost on fine roots growth – Decline in fine root growth as the result of prolongation of soil frost/lower soil temperature	Repo et al. (2014)
Boreal forests in northern Sweden (64°14′ N, 19°46′ E)	Snow removal/soil frost manipulation experiment in a Norway spruce stand, 3 m × 3 m plots, including triplicates of three treatments: deep soil frost, shallow soil frost, ambient Start 2002	Summer soil DOC concentration, heterotrophic CO_2 production in soil	– Higher DOC concentrations (after 7 years) and higher rates of heterotrophic CO_2 production (after 3 years) during summer in deep soil frost plots compared to control, in the surface soils – Both colder soil temperatures and longer durations of soil frost significantly contributed to explain the variations in both DOC and heterotrophic CO_2 production – Significantly higher DOC concentration in the deep soil frost treatment compared with both ambient and shallow soil frost (after 6 years at 10 cm depth) – Strong positive correlation between duration of soil frost and DOC concentration	Haei et al. (2013)
		Soil DOC concentration in spring and summer	– More labile DOC in the surface soil of deep soil frost treatment plot – Lability of soil water DOC strongly and positively correlated to the duration of soil frost	Haei et al. (2010)
		DOC lability (as assessed by UV-Visible spectroscopy)	– Increase in spring CO_2 concentration and decrease in summer CO_2 concentrations in response to increase in maximum soil frost depth (after 2 years)	Haei et al. (2012)
		CO_2 concentration and emission during spring and summer	– Negative correlation between the average CO_2 emission rates to the atmosphere in the growing season and maximum soil frost depth in the preceding winter (after 2 years)	Öquist and Laudon (2008)
		Annual cellulose decomposition	−46 % reduction in the annual cellulose decomposition in the deep soil frost treatment compared to ambient treatment (after 9 years of manipulation)	Kreyling et al. (2013)
		Vegetation cover, fine root biomass	−50 % decline in the total vegetation cover and 50 % lower fine root biomass in the snow removal treatment plots (after 8 years).	Kreyling et al. (2012)
Montane heathlands in southern Norway (59°01′ N, 8°32′ E)	Snow removal treatment Two consecutive winters (2005–2006)	DOC concentration, DOC lability	– Increase in soil solution DOC and change in DOC quality towards more lability as induced by soil frost	Austnes et al. (2008)
Temperate forests in southeastern Germany (50°03′ N, 11°51′ E)	Snow removal (3 snow removal plots and 3 control plots, 20 m × 20 m) in a Norway spruce stand Winter 2005–2006	Soil solution DOC concentration	– No soil frost effect on DOC concentrations, ^{14}C signature of DOC and annual fluxes of DOC in forest floor percolates	Hentschel et al. (2009)
		Lignin, plant and microbial sugars, microbial biomass (phospholipid fatty acid (PLFA))	– No clear frost effect on lignin contribution to TOC – Significant decline in plant- and microbial sugar contribution to soil organic matter at the snow removal plots – No frost effect on soil microbial biomass	Schmitt and Glaser (2011)

Table 1. Continued.

Biome	Design/time	C-compound	Effect	Reference
		Total soil respiration and heterotrophic respiration (assessed by radiocarbon signature)	– Frost induced reduction in soil respiration leading to less annual C emission. 14 % of the difference in annual C emission attributed to the frost period and 63 % to the summer. – Significant reduction in heterotrophic respiration as result of soil frost	Muhr et al. (2009)
		Fine root biomass, root longevity	– $\sim$ 30 % increase in fine root mortality due to soil frost (can to some degree be compensated by frost stimulated fine root growth) –3 times decrease in root longevity as affected by soil frost	Gaul et al. (2008)
Northern hardwood forest in New Hampshire, USA (43°56′ N, 71°45′ W)	Two occasions of two-year snow removal treatment (by shoveling), 10 m × 10 m plots in 2 sugar maple and 2 yellow birch dominated stands (totally eight plots including one control and one insulation) Winters 1997–1999 Winters 2002–2004	Soil solution DOC	–1997–1999: No freezing effect on soil solution DOC – 2002–2004: Soil frost induced increase in DOC concentration changes not consistently significant	Fitzhugh et al. (2001) Groffman et al. (2011)
	Two occasions of two-year snow removal treatment (by shoveling), 2 plots of 10 m × 10 m in 4 forest stands, 2 sugar maple and 2 yellow birch dominated stands, one snow-removal plot (by shoveling) and one control at each site, minirhizotrons installed at each of the plots prior to the start of experiment Winters 1997–1999	fine roots (< 1 mm diameter)	– Higher overwinter root mortality at the snow removal plots compared to the controls, in both years – Earlier fine root production peak in the snow removal plots, in the following growing season – No significant change in fine root biomass – No difference in root mortality response between the species	Tierney et al. (2001)
	Two-year snow removal treatment (by shoveling), 10 m × 10 m plots in 2 sugar maple and 2 yellow birch dominated stands (totally eight plots including one control and one insulation), 3–5 gas flux chambers in each plot, weekly measurements in early spring and monthly measurements otherwise Two winters 1997–1999, following a recovery winter 1999–2000	CO_2, CH_4	– Significantly lower fluxes of CO_2 during winter – 11, 9 and 15 % of annual fluxes of CO_2 represented by winter in 1998, 1999 and 2000, respectively – Significantly lower fluxes of CH_4 during winter – Significant reduction in CH_4 uptake during the winter/spring transition period (around snowmelt), in both soil types and during both treatment winters –18, 17 and 13 % of annual fluxes of CH_4 represented by winter in 1998, 1999 and 2000, respectively	Groffman et al. (2006)
	Four sites, total eight plots (12 m × 12 m), one control and one snow removal plot at each site, root growth measurements using minirhizotrons; removal of soil blocks and separation of fine roots (< 2 mm) followed by root vitality assay Winters 2002–2003 and 2003–2004	Fine root vitality and growth	– Reduced vitality of first- and second-order roots in the snow removal treatment (organic soil) – Generally higher annual root growth in the snow removal plots, with maximum in early summer and in surface soil	Cleavitt et al. (2008)

Table 1. Continued.

Biome	Design/time	C-compound	Effect	Reference
Alpine forest in Sichuan, China (31°15′ N, 102°53′ E)	Two treatments: with and without snow removal, 5 replicates (5 m × 5 m plots). The snow removal plots covered with roofs with plastic film coverage, and watered three times to simulate rain and snowmelt. The study period divided into 5 periods: before snow-cover, early snow-cover, deep snow-cover, snow-cover melting and early growing period Winter 2009–2010	Soil DOC, soil microbial biomass carbon	– Snow removal led to increased soil DOC during deep snow-cover period, snowmelt and early growing season – Snow removal increased microbial biomass carbon during deep snow-cover as well as during the snowmelt period	Tan et al. (2014)
Cool-temperate alpine bog in northern Italy (46°21′ N, 11°44′ E)	Snow-cover manipulation with following treatments: no manipulation, snow removal at the end of winter, snow removal in spring, snow addition in spring, removal of all aboveground plants with no snow manipulation. Snow removal by plastic shovel Following measurements at several occasions from late spring to early autumn 2008–2009	Ecosystem respiration (mg CO_2 m^{-2} h^{-1}), Soil DOC, microbial biomass carbon	– No treatment effect of snow manipulation on the measured variables	Bombonato and Gerdol (2012)
Boreal oligotrophic mire in northern Sweden (64°15′ N, 19°46′ E)	Sampling of soil water at 5 occasions stated before freezing the surface and ended after complete thaw, sampling depths: 0, 5, 10, 20, 30, 50, and 70 cm below the bottom of the concrete soil frost, six sampling areas (3 m × 3 m) Winter 2001–2002	Mire DOC concentration during winter	– Increase in DOC concentration in the soil water profile of mire under the concrete ice, when the soil frost reached almost the maximum depth, compared to the start of frost formation	Ågren et al. (2012)
Temperate deciduous forest in Western Michigan (42°24′ N, 85°24′ W)	Snow-pack manipulation, three treatments: snow removal, snow addition and ambient ($n = 3$ for each treatment), monthly DOC measurements, near surface CO_2 measurements 20 Sep–5 Apr 2008	DOC concentration, CO_2 concentration, bacterial and fungal community structure	– Lower DOC concentration in ambient and snow removal treatments compared to the snow addition prior to spring-thaw, and similar concentrations among the treatments at the end of experiment – No evidence for an increase in respiration sensitivity to freezing temperatures – Changes in both bacterial and fungal communities by the snow treatments during winter season – Only change in the bacterial community in response to snow-pack treatment was prolonged into the spring-thaw period	Aanderud et al. (2013)
Colorado Rockies, Summit County, Colorado	Soil carbon amendment in deciduous and coniferous forests, 9 locations in each forest type: Snow removal plots ($n = 3$), undisturbed plots ($n = 3$) and carbon addition plots ($n = 3$). Snow-pits into soil for the carbon amendment and snow removal plots, carbon amendment in form of glucose addition; $\delta^{13}C$-CO_2 sampling and CO_2 flux calculations at 24 h and 30 days after carbon addition Mid-Feb 2003	CO_2 flux, $\delta^{13}C$-CO_2	−52–160 % increase in CO_2 fluxes in snow-covered carbon amended soils compared to control site within 24 h after carbon addition, which remained 62–70 % higher after a month – Shift in $\delta^{13}C$-CO_2 towards glucose value indicating the preferential use of added carbon and presence and activity of heterotrophic community below 0 °C	Brooks et al. (2005)

Table 2. Controlled laboratory experiments on the effects of winter conditions and soil freezing on organic and inorganic carbon.

Biome	Design/time	C-compound	Effect	Reference
Boreal forests in northern Sweden (64°14′ N, 19°46′ E)	Incubation temperatures: 0, −6 and −12 °C; incubation duration: 2, 4 and 6 months, water content: 30, 60 and 90 % water holding capacity, freeze–thaw cycles (FTC): 1, 4 and 7 cycles, thawing: 5 °C, 48 h	DOC, DOC quality, C : N	– Higher DOC concentrations and higher DOC lability at lower temperatures – Frost duration and frequency of FTC (alone and in interaction with other factors) not influential for DOC concentration and quality – Initial soil water content prior to freezing significantly important for DOC concentration and lability	Haei et al. (2012)
		Basal respiration, microbial growth and microbial composition (PLFA)	– Lower microbial growth and lower soil respiration rate at longer frost duration – Higher respiration rate in moister soils – Interaction between soil water content and frost duration significantly influential for soil respiration rate as well as fungal and bacterial growth – Higher fungal to bacterial growth rate ratio at lower temperatures – ∼ 30 % decline in total PLFA concentration as the results of the longer frost duration and lower temperature – A clear shift in the PLFA composition at 0 °C with an abundant of fungi and gram negative bacteria	Haei et al. (2011)
Boreal forests in northern Sweden (64°11′ N, 19°35′ E)	Incubation temperatures (duration (days)): −9 °C (160), −4 °C (99), +4 °C (10) and +9 °C (6); addition of ^{13}C glucose and N and P nutrients	Newly synthesized biomass (^{13}C compounds, anabolic compounds), ^{13}C-CO_2 (catabolic compound)	– No difference in ^{13}C allocation into catabolic and anabolic compounds between the frozen and unfrozen soils – A first phase of slow increase in CO_2 production followed by a second phase of acceleration in CO_2 production at all tempeartures – The only metabolic change was increase in the production of glycerol and increase in the fluidity of the synthesized cell membrane at frozen conditions	Drotz et al. (2010)
Montane heathlands in southern Norway (59°01′ N, 8°32′ E)	Undisturbed soil columns, 2 week treatment, freezing temperature: −5 °C, Thawing temperature: +5 °C, Four treatments: 1. Fast cycling: four 25 h freezing, with 60 h thawing in between, 2. low cycling: one 123 h freezing, 3. Permanent frost, 4. Permanent thaw	DOC, DOC quality	– Increased concentrations of DOC and shift towards higher quality as the result of permanent frost	Austnes and Vestgarden (2008)
		CO_2 and DOC in soils with different vegetation cover	– Increase in both DOC concentration and CO_2 emission after permanent freezing, and depending on the vegetation cover in the order *Sphagnum* > *Calluna* > *Molinia*	Vestgarden and Austnes (2009)

Table 2. Continued.

Biome	Design/time	C-compound	Effect	Reference
Taiga soils close to Fairbanks, Alaska; Tundra soils, north of the Brooks Range in Alaska (68°38′ N, 149°38′ W)	Incubation of soil samples at +5, −2 and −5 °C for 31 days (water holding capacity adjusted to 50 %, additional taiga soil samples adjusted to 10 % water holding capacity to check the moisture effect), CO_2 measurements 3–5 times	CO_2 respiration rate	– Highest and lowest respiration rates at +5 and −5 °C, respectively – More respiration in the taiga soils with higher water content	Clein and Schimel (1995)
Sub-arctic heath tundra in northern Sweden (68°20′ N, 18°50′ E)	Mesocosms containing the entire organic soil layer and rooted vegetation, sampled in summer and went through sample preparation procedures, i) a single deep freeze treatment using a growth chamber with −10 to −15 °C air temperature, for 1–2 days, ii) a freeze–thaw treatment composed of similar freezing condition as deep freeze treatment as well as a 20–25 °C darkened area for thawing (5 freeze–thaw cycle, each cycle 1–2 d)	DOC, microbial biomass carbon, CO_2 efflux	– Decrease in microbial biomass carbon and increase in DOC after multiple freeze–thaw cycles, but no effect in the deep freezing treatment – Consistently low rates of CO_2 efflux in the deep freezing treatment, 9 times higher fluxed after thawing, high fluxes in thaw periods of the multiple freeze–thaw cycles – Strong correlation between soil temperature and CO_2 flux rates	Grogan et al. (2004)
Temperate forests in southeastern Germany (50°08′ N, 11°52′ E)	Permanent soil frost, duration: 2 weeks, freezing temperatures: −3, −8 and −13 °C	DOC concentration, DOC lability	– Increased DOC concentration at −8 and −13 °C, but no effects at −3 °C – No frost effect on DOC lability	Hentschel et al. (2008)
	Soil columns from a mature Norway Spruce forest (organic soil and organic/top mineral soils), stored at field moisture at +5 °C for 2 months before freezing treatment, freezing temperatures: −3, −8 and −13 °C (control at +5 °C), treatment at each freezing temperature included 3 FTCs, 2 week freezing and 1 week thawing at +5 °C Year 2005	CO_2 flux	– Increased emissions of CO_2 during the thawing period – Increase CO_2 fluxes in response to the severe freezing temperarture, but decline after repeated FTCs	Goldberg et al. (2008)
Northern hardwood forest in New Hampshire, USA (43°56′ N, 71°45′ W)	Freeze-treatment of organic soil samples from stands of sugar maple and yellow birch, freezing temperatures: −13 and −3 °C (control samples at laboratory temperature), freezing duration: 10 days followed by 3 week incubation at 20–25 °C (weekly sampling) Year 1997	CO_2	– Stimulated CO_2 production as the result of severe freezing, less effect of mild freezing (after one-week thawing) – Small but significant species effect on CO_2 production with higher rates in birch samples after one-week thawing	Neilson et al. (2001)
	Incubation of soil cores of surface organic soil from 2 forests: sugar maple (Acer saccharum) and American beech (Fagus grandifolia) forest, and a red spruce (Picea rubens) and balsam fir (Abies balsamea) forest, freezing temperatures: −15, −0.5 and +5 °C, freezing duration: 1 week, followed by snowmelt simulation at +5 °C and with snow-cover	DOC, CO_2 and CH_4	No significant changes on DOC and cumulative fluxes of $CO_2 + CH_4$ – Total cumulative fluxes of C (DOC, CO_2 and CH_4) at −15 °C significantly lower (25–50 %) than in +5 °C – A tendency towards higher C losses in red spruce-balsam fir forest soils, but no significant differences between the two forest types	Reinmann et al. (2012)

Table 2. Continued.

Biome	Design/time	C-compound	Effect	Reference
	Soils of organic horizon placed in columns and subjected to one of the temperatures −15, −0.5 and +5 °C, then covered with snow and melted at +5 °C	Fluxes of C compounds, Dissolved Organic Matter (DOM) quality, leaching of labile DOM	– Decline in the fluxes of all forms of C during snowmelt, indicating that a limited soil pool was flushed – Increase in the aromatic content of DOM – Little effect of mild freezing, but delayed leaching and a flush of labile DOM as the result of severe freezing	Campbell et al. (2014)
	Installation of sugar maple and yellow birch seedlings, with intact root systems, into pots with reconstructed root profiles, horizontal minirhizotron tubes installed in the pots to measure the root dynamics, sugar maple seedlings exposed to −1 and −5 °C for 5 weeks (a control at +3 °C for the same duration included), yellow birch seedlings kept at −4 °C for durations of 5 weeks, 10 weeks and a freeze–thaw treatment (5 weeks freezing and a one-week thawing to +3 °C), and a control at +3 °C	Fine root dynamics	– No effect of mild freezing (to −5 °C) on fine root dynamic in the potted tree seedlings – No significant difference between the mild freezing treatments and controls, even regarding the freezing duration	Tierney et al. (2001)
Sub-arctic heath in northern Sweden (68° N, 18′ E)	Two types of mesocosms: dwarf shrub heath and graminoid-rich heath (17 cm × 11 cm), three treatment (8 replicates each): 1. Constantly frozen at −4 °C, 2. Unfrozen at +2 °C, 3. Freeze–thaw: 18 FTCs including 9 h daylight at +2 °C and 15 h darkness at −4 °C	CO_2 emission, microbial C	– Significantly lower respiration in mesocosms kept at −4 °C – Respiration in freeze–thaw treatment was constantly lower than unfrozen and higher than frozen treatments, respectively – Decreasing respiration rates by time in the freeze–thaw treatment – Decrease in microbial biomass carbon only in the freeze–thaw treatment	Larsen et al. (2002)
Poudre Canyon, Colorado (41° N, 106° W)	– Chamber respiration experiment for six treatments (*n* = 5 for each treatment): Autotrophic and heterotrophic respiration, autotrophic respiration, heterotrophic respiration, no organism respiration in soil, autotrophic respiration in vermiculite, no organism respiration in vermiculite; four measurements during the one-month experiment – Soil collection in Apr 2014	Soil CO_2 efflux	– Heterotrophic respiration, main contributors to the soil CO_2 efflux, accounting for about 75 % of the total carbon efflux, during the simulated winter conditions	Beverly and Franklin (2015)

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◄| |►
◄ ►
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Table 3. Time-series of dissolved organic carbon in soil and water, CO_2 and winter climatic variables in mid to high latitude regions.

Biome	Design/time	C-compound	Effect	Reference
Boreal forests in northern Sweden (64°14′ N, 19°46′ E)	Datasets of climate, discharge and stream (DOC) in a forest dominated catchment (Partial Least Square (PLS) modelling) 1993–2007	Stream (DOC) during snowmelt	– Longer and colder winter climatic conditions followed by higher maximum stream (DOC) in spring snowmelt	Haei et al. (2010)
	Datasets of climate, discharge and stream (DOC) in a forested catchment 1993–2007	Snowmelt stream (DOC) (average, maximum and at maximum discharge)	– Higher snowmelt concentrations following long winters	Ågren et al. (2010)
Boreal oligotrophic mire in northern Sweden (64°15′ N, 19°46′ E)	Datasets of hydrological and meteorological variables and spring DOC concentration in a stream draining the mire 1993–2007	Snowmelt stream (DOC)	– Increase in stream DOC during spring following colder winter soils	Ågren et al. (2012)
Eight mid-to-high latitude catchments (three in Scotland, Two in the USA, two in Canada, and one in Sweden) (44–64° N)	Time-series of climate data, discharge and DOC (3–10 years depending on data availability)	Annual and seasonal export of water and DOC	– Increase in the export of water and DOC during warmer winter and consequently decline in spring and summer export (shift from a dominant spring export towards a more evenly distributed export during a year) – Decrease in the coupling between the export of water and DOC in spring and its increase in winter time	Laudon et al. (2013)
Simojoki river system in northern Finland (65°37′ N, 25°03′ E)	Datasets of temperature, precipitation and frost depth, discharge and TOC 1971–2008	Spring snowmelt TOC concentrations at the river outlet	– Significantly lower average TOC concentrations following harsher winters with deeper maxima soil frost	Lepisto et al. (2014)
Boreal catchments of northern Latvia and Estonia (57°44′ N, 25°14′ E)	Long-term changes of TOC concentration in Salsa River studied by non-parametric Mann–Kendall test 1996–2005	TOC concentration	– Highest concentrations of TOC during warmer winters with most of precipitation as rain on seasonal basis, strongest correlation between TOC concentration and discharge during winter	Klavins et al. (2012)
Sub-alpine meadows in Sierra Nevada, USA (38° N, 119° W)	Changes in CO_2 fluxes with regards to onset of spring and length of snow-free period: At 4 transects, triplicates of soil collars inserted at 3–5 cm soil depth at 3 distinct hydrological regions (wet, dry and intermediate), soil CO_2 efflux measured from collars at midday, weekly at the first half of growing season and biweekly later 2011–2013 (year 2012 and 2013 with extreme winter precipitation variation)	Surface soil CO_2 flux	– Earlier onset of spring in 2012 and 2013 followed by several frost events after the snowcover had disappeared. – Longer duration of growing season in both years 2012 and 2013 compared to year 2011 (by 57 and 61 days, respectively) –100 % increase in soil respiration in both years 2012 and 2013 compared to year 2011	Arnold et al. (2014)
Sub-arctic Canadian Shield Catchment in northwestern Canada (62° N, 114° W)	Weekly/biweekly sampling of a representative stream, flow and DOC measurements 15 Mar 2011–20 Apr 2013	DOC flux	– 2011–2012: A water year with more rain in the fall and higher winter stream flow (fall/winter stream flow accounted for 69 % of the annual stream flow), higher winter DOC flux (proportional to the stream flow) – 2012–2013: A year with zero or very low winter flow, lower winter DOC flux	Spence et al. (2015)

Table 3. Continued.

Biome	Design/time	C-compound	Effect	Reference
Temperate forest–steppe ecotone in northern China (42° N, 117° E)	Soil respiration measurements using soil CO_2 flux systems, soil CO_2 effluxes measured every 15–20 days during growing season and every month during winter (except for Feb), soil temperature and water content measurements, triplicate plots for each of three forest types, two shrubs and two meadow grasslands Jun 2006–Oct 2007	CO_2 efflux	– Mean winter soil CO_2 efflux 3.77–7.27 % of the growing season efflux – No significant difference between winter soil CO_2 efflux among different ecosystems – No obvious relationship between winter soil CO_2 efflux and soil temperature – Significant difference in growing season CO_2 efflux among the ecosystems types, with the highest soil respiration rate in one of the meadow grasslands – No significant effect of soil temperature and water content on growing season's soil respiration, but significant correlation between soil respiration and soil organic carbon density – Exponential increase in soil respiration rate with soil temperature over the year at all ecosystems types. – Soil temperature and soil water content explained 86–94 % and 54–80 % of annual temporal changes in soil respiration, respectively – Winter soil CO_2 efflux accounted for 3.48–7.30 % of the annual soil respiration based on interpolation of measurements	Wang et al. (2010)
Mountain forest in the Northern Limestone Alps in Western Austria (47°34′ N, 11°38′ E)	Measurements of root respiration through trenching (three plots), and winter soil respiration (CO_2 efflux) through snow-cover using three methods (three plots): 1. Closed dynamic chamber on the snow surface (every third week from the start of experiment), 2. Diffusional flux calculation based on conductance properties of snow-cover and CO_2 gradient between the soil surface and snow surface (start 12 Dec 2005), 3. Diffusional flux calculations based on CO_2 concentration profiles through the snow-cover (start Mar 2006) Mid Nov 2005–late Apr 2006	CO_2 efflux, root respiration	– Highest CO_2 efflux in early winter, decreasing until the end of snow-cover – Accumulated CO_2 efflux from snow-covered soils accounted for 12 % of the total annual soil respiration. –13–50 % contribution of root respiration to the total soil respiration during winter. –38 % flux underestimation by the closed chamber methods due to lateral diffusion and retention of CO_2 within the snow-cover, similar estimates based on the two other methods	Schindlbacher et al. (2007)
	5 year time-series study of the impacts of natural variations in snow cover on soil CO_2 efflux, triplicates of untreated control plots (2 m × 2 m), soil temperature and soil moisture measurements at 5 and 15 cm soil depth and manual snow depth measurements; measurements of soil CO_2 efflux using permanently installed close chambers, every 2 weeks, during the snow free season; measurements of soil CO_2 efflux based on CO_2 concentration profiles in the snow-cover to the soil surface, every third week, during snow-cover period Nov 2007–Dec 2012	Soil CO_2 efflux	– The effects of variations in the soil temperature was not mostly reflected on CO_2 efflux which in turn decreased gradually throughout the winter due to depleting carbon substrate – Cumulative CO_2 efflux beneath snow-cover accounted for 6–12 % of the annual efflux – Higher CO_2 efflux during the shortest winter (15 % of the annual efflux)	Schindlbacher et al. (2014)

Table 3. Continued.

Biome	Design/time	C-compound	Effect	Reference
Taihang Mountain, Hebei Province, North China (37°54′ N, 114°14′ E)	Three sites: grassland, shrubland and plantation, three plots in each site (10 m × 10 m), soil respiration measurement using an automated soil CO_2 flux system (dynamic closed chamber system) Jul 2012–Jun 2013 (once a month)	Soil respiration rate	– Maximum soil respiration rates in midday (at 12:00 or 14:00 LT) and in Jul or Aug for all sites – Minimum soil respiration rates in Feb – Winter soil carbon flux contributed 4.8–7.1 % to the annual soil respiration rates	Shen et al. (2014)
Northern foothills of the Brooks Range, Alsaka (68°37′ N, 149°18′ W)	Measurements of CO_2, water and energy using eddy covariance systems at three tundra types Sep 2007–May 2011	CO_2 flux	– Maximum CO_2 uptake during Jul in the three tundra types – The three tundra types as CO_2 sink during growing season – Net growing season's CO_2 accumulation lost/respired during the snow-cover period – In the early spring, the switch from CO_2 source to sink strongly regulated by the number of warmer day, so that warmer springs promote the increase in net CO_2 uptake – During snow season (Nov–Apr), negative correlation between snow depth and CO_2 flux to the atmosphere	Euskirchen et al. (2012)
Subalpine forest in the Rocky Mountains, Colorado (40°1′ N, 105°32′ W)	Eddy covariance measurements of ecosystem respiration rate; beneath-snow measurements of soil respiration rate using a multi-inlet air-sampling system, with 11 chambers in total (4 chambers at tree area, 7 at open area and 3 above the snow to measure atmospheric (CO_2)) Winter months of 2003–2004	Beneath-snow CO_2 concentration and flux, Eddy fluxes of CO_2	– Fairly constant beneath-snow (CO_2) despite increasing snow-pack depth during winter (start 20 Nov), followed by an increase during a snow-melt event (20 march), a few days of (CO_2) reduction with decrease in depth and density of snow (beginning of Apr), and a large increase in late spring (until early May) – Estimation of 35–48 % contribution of winter soil respiration to the total wintertime ecosystem respiration – Winter soil respiration accounted for 7–10 % of the total annual ecosystem respiration	Monson et al. (2006a)
	Six-year record of net ecosystem CO_2 exchange (NEE) (eddy covariance and beneath-snow measurements) Nov 1998–Oct 2004	CO_2 flux, NEE	– Correlation between interannual variations in late winter cumulative NEE with variation in mean soil temperature and the cumulative winter snow-pack – Shallower snow-cover resulted colder soils and lower rate of soil respiration – Susceptibility of soil respiration rate to snow-depth attributed to a low-temperature adapted (narrow temperature range) microbial community – Late-winter NEE over the six years accounted for 21 % of the average cumulative annual NEE at the site	Monson et al. (2006b)
Forest soils near the Arctic treeline in northwest Alaska (67°29′ N, 162°12′ W)	Five forest and two treeline sites, measurements of subnivean (CO_2), soil temperature and snow depth along a linear transect at each site, with atmospheric (CO_2) at start and end of transect. Flux estimations using diffusion gradient approach Late winters 2007–2009	CO_2 flux	– Greater snow depth and soil temperature in the forest sites compared to the treeline sites, especially in years with higher snowfall – Similar patterns of soil temperature, snow depth and estimated CO_2 efflux –5 sites showed increasing patterns of CO_2 efflux during the years, while the other 3 site (including 2 treeline sites) showed just very small changes – The forest soils lost more C during late winter compared with the treeline sites	Sullivan (2010)

Table 3. Continued.

Biome	Design/time	C-compound	Effect	Reference
Sub-alpine forests near Fraser Colorado, USA (39°4′ N, 105°52′ W)	−50 and 300 yr forest stand – Sampling at 5 blocks in each stand, each block consisting of 2 cut and unharvested pairs Snow seasons 2002–2003 and 2003–2004	Soil surface CO_2 efflux through snow	– Same pattern of soil surface CO_2 flux in the two sites, with lower value in Jan and highest in May for both study years −13 % lower under-snow soil CO_2 efflux in the younger forest during winter months	Hubbard et al. (2005)
Larch forest in Greater Khingan Mountains, Northeast China (50°56′ N, 121°30′ E)	5 collars (3–7 cm depth) to measure soil respiration (using LI-8100A automated soil CO_2 flux system), every day measurements between 9–11 a.m., 5 collars to measure heterotrophic respiration (using the trenching method), temperature and moisture measurements in the open air an 5 cm soil depth Mid-Oct–early Nov 2011 (three snow events occurred during this period)	Soil respiration, heterotrophic respiration	– Linear declining trend for both respiration and heterotrophic respiration during the measurement period – Exponential correlation between soil respiration and soil temperature – A "freeze–thaw critical point" was proposed. The Q_{10} above this point was much higher than below it	Du et al. (2013)
Colorado Rockies, Summit County, Colorado	Biweekly measurements of winter CO_2 flux at 5 transects (10 locations each), at snow surface and 25 cm depth increments through snow to the soil surface Jan–May 2003	Winter CO_2 flux through snowpack	– Overwinter subnivean CO_2 flux was positively and strongly correlated with soil carbon content	Brooks et al. (2005)

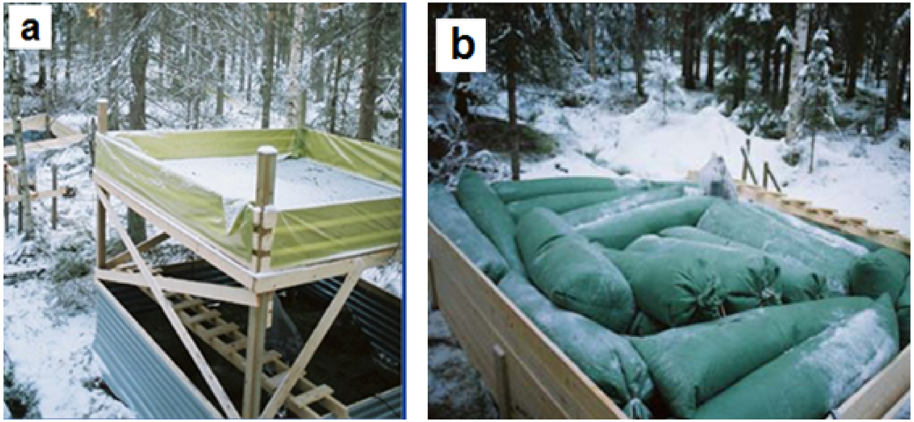

Figure 1. Field-scale soil frost manipulation experiment started 2002 in boreal forests of northern Sweden: **(a)** Deep soil frost treatment plot and **(b)** Shallow soil frost treatment plot (see Öquist and Laudon (2008) and Haei et al. (2010) for details).

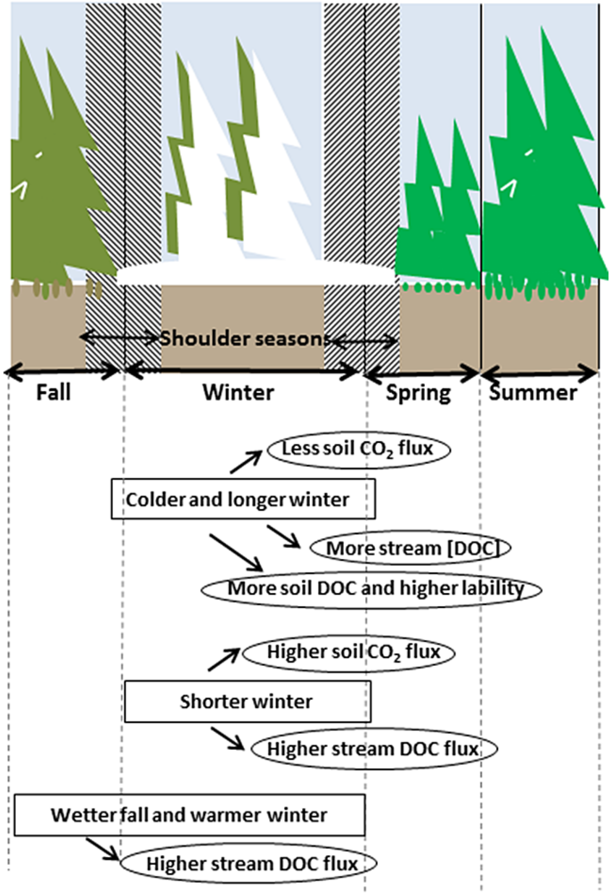

Figure 2. Summary of changes in the winter climate and carbon dynamics, during fall-winter shoulder season, winter and winter-spring shoulder season.

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Carbon dynamics and changing winter conditions

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