



The current state of CO₂ flux chamber studies in the Arctic tundra: A review

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**Anna-Maria Virkkala** 

University of Helsinki, Finland

Tarmo Virtanen

University of Helsinki, Finland

Aleksi Lehtonen

Natural Resources Institute Finland, Finland

Janne Rinne

Lund University, Sweden

Miska Luoto

University of Helsinki, Finland

Abstract

The Arctic tundra plays an important role in the carbon cycle as it stores 50% of global soil organic carbon reservoirs. The processes (fluxes) regulating these stocks are predicted to change due to direct and indirect effects of climate change. Understanding the current and future carbon balance calls for a summary of the level of knowledge regarding chamber-derived carbon dioxide (CO₂) flux studies. Here, we describe progress from recently (2000–2016) published studies of growing-season CO₂ flux chamber measurements, namely GPP (gross primary production), ER (ecosystem respiration), and NEE (net ecosystem exchange), in the tundra region. We review the study areas and designs along with the explanatory environmental drivers used. Most of the studies were conducted in Alaska and Fennoscandia, and we stress the need for measuring fluxes in other tundra regions, particularly in more extreme climatic, productivity, and soil conditions. Soil respiration and other greenhouse gas measurements were seldom included in the studies. Although most of the environmental drivers of CO₂ fluxes have been relatively well investigated (such as the effect of vegetation type and soil microclimate on fluxes), soil nutrients, other greenhouse gases and disturbance regimes require more research as they might define the future carbon balance. Particular attention should be paid to the effects of shrubification, geomorphology, and other disturbance effects such as fire events, and disease and herbivore outbreaks. An improved conceptual framework and understanding of underlying processes of biosphere–atmosphere CO₂ exchange will provide more information on carbon cycling in the tundra.

Keywords

Arctic, tundra, chamber, net ecosystem exchange, gross primary production, ecosystem respiration

1 Introduction

Tundra regions are expected to experience stronger climate warming than other regions in the world (Hinzman et al., 2013; Stocker et al.,

Corresponding author:

Anna-Maria Virkkala, Department of Geosciences and Geography, University of Helsinki, P.O. Box 64 (Gustaf Hållströmin katu 2), Helsinki, FI 00014, Finland.

Email: anna-maria.virkkala@helsinki.fi

2013). They are also highly sensitive to environmental change, which may potentially alter their ecological dynamics (Hinzman et al., 2005; McGuire et al., 2009; Post et al., 2009). Higher air temperatures have already been observed to alter permafrost extent (Osterkamp and Romanovsky, 1999; Schuur et al., 2009), vegetation distribution (Elmendorf et al., 2012; Forbes et al., 2010; Hudson and Henry, 2009; Tape et al., 2006), and hydrological cycles (Mernild et al., 2012; Overeem and Syvitski, 2010; Smol and Douglas, 2007). These changes are tightly linked to the tundra carbon cycle which plays an important role in the global carbon balance: northern tundra regions store approximately 50% of global soil organic carbon (SOC) stocks (Hugelius et al., 2014; McGuire et al., 2009; Tarnocai et al., 2009). Whether tundra regions will act as a carbon sink, or as a carbon source, in a warmer climate remains uncertain (Belshe et al., 2013; McGuire et al., 2012; Sitch et al., 2007).

The SOC stocks and the carbon balance are regulated mainly by CO₂ and CH₄ exchange between the biosphere and the atmosphere (McGuire et al., 2010b). Moreover, the lateral transport of organic and inorganic carbon in soil water transfers carbon to streams and rivers in a dissolved or particulate form (McGuire et al., 2009, 2010a; Parmentier et al., 2017). Two processes, or fluxes, dominate the biosphere–atmosphere exchange: CO₂ uptake by ecosystems via photosynthesis (GPP: gross primary production) and CO₂ release to the atmosphere via plant and microbial respiratory losses (ER: ecosystem respiration) (Callaghan et al., 2004). The CO₂ balance between these two fluxes is called NEE (net ecosystem exchange).

Future climate warming can affect CO₂ fluxes in multiple ways (Arens et al., 2008; Biasi et al., 2008; Bokhorst et al., 2010). On the one hand, warming might accelerate soil respiration by heterotrophs, that is, the microbial decomposition of organic matter, thus increasing respiratory carbon losses (Grogan

and Chapin, 2000; Nadelhoffer et al., 1991). These emissions may be multiplied if permafrost soils thaw and the carbon stored therein will become available for decomposition (Kuhry et al., 2010; Van Huissteden and Dolman, 2012). On the other hand, increases in temperature, greater release of available soil nutrients via accelerated decomposition, and a longer growing season have the potential to stimulate GPP and strengthen the carbon sink (Cahoon et al., 2012b; Leffler et al., 2016). Changes in the CO₂ fluxes can therefore either increase or decrease NEE and thus create either a negative or positive feedback to global warming. A recent tundra meta-analysis based on 54 studies suggested that there has been an increase in the CO₂ source due to higher ER, resulting in amplified carbon losses to the atmosphere in warmer conditions (Belshe et al., 2013).

Though climatically controlled, the magnitudes, directions, and feedbacks of GPP and ER are ecosystem- and scale-dependent (Oberbauer et al., 2007; Pare and Bedard-Haughn, 2012). Tundra landscape heterogeneity (Fletcher et al., 2012; Post et al., 2009; Virtanen and Ek, 2014) is apparent at multiple scales. At the landscape scale, diverse environmental conditions and vegetation types create mosaic of ecosystems, for example, bogs and barrens. These ecosystems, in turn, are made up of diverse plant-communities, such as heaths, tussocks, or hummocks. At this fine scale, environmental conditions can change within only a few meters (Aalto et al., 2013). Such variation might offset climatological effects and buffer climate change-induced modifications in CO₂ fluxes (Post et al., 2009). For example, the environmental gradients of soil moisture are an important driver of CO₂ fluxes (Nobrega and Grogan, 2008; Oberbauer et al., 2007; Sharp et al., 2013). However, the fine-scale variation of CO₂ fluxes is not yet fully understood. This may hinder our ability to predict the future carbon balance.

GPP, ER, and NEE are studied with various methods in the field. There are two widely used

techniques to measure CO₂ fluxes between ecosystems and the atmosphere: the micrometeorological eddy covariance (EC) technique, and chamber measurement techniques. EC measures fluxes continuously at an ecosystem scale in areas between 100 m² to 10,000 m², thus averaging over fine-scale heterogeneity (Kade et al., 2012; Maanavilja et al., 2011). However, using detailed land cover and wind direction information, flux sources can to some extent be estimated by footprint modeling techniques (Fox et al., 2008; Soegaard et al., 2000). Studies investigating individual plant communities and fine-scale spatial variability (100–10,000 cm²) in the tundra are usually conducted using chambers. Both abovementioned methods have their limitations. The costs of setting up and maintaining an EC tower are higher than for the chamber method. Additionally, EC requires more electricity, technical knowledge, and understanding of surface-layer meteorology; whereas chambers are widely used due to low power consumption and simple operation. However, manual chamber measurements are laborious. With the chamber method, the different components of CO₂ exchange can be studied, thus providing important data on the processes regulating biosphere–atmosphere interactions (McGuire et al., 2012).

In order to understand CO₂ fluxes at multiple scales, reviews, and meta-analyses are important to summarize the current knowledge. Comprehensive works exist on the Arctic carbon cycle as a whole (McGuire et al., 2009; Parmentier et al., 2017), on the vulnerability of permafrost carbon (Abbott et al., 2016; Ping et al., 2015; Schuur et al., 2008), and on the CO₂ and carbon balance of tundra regions during the past 20–40 years (Belshe et al., 2013; McGuire et al., 2010a, 2012; Oechel et al., 1993, 2000). Although these analyses include chamber studies, the main focus has been on the effects of large-scale drivers and temporal changes on CO₂ fluxes. To our knowledge, no previous reviews or meta-analyses focus on chamber

studies of GPP, ER, and NEE with an emphasis on fine-scale vegetation and soil variables.

In this review, we synthesize the progress of chamber-derived growing season CO₂ flux studies in terrestrial Arctic tundra. We focus on chamber studies as they have been and will continue to be a central and cost-efficient method to study the underlying processes in CO₂ exchange, and are able to account for the fine-scale spatial variability of these processes. GPP and ER are the most important fluxes considered (Cahoon et al., 2012b; Illeris et al., 2004), as they are processes that govern the net exchange of CO₂ between an ecosystem and the atmosphere. Furthermore, the balance of these two, NEE, is also incorporated in the review. We review the study areas and study designs where GPP, ER, and NEE are investigated and identify environmental conditions not sufficiently covered by these studies. Our aim is to examine the explanatory variables used and whether they correspond to mechanisms of known importance. Section II will give a short introduction to the tundra carbon cycle and Sections III to VI encompass a systematic review of 93 articles found via ISI Web of Science (WoS) and subsequently from the references therein. We include recent publications only (studies published 2000–2016: see online Supplementary Material 1 & 2, S1 & S2) to determine the current state of CO₂ flux chamber studies in the tundra.

II Carbon cycle in a tundra environment

The spatial extent of Arctic tundra regions (from hereon, tundra regions) can be defined in various ways. Here, we consider the tundra as a biome of treeless vegetation and their adjacent tree-line areas in the Arctic and oro-Arctic regions (as suggested by Virtanen et al., 2016). Sub-Arctic and Arctic peatlands were included in the review whilst boreal regions were excluded as we concentrated on tundra

patterns and processes only. Thus defined, tundra regions cover 8.7% of global terrestrial areas (Dinerstein et al., 2017) and are characterized by low summer temperatures and long winters (Billings and Mooney, 1968).

Due to low solar energy input and harsh climatic seasonality, primary production, respiration, and decomposition rates are slow. Significant seasonal cycles in these processes exist largely due to snow cover and the short, two-to-four-month growing season (Leffler et al., 2016; Van der Molen et al., 2007). Photosynthesis only occurs during the summer, whereas decomposition and respiration occur throughout the year, albeit at slower rates in winter (Larsen et al., 2007). The growing season is the most active season for GPP and ER, although spring and autumn CO₂ fluxes can contribute up to 19% of annual GPP (Larsen et al. 2007). GPP and ER may fluctuate on inter-annual and longer time scales due to the variations in for example, climatic parameters. Diurnal cycles are also notable: daytime GPP usually offsets ER, but at night ER becomes dominant (López-Blanco et al., 2017). NEE, defined as $NEE = ER - GPP$, is usually a small difference between two large fluxes which makes it sensitive to small changes. Based on observations, tundra regions can be either CO₂ sources or sinks with large temporal variation on inter-annual and decadal scales (López-Blanco et al., 2017). Typical NEE values are, for example, -79 to -41 g C m⁻² yr⁻¹ in a Russian erect shrub tundra–wetland complex (Marushchak et al., 2013), -4 to -53 g C m⁻² yr⁻¹ in a Fennoscandian fen (Aurela et al., 2004), and -2.3 g C m⁻² yr⁻¹ in an Arctic valley in Greenland (Soegaard et al., 2000), with negative values indicating a net carbon uptake by ecosystems. These estimates are smaller than for the neighboring boreal and temperate regions, but they have the potential to change in a warmer climate (Hartley et al., 2012; Parker et al., 2015).

Although tundra regions lack the trees that dominate carbon exchange in forested

ecosystems, they have highly variable vegetation patterns. One of the most common ways to describe tundra vegetation is the Circumpolar Arctic Vegetation Map (CAVM; e.g. Pearson et al., 2013; Raynolds et al., 2008) created by Walker et al. (2005). They divide the Arctic based on the general appearance of vegetation into the following habitat-scale physiognomic categories and further into specific mapping units based on plant functional types (PFTs): barren (B), graminoid (G), prostrate-shrub (P), erect-shrub (S), and wetland (W) tundra, all of which have distinct CO₂ flux patterns (Figure 1). GPP usually exceeds ER, leading to a net uptake of carbon (negative NEE) during the growing season in all CAVM categories except in barren vegetation types. In general, deciduous shrubs and graminoids have the highest GPP due to high leaf area and vegetation cover, with graminoids having even larger ER due to their faster metabolism (Cahoon et al., 2012b; Hobbie, 1996; Nobrega and Grogan, 2008; Oberbauer et al., 2007). Yet, the annual leaf development cycle of deciduous plants shortens their carbon uptake period in the early and late growing season. Evergreen shrubs and cryptogams, on the other hand, start photosynthesizing as soon as the ground is snow-free (Douma et al., 2007; Street et al., 2012b).

III Study designs and locations

I Overview of the studies

During the twenty-first century, most of the studies have focused on the effects of climate warming and related feedbacks on CO₂ fluxes (Biasi et al., 2008; Boelman et al., 2003; Welker et al., 2004), differences between vegetation types (Shaver et al., 2007; Williams et al., 2006), hydrological effects (Dagg and Lafleur, 2011; Nobrega and Grogan, 2008), and growing season dynamics (Bäckstrand et al., 2008; Larsen et al., 2007). The effect of permafrost thaw on CO₂ fluxes has not received a lot of attention until lately (Natali et al., 2011; Schuur

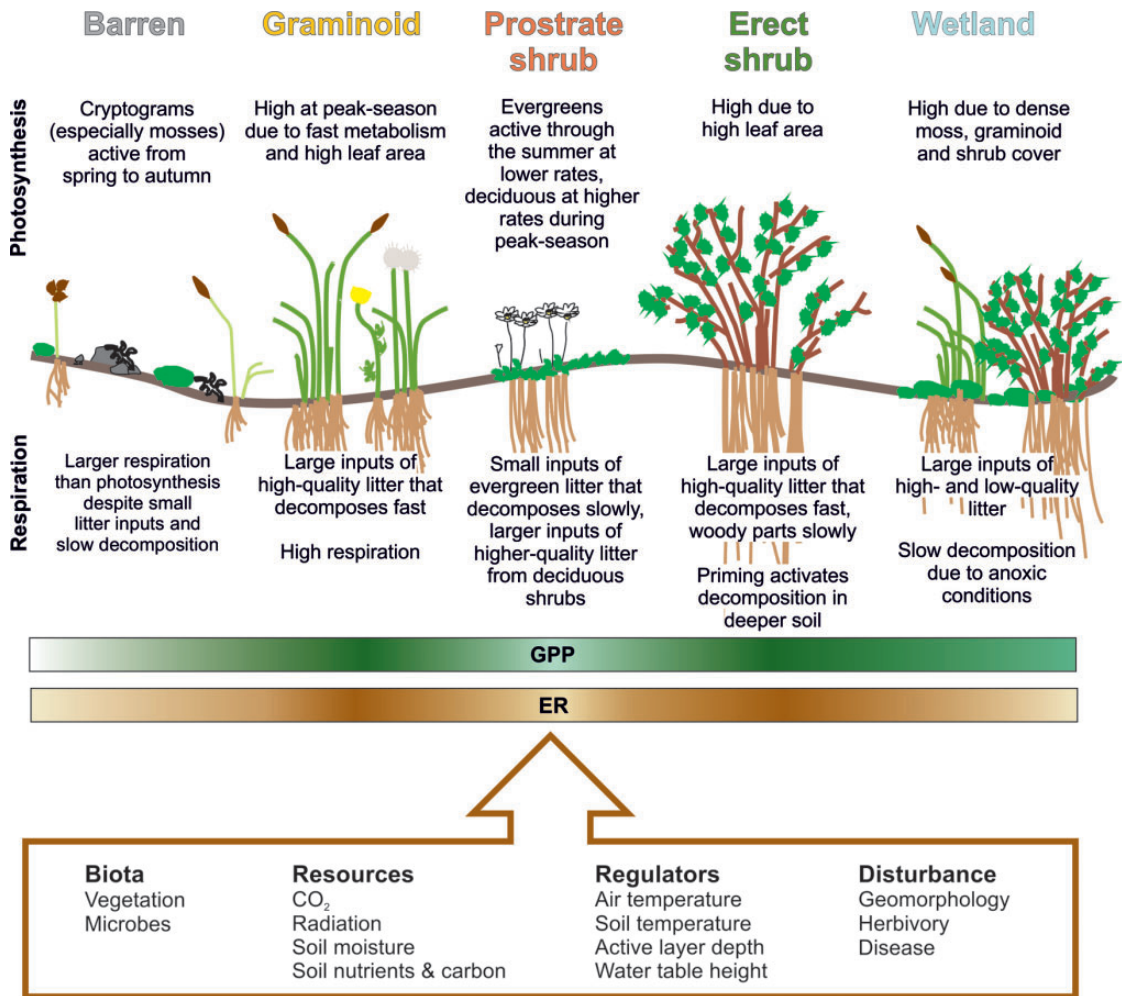


Figure 1. CO₂ fluxes are regulated by biota, resources, regulators, and disturbance, and vary depending on CAVM (Circumpolar Arctic Vegetation Map) categories resulting in different carbon balances. CAVM represents only the major vegetation units and is developed for landscape or circumpolar scales, although in reality most tundra landscapes are mosaics of several of these types and their subtypes (Walker et al., 2016). The GPP (gross primary production) and ER (ecosystem respiration) bars represent their rates: the darker the shade, the faster the process. Increased GPP is often linked to higher plant respiration rates and, therefore, increased ER (Johnson et al., 2000). Increased GPP also stimulates the rate of litter production, resulting in higher heterotrophic respiration rates (Boelman et al., 2003).

et al., 2009; Vogel et al., 2009). The most cited articles (>100 citations) within the literature reviewed focused on the effects of experimental warming and permafrost thaw on CO₂ fluxes and their spatial variation (S3).

The geographical distribution of observations in the CO₂ flux chamber studies is

clustered in Alaska (32 out of 93 studies) and Fennoscandia (27), with smaller clusters scattered across Greenland (18), Russia (13), and northern Canada and Svalbard (8, Figure 2(a), S4). The observation sites do not cover the environmental variation or the extreme conditions found in the Arctic (Figure 2(b)). Extreme

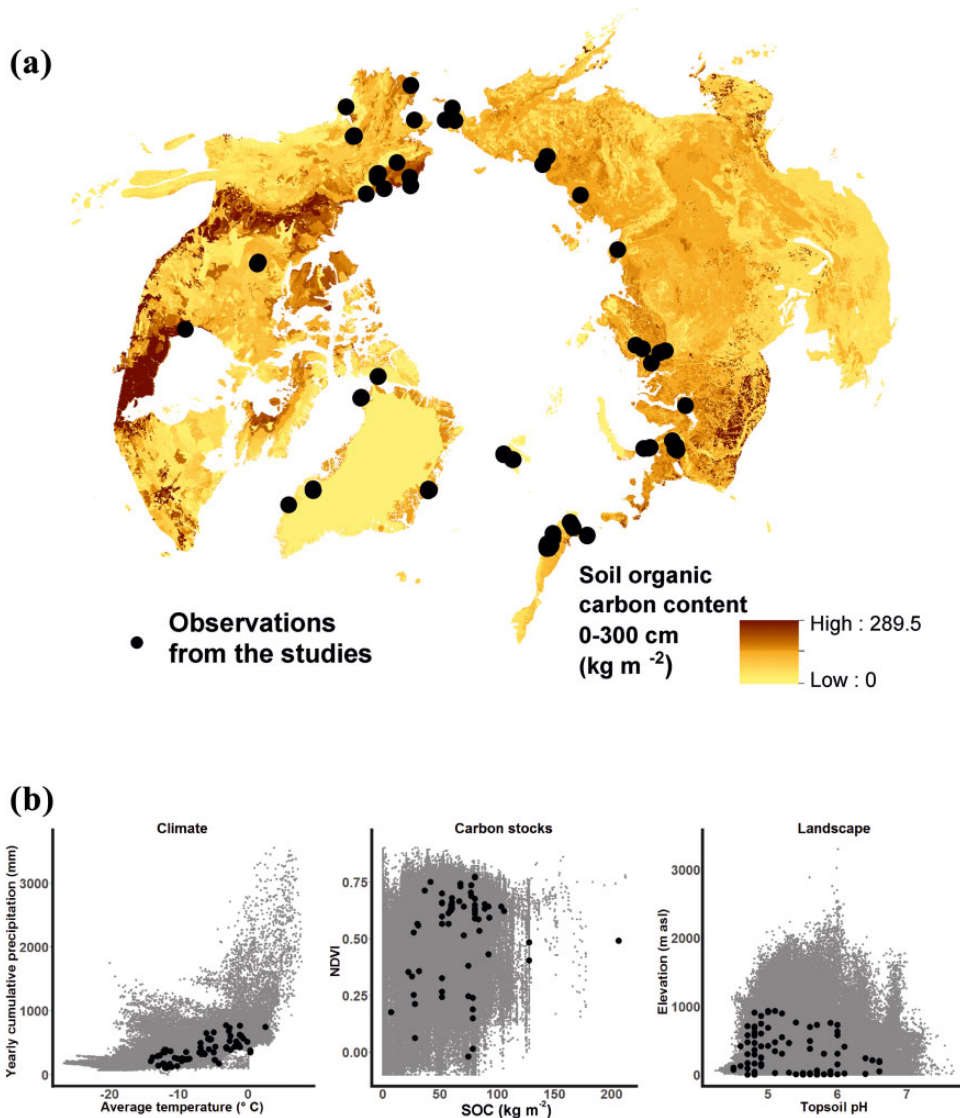


Figure 2. (a) The spatial distribution of the observations in the study with a base map of soil organic carbon content. (b) The environmental conditions of the observations (in black) versus the environmental conditions in the Arctic tundra (in gray). The data acquired from WorldClimv2 (1970–2000), Soilgrid (topsoil pH), NCSCDv2 (soil organic carbon, SOC), TERRA/MODIS NDVI -product (July, 2015), and GTOPO DEM (elevation). The Arctic area was defined by Ecoregions (Dinerstein et al., 2017). See S2 for more details.

conditions are generally found in the middle and eastern parts of Russia, and along coastlines and islands of northern Canada and Greenland. The environmental conditions in Alaska and Fennoscandia are characterized by relatively

high precipitation, semi-oceanic climates, and acidic or mildly acidic soil conditions. In addition to these spatial limitations, continuous sampling of CO_2 fluxes remains a challenge (McGuire et al., 2012). While there are many

studies with measurements from multiple growing seasons (Arens et al., 2008; Olivas et al., 2010), there are not many year-round observations (S4). The cold season (autumn, winter and spring) has been included in some studies, mainly in order to understand the role of non-growing season versus growing season CO₂ fluxes and their drivers (Grogan and Jonasson, 2005; Kade et al., 2012; Larsen et al., 2007).

CO₂ flux chamber studies are usually based on relatively small data sets (median number of sites studied four). With small data sets, all environmental gradients (e.g. topography, radiation, hydrology, productivity) are difficult to cover. Often, studies are designed to simplify and understand the variation with the help of different classifications mainly based on vegetation (e.g., Christensen et al., 2000, on Cassiope, hummock, continuous fen, grassland, and *Salix arctica*), soil moisture (e.g., Welker et al., 2000, on dry and wet), or a combination of these two (e.g., Dagg and Lafleur, 2010, on dry birch, mesic birch, dry tussock, wet tussock, dry heath, mesic heath, wet sedge). The topographic gradient has been considered mostly in the peatland studies with microtopographically varying hummocks and hollows (Poyatos et al., 2014), though there are some coarser scale toposequence studies (Williams et al., 2006).

Based on our findings, future research should focus more on extreme conditions. Areas of high precipitation and low temperatures (e.g., southeastern parts of Greenland) or high temperatures (e.g., southern Alaska) should also receive further attention. Additionally, neutral conditions (topsoil pH > 6, e.g., along the coastlines of Nunavut and Siberia) and higher elevations (e.g., in eastern Siberia) need to be considered. Relatively large SOC stocks are found in the Northwestern or Yukon Territories in Canada, which have not received much consideration. As fluxes in Alaska and Fennoscandia are the most studied and cited, it seems that our understanding of CO₂ fluxes is limited to these regions and important knowledge

regarding for example High-Arctic environments has not been adequately considered. We realize that logistical and infrastructural reasons are, to some extent, responsible for this pattern, but this may potentially lead to misinterpretations of the CO₂ exchange of the whole tundra region. Moreover, studies in calcareous regions are needed as the higher availability of nutrients in neutral areas may cause CO₂ fluxes to vary more than in acidic landscapes with low nutrient availability (Williams et al., 2006). Furthermore, we emphasize the need for better observational studies to understand the spatio-temporal variation of CO₂ fluxes along environmental gradients as the drivers and dynamics might change due to global warming (Shaver, et al., 2013; Zamolodchikov, 2015). We encourage future studies to measure CO₂ fluxes from various topographical conditions from fine, 1–10 m (Scherrer and Körner, 2011), to ecosystem and landscape scales, 10–1000 m (Billings, 1973), as the response of biota to climate warming varies depending on topographic position.

2 CO₂ flux chamber measurement methods

Various chamber systems have been used for studying CO₂ fluxes. Most of the tundra CO₂ flux studies were conducted with manual chambers while automated systems are still rare (11 studies) because of the high costs and infrastructure challenges (S4; e.g. Griffis et al., 2000; López-Blanco et al., 2017; Natali et al., 2011; Poyatos et al., 2014).

Chamber size plays an important role when studying CO₂ fluxes. Tundra regions are microtopographically heterogeneous and, therefore, smaller chambers (<50 cm in diameter) are more practical. However, with a larger chamber, the erroneous influence of chamber edges on measurements decreases. Based on our literature survey, chamber sizes (when measured from edges or diameter of the chamber) and heights vary from 15 to 100 cm. The average height is relatively low, limiting the vegetation

type studied (S4). Regardless of chamber type and size, the air-proof sealing of the chamber into the ground is an important step when measuring fluxes (Hutchinson and Livingston, 2001). Traditionally, plastic or aluminum collars are put into the ground (depth 2–10 cm) and chamber placed atop of them. Collars are positioned into the ground just minutes, days (Dagg and Lafleur, 2011; Stewart et al., 2013) or weeks before the measurement (Nykänen et al. 2003; Heikkinen et al. 2002), or in the preceding year (Grogan and Jonasson, 2005). However, placing the collars into rocky soils or soils with long horizontal aboveground shoots and roots typical to some tundra plants (e.g., *Empetrum hermaphroditum*, *Dryas* sp.) without cutting them is a challenge. A method that uses the combination of a plastic skirt and metal chains instead of, or in addition to, collars has been developed and is widely used in the studies (Street et al., 2007, 2012a).

We stress the need for long-term measurements of CO₂ fluxes with automated chambers, as they provide important information about local carbon cycle dynamics and episodic events in the Arctic. Moreover, we recommend researchers to carefully consider the chamber size used, and the timing and placement of the collar into the ground. Measurement devices and calculation techniques also have an impact on the measured fluxes. For example, CO₂ fluxes may be underestimated when using linear regression as compared to nonlinear methods (Kutzbach et al., 2007).

3 Studied fluxes

From the global carbon balance perspective, NEE is an important flux variable to study as it describes whether the environment is acting as a CO₂ sink or source (Belshe et al., 2013). Yet, NEE itself is not a process but a balance between two simultaneous processes, GPP and ER, that are more strongly linked to environmental drivers. Although studying NEE is

crucial, many articles state that the future carbon balance is regulated by ER (Biasi et al., 2008; Cahoon et al., 2012b) or soil respiration (Knowles et al., 2016; Luo et al., 2016). Despite this, soil respiration was measured in relatively few studies (15) together with GPP, ER, and NEE. Moreover, CO₂ fluxes are linked to other biogeochemical (N₂O, CH₄, and H₂O) fluxes. Methane (CH₄) fluxes were studied in 24 studies, out of which most of the measurements were from wetlands (S4). Other fluxes, such as nitrous oxide (N₂O; e.g., Brummell et al., 2012; Kelsey et al., 2016) or water (H₂O; e.g., Douma et al., 2007) were studied even less in CO₂ flux chamber studies, partly because according to current knowledge, N₂O emissions are significant in only non-vegetated patches with high soil organic matter content (Marushchak et al., 2011). They are increasingly measured alone (Flessa et al., 2008; Gil et al., 2017; Voigt et al., 2017), without CO₂ exchange measurements. Chamber-derived CO₂ fluxes have also been investigated together with EC and leaf cuvette methods (Heikkinen et al. 2002; Vourlitis et al. 2000). Studies with EC aimed to (a) describe the annual variation of CO₂ fluxes more reliably, and (b) test the upscaling potential of chambers for EC measurements with varying success in summer- and winter-time (Kade et al., 2012; Maanaviija et al., 2011; Marushchak et al., 2013). In total, EC was used in 11 studies and leaf cuvette measurements 5 (S4).

Based on our findings, we suggest that future studies should incorporate soil respiration measurements into CO₂ flux chamber studies. However, there is no standard way of measuring soil respiration and most of the methods cause disturbance to the ground, or require laboratory work (Kuzyakov, 2005). Clipping the vegetation was a widely-used method in the investigated articles (Illeris et al., 2004; Nobrega and Grogan, 2008). In some articles, soil respiration was quantified from a non-vegetated soil close to other CO₂ flux measurements (Arens et al.,

2008) or with incubation methods (Ylänne et al., 2015). Despite the disturbance caused by clipping, this might be a cost-efficient method for soil respiration measurements, providing there is a sufficient waiting period between the clipping and the measurements (Illeris et al., 2004). Incubation methods will provide robust information on the soil CO₂ emissions for more precise analyses. In addition to soil respiration measurements, the inclusion of non-CO₂ greenhouse gas measurements would provide better understanding of climate forcing, especially in wet regions (CH₄) and non-vegetated areas (N₂O) (e.g., Brummell et al., 2012). Furthermore, the incorporation of multiple flux measurement methods will provide more reliable and increasingly detailed information on the spatial and temporal variation of CO₂ fluxes (Myklebust et al., 2008).

IV Environmental drivers studied to explain fluxes

GPP, ER, and NEE are affected by multiple variables which can be divided into four categories: (a) biota, where the processes occur, (b) resources which are consumed by the biota, (c) regulators which affect the metabolic processes, and (d) disturbance which often destroys the biota and therefore influences the fluxes (Figures 1 and 3). Here, we review how these four categories and their variable classes have been included in studies (Table 1). The environmental drivers used to explain fluxes varies depending on the research questions and study designs, yet we assume that with a systematic review (S2 & S4) of the environmental drivers measured in the studies, we can highlight overall research gaps.

I Climate

Air temperature and solar radiation are the most important climatic variables explaining CO₂ fluxes, both spatially and temporally, as temperature controls the metabolic activity of biologic

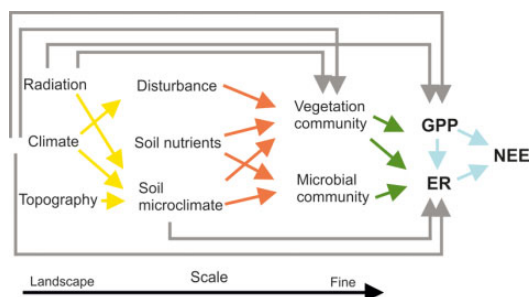


Figure 3. The hierarchy and most important relationships of the environmental drivers regulating GPP (gross primary production), ER (ecosystem respiration), and NEE (net ecosystem exchange) from landscape to fine scale. The arrows represent the main direction of the effect, and the colors of the arrows have no meaning. The resource variables have mostly a direct link to GPP and ER, but regulators and disturbance affect the biota, and thus, GPP and ER.

organisms and energy from the sun drives photosynthesis (López-Blanco et al., 2017; see also Figure 1). Air temperatures and photosynthetically active radiation (PAR, or photon flux density PPFD) in the chamber and/or in the vicinity of loggers are almost always included in the studies, and are often used in the models explaining GPP, ER, and NEE (Karelin et al., 2013; Shaver et al., 2013; Williams et al., 2006).

CO₂ fluxes are driven by soil microclimate which varies spatially over short distances. Soil temperature does not have a direct effect on GPP but it is an important driver of ER (Larsen et al., 2007) as it stimulates soil respiration and decomposition (Grogan and Chapin, 2000). Soil moisture has been identified as a limiting factor for GPP (Nobrega and Grogan, 2008) and for soil and plant respiration, especially at the soil moisture extremes (Dagg and Lafleur, 2011; Giblin et al., 1991; Illeris et al., 2003). The importance of soil microclimate has been recognized in the studies: the temporally varying soil temperature, active layer depth (or thaw depth), soil moisture, and water table height are included in approximately 80% of the studies

Table 1. Environmental categories and classes used to explain CO₂ fluxes. Leaf area index (LAI) measures the amount of leaf area in a canopy per unit ground area (m²/m²; Asner et al., 2003). The normalized difference vegetation index (NDVI) derived from remote sensing describe the amount of green biomass and/or LAI. Numbers in parentheses indicate the number of studies (0–93) to include the environmental categories/classes.

Categories	Climate (91)	Vegetation (79)	Soils (54)	Disturbance (38)
Classes	Air temperature (80) Radiation (72) – Photosynthetically active radiation (PAR) Soil microclimate (81) – topsoil temperature – active layer depth – moisture – water table height	Biomass (75) – cover, biomass, LAI – remotely sensed parameters (NDVI) Plant traits (35) – leaf N – leaf cover/area – vegetation height Growth & phenology (17) – shoot, root, leaf, biomass growth – phenology	Soil nutrients (36) – C, N, P – pH – litter biomass Physical properties (41) – soil type, texture – organic layer depth Microbes (8) – microbial biomass, activity, community structure	Geomorphology (24) – permafrost thaw, cryoturbation, fluvial processes Herbivory (13) – small & large mammals – birds – insect outbreaks Disease (1) – plant pathogens

(Figure 4). Soil temperature is also often used when modeling ER and NEE, sometimes together with other soil microclimatological variables such as active layer depth or water table height (Christensen et al., 2000; Segal and Sullivan, 2014). Water table height is an important variable, especially in the peatlands, as it controls the anoxic conditions needed for CH₄ emissions.

2 Vegetation

Vegetation plays an important role in controlling the variation of CO₂ fluxes as GPP and, partly, ER are processes occurring within the plant (Johnson et al., 2000). The reviewed studies always provide some information on the dominant species with varying degrees of additional data on vegetation properties (e.g., biomass, leaf area index (LAI)). We collected data on the dominant and secondary species in each

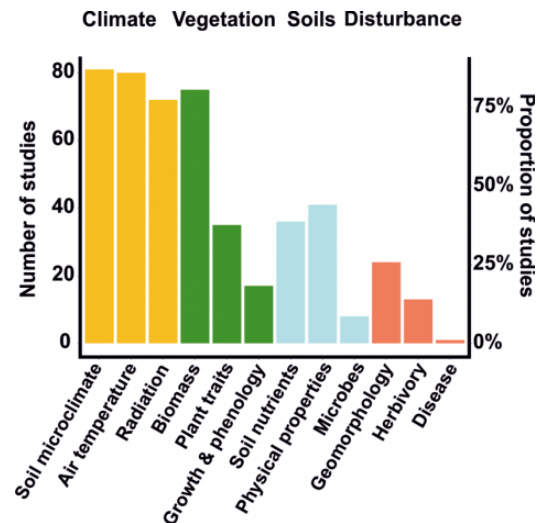


Figure 4. Number and proportion of studies in which each environmental class was used. Climatological variables and biomass were studied the most, whereas other vegetation properties, soils, and disturbance the least.

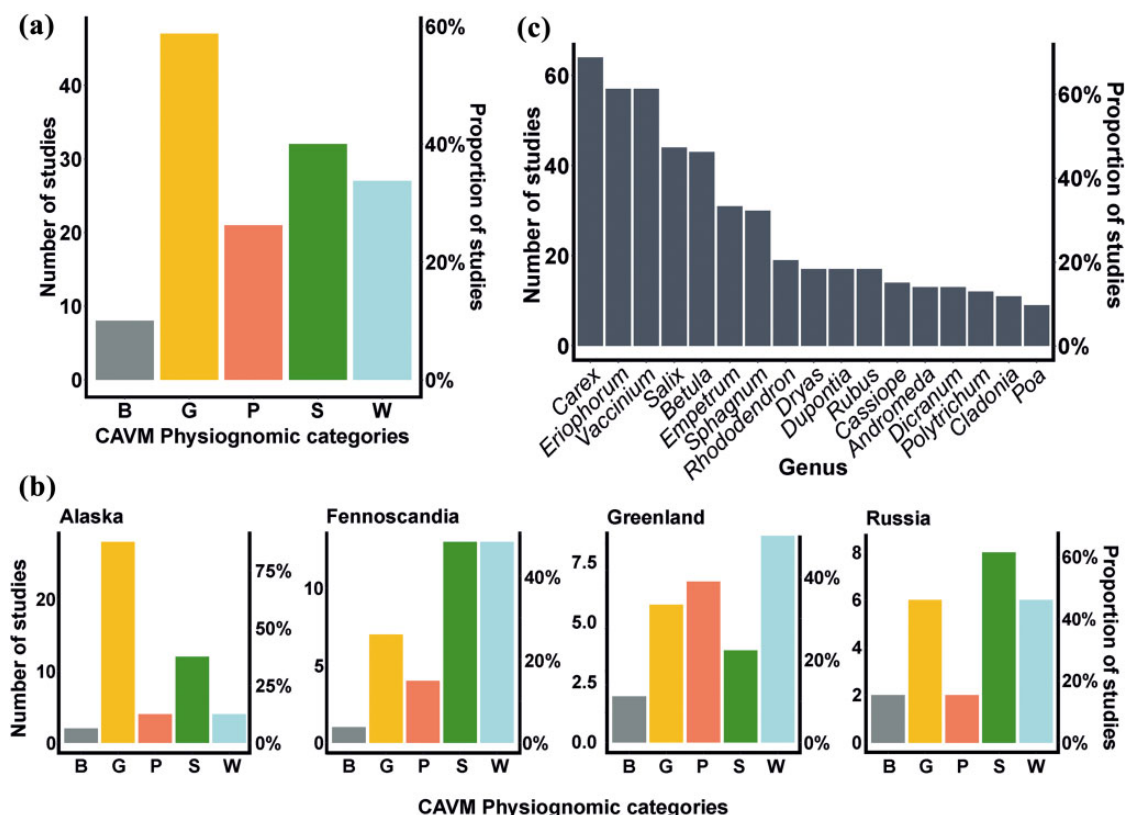


Figure 5. (a) Number and proportion of studies with observations from different CAVM (Circumpolar Arctic Vegetation Map) categories in the Arctic tundra (B = barren, G = graminoid, P = prostrate shrub, S = erect shrub, W = wetland). (b) Number and proportion of studies with observations from the most dominant genera. (c) Number and proportion of studies with observations from different CAVM categories per most intensively studied regions. The vegetation data is based on the dominant and secondary species informed by the authors, which was then used to classify the vegetation into CAVM categories. Note the differing proportions on the y-axis.

measurement plot from the articles and further divided it into CAVM categories (S2, S5). In many of the studies different measurement sites within the study area belonged to several CAVM categories.

Most of the research has been conducted for the most dominant vegetation types and species in the Arctic: on graminoid-dominated meadows (with species *Carex* sp., *Eriophorum* sp. in >20 of the studies) and prostrate shrub and erect shrub heaths (with species *Betula nana*, *Empetrum* sp., *Vaccinium vitis-idaea*, *V. uliginosum* in

approximately 10–30 of the studies Figure 5(a), S5). Fewer studies included cushion plants, forbs, or mosses and lichens (despite some observations from *Cassiope* sp., *Potentilla* sp., *Sphagnum* sp., *Dicranum* sp., *Cladonia* sp., Figure 5(c), S5). There are relatively large differences among measured vegetation types in the most researched areas (Figure 5(b)). Despite the important role of *Betula nana*, taller low-shrubs such as *Salix* sp. and in some regions *Juniperus communis* and *Alnus* sp. species are also crucial in the shrubification of the Arctic, yet they were

included in only a small amount of studies. Indeed, based on article keywords, very few studies aimed to study the effects of shrubification on CO₂ fluxes (Cahoon et al., 2012b, 2016). Barren vegetation types, which cover 25% of the region, are only included in less than 10% of the studies, but have received more attention in Antarctica (Thomazini et al., 2016; Zhu et al., 2014).

Although *Eriophorum*, *Carex*, or *Betula nana*-dominated vegetation types have been relatively well studied they need to be investigated more thoroughly in different environmental conditions as CO₂ flux observations of tundra shrubs and sedges, together with moist meadows by streams, contain the largest and most varying CO₂ fluxes (Williams et al., 2006). Additionally, these are also key sites for CH₄ dynamics. Moreover, we stress the need for studies focusing on shrubification effects with a diverse combination of taller low-shrub species. In the CAVM region, low-shrub tundra can be found from European Russia, northwestern Siberia, and the Yukon-Kuskokwim River delta, as well as in southwestern parts of Greenland and locally along rivers and tree lines. Regionally, more observations are needed from wetlands in Alaska and prostrate shrubs in Siberia (Figure 5(b)). Although having only low CO₂ flux rates, we highlight the need for more studies in barren soils as these are underrepresented and their spatial coverage might increase resulting from melting glaciers (Mernild et al., 2012).

In addition to PFTs and plant species, other data on vegetation have been used to understand CO₂ fluxes in different environments (Cornelissen et al., 2003). Plants use carbon for growth and, therefore, plant biomass can be measured to understand carbon sequestration and allocation patterns (mass-ratio hypothesis; Grime, 1998). In addition to biomass measurements, LAI and normalized difference vegetation index (NDVI) have been used to link the amount of photosynthesizing leaves to carbon use patterns, out of which LAI has often been found to be the

best predictor of CO₂ dynamics (Marushchak et al., 2013; Shaver et al., 2007; Street et al., 2007). NDVI and LAI measurements were included in approximately 25 studies and biomass sampling in 45 (S4). Plant traits (leaf N, vegetation height, see Dorrepaal 2007) were studied less than biomass (Figure 4), although the relationship between leaf N and CO₂ fluxes has received increasing attention (Street et al., 2012).

Based on our findings, we firstly highlight the need for more detailed analysis of vegetation properties and CO₂ fluxes. For example, the relationship between plant traits or growth and CO₂ fluxes remains uncertain (De Deyn et al., 2008). Additionally, there is a need to study the linkages of ER and biomass, as higher biomass is linked to higher GPP but not as clearly as to ER (Boelman et al., 2003; Douma et al., 2007; Poyatos et al., 2014). Lastly, we stress the need for vegetation data-based upscaling, particularly to landscape scales, which remains a challenge in carbon cycle studies (O'Rourke et al., 2015). Although chamber-derived GPP, ER, and NEE have been linked to field-observations of spectral properties of vegetation and LAI (Boelman et al., 2003; Williams et al., 2006), this relationship has seldom been used to upscale results to larger areas with aerial or satellite imagery (Marushchak et al., 2013). More research of CO₂ fluxes and remote sensing-based indices at multiple resolutions (e.g., WorldView, Landsat, MODIS, see e.g., Curasi et al., 2016) is called for to develop the upscaling methodology. Recent progress of unmanned aerial vehicles (UAVs) offers CO₂ flux researchers new opportunities for fine spatial and hyperspectral resolution imagery data (Anderson and Gaston, 2013). To our knowledge, there are no published studies utilizing UAVs for CO₂ flux chamber measurements in the tundra.

3 Soils

GPP, ER, and NEE are regulated by soil physical, chemical, and biological properties which

vary greatly over short distances (Arnesen et al., 2007; Wang et al., 2010). Soil physical properties, particularly soil type, texture, and organic layer depth influence overall soil conditions (Buchmann, 2000; Grand et al., 2016) and are connected to soil temperature, depth of the active layer, and vegetation properties. Soil nutrients are an important resource for plants and soil microbes, therefore affecting GPP and ER (Grogan and Jonasson, 2005). Soil N together with P limit tundra productivity, leading to increases in GPP if nutrients are added to the soil (Arens et al., 2008; Shaver et al., 1998). Soil microbes (heterotrophic respiration) control soil respiration together with plant roots (autotrophic respiration) and, therefore, partly ER (Segal and Sullivan, 2014). Soil data is included in fewer studies than climate and vegetation data: soil type descriptions are included in 15 studies, litter biomass estimates in 7 studies, soil nitrogen data in 18, and SOC measurements in 15 of the studies (S4). Data from the soil microbes is included in eight studies.

We recommend future studies to at least describe the soil type (Jones et al., 2010) and organic layer depth to provide information on soil physical and chemical conditions (see e.g. Biasi et al., 2008). The inclusion of soil data is needed in spatial study designs as soil properties vary especially spatially. We highlight the need for better understanding of CO₂ flux–nutrient and SOC relationships (Williams et al., 2006) as recent studies have discovered the respiratory losses and carbon sequestration to soils to depend on soil geochemistry (Doetterl et al., 2015). Thus, including soil nutrient data, of for example N and P, also increases knowledge of the linkages between different biogeochemical cycles in the Arctic. We stress the need for easily measurable indicators of soil quality (e.g., soil pH, the color, or depth of organic matter, e.g., White et al., 2004). Microbial activity should receive more attention as it is not yet fully understood how microbial communities and their functioning regulate ER and NEE and

how they will respond to environmental change (Biasi et al., 2008; Hultman et al., 2015; Xue et al., 2016).

4 Disturbance

Geomorphological processes create disturbance that leads to heterogeneous abiotic and biotic conditions (Le Roux and Luoto, 2014) potentially shaping CO₂ fluxes (Vogel et al., 2009). There is a small but increasing amount of publications that focus on the effect of fluvial processes (Curasi et al., 2016; Oberbauer et al., 2007), cryoturbation, for example as in patterned ground and hummocks (Heikkinen et al., 2002; Maanavilja et al., 2011), and permafrost, for example as in palsas mires (Bäckstrand et al., 2010; Nykänen et al., 2003), on CO₂ fluxes. Most of these studies have been conducted in northern Fennoscandia, though there is an increasing number of studies of permafrost thaw from Alaska (Natali et al., 2011; Schuur et al., 2009).

CO₂ fluxes are mediated by biological disturbance (Falk et al., 2015; Sjögersten et al., 2011; Susiluoto et al., 2008). The tundra is grazed by large and small herbivores which can alter species composition, above- and below-ground biomass and litter quality and, therefore, CO₂ fluxes (Cahoon et al., 2012a; Metcalfe and Olofsson, 2015; Ylänne et al., 2015). Herbivory was included in 13 studies with a focus on larger herbivores such as reindeer and muskoxen (S4). Larval outbreak was included in one study (but see new studies by Lund et al., 2017; Dahl et al., 2017). In addition to herbivory, disease outbreaks (plant pathogens) can modify CO₂ fluxes but they have only been studied to a rather limited extent in one study. Olofsson et al. (2011) demonstrated GPP to decrease during the growing season due to an outbreak of a parasitic fungus, *Arwidssonia empetri* in northern Sweden. Presently, intensive insect outbreaks are rare in the tundra, but this might change if the climate warms (Abbot et al., 2016).

Fire is an important disturbance in boreal regions, but has had only minor effects on tundra carbon cycling since the early Holocene (Kasischke and Turetsky, 2006). However, models predict an increasing amount of tundra fires in a warmer climate which has already been observed in Alaska (Hu et al., 2010; Krawchuk et al., 2009), but still the effect of fire disturbance on tundra carbon cycling has received relatively little attention. Although there are studies considering the SOC stocks before and after a fire (Bret-Harte et al., 2013; Mack et al., 2011), there are no CO₂ flux chamber studies related to fire in the tundra (but see e.g., Köster et al., 2016, on boreal regions).

The disturbance regime of the studied region is often well described in the study site description (e.g., Vourlitis et al., 2000), but it should be better incorporated into analyses due to predicted changes in occurrence in a warmer climate (Aalto et al., 2014; Koven et al., 2011). Moreover, we need more comprehensive analysis of the effect of disturbance in different conditions (e.g., in nutrient-rich vs. nutrient-poor environments, or high vs. low-Arctic) as the response of an ecosystem to for example drought, increased herbivory, or fire differs depending on the location.

V Towards a conceptual framework

Conceptual frameworks to explain and describe the drivers and mechanisms of fine-scale spatio-temporal variation of CO₂ fluxes are lacking (Bardgett and Wardle, 2010; Callaghan et al., 2004; Xue et al., 2016). Tundra ecosystems are complex and heterogeneous, so to be able to predict future changes, we first need to create a good understanding on the current processes and variables affecting CO₂ fluxes. Firstly, we highlight the need for theoretical, analytical, and process-based justification for the choice of measured variables. Secondly, we stress the importance of understanding the direct and

indirect relationships among the variables (e.g., the importance of topography, Figure 3). Most of the reviewed publications include data on biota (vegetation), resources (radiation, soil moisture), and regulators (air and/or soil temperature) as these variables vary greatly both spatially and temporally (S4). Out of these drivers, air temperature, PAR, vegetation type, LAI and, occasionally, soil temperature and moisture and NDVI were the most important factors affecting CO₂ fluxes. Other environmental variables measured depend on the study location and design, and research questions. Measuring disturbance is challenging as disturbance often occurs as episodic events. Still, we encourage the investigators to describe the disturbance regime of the plot by for example collecting herbivory data or describing the active geomorphological processes.

I Standardized methodology for site description of chamber studies

The description of the measured sites varies between the studies. Both species-level as well as PFT descriptions are used in the literature. For example, classifications of meadow-heath (Oberbauer et al., 2007) and more precise groups based on the dominant species, that is, *Betula nana* and *Dryas octopetala* (Shaver et al., 2007), have been used in the studies. Because of the importance of vegetation in the carbon cycle, standardized and easily comparable descriptive information on vegetation is crucial in order to understand CO₂ fluxes. Although the vegetation data given by CO₂ flux researchers is descriptive, we encourage the investigators to use widely used plant community classifications in addition to their own. A comprehensive system for the grouping of plants with similar links to environmental conditions can reduce the complexity of the systems (Otieno et al., 2009). Here, we used CAVM (Walker et al., 2005) which was

developed for biogeographic and landscape-scale purposes. It has been successfully applied to the carbon cycle studies and allows researchers to easily compare results (Arndal et al., 2009; Biasi et al., 2008; Douma et al., 2007). An even more precise hierarchical floristic classification system than CAVM which is based on a smaller habitat-scale has been developed by Mucina et al. (2016), but is currently available only for Europe. In addition, the Arctic Vegetation Archive (AVA) aims to combine Arctic vegetation data at plot-scale but is still under progress (Walker et al., 2016).

Despite a common grouping system and characteristic vegetation types, smaller wet patches, stream channels, and transitional zones are equally important in the patchy tundra vegetation. Fletcher et al. (2012) have shown that the most abundant vegetation types (e.g., *Betula nana* or *Empetrum* heath) have a higher GPP than their mixed vegetation types (e.g., *Betula*–*Empetrum* heath). Therefore, measuring also less abundant transition zones and providing species cover data on the dominant and secondary species to locate them is important. Currently, species cover data is included in approximately only 50% of the studies, and cryptogram (mosses and lichens) data in even less. Cryptograms cover large areas in the Arctic, and the crucial role of mosses in the carbon cycle has been identified, especially during spring when leaves of deciduous vascular plants are not yet fully developed but mosses are already photosynthesizing (Douma et al., 2007). Cryptogram quantification using remote sensing and LAI determination are much less studied as they are methodologically even more challenging than vascular plants. However, high-resolution satellite and UAV imagery might provide tools for robust vegetation characterization in the future (Fraser et al., 2016). In addition to standardized vegetation characterization, chamber researchers need a common platform, similar to Fluxnet created for EC studies (Baldocchi

et al., 2001; Chu et al., 2017), to share data and develop methods and guidelines.

VI Summary and future research needs

Environmental variation can affect tundra CO₂ fluxes in multiple ways. These effects are not yet fully understood due to limitations posed by study locations, designs, and environmental variables measured to explain chamber-derived CO₂ fluxes (Table 2). Even though study locations cover the environmental variation relatively well, more research is needed in extreme conditions (such as high precipitation and low temperatures, high topsoil pH, high SOC stock conditions). Study designs should focus on covering spatial variation in environmental conditions, vegetation, and soils, within and between study areas. Additionally, both ends of the productivity gradient (low-shrubs and barren vegetation types) should be studied more thoroughly.

Ecologically and physically relevant variables have been included in the reviewed studies to varying degrees and some topics require new research more urgently than others. Chamber-derived CO₂ fluxes should be explained not only by microclimate and vegetation type, but also by other fluxes, soil microbes, nutrient availability, and disturbance data, to better understand ecosystem functioning. As tundra regions are typically nutrient-limited thus responding strongly to changes in nutrient availability, more studies on the relationship of soil nutrients and microbes with GPP, ER, and NEE measurements are urgently needed. Simultaneous measurements of other greenhouse gases and soil respiration together with CO₂ fluxes are particularly urgent themes as changes therein might be crucial in determining the future carbon balance.

Finally, studies of CO₂ fluxes should focus on the sensitive processes—along with their transitions and thresholds in the ecosystem—that have the potential to change the carbon

Table 2. Chamber-derived CO₂ fluxes and environmental categories studied, their knowledge level, research gaps, and importance of the topics in the global change context.

Category	Knowledge level	Future research needs	Mechanisms	Importance
Fluxes	Good	Combination of soil respiration and NEE. Linkages to other greenhouse gas fluxes. Upscaling of fluxes.	Soil respiration & ER define NEE in a changing climate and disturbance regime. The role of other gas fluxes in global change. More detailed information on spatio-temporal variation and hot spots.	Urgent
Climate	Very good	Temperature extremes.	Climate warming and changes in precipitation.	Less urgent
Vegetation	Good	Growing-season length. Barren and low-shrubs. Cryptograms.	Changes in dynamics. Shrubification, vegetation shift. The role of mosses.	Moderate
Soils	Poor	Soil nutrients, SOC stocks and fluxes.	Substrate quality important for GPP, regulates temperature sensitivity of ER. Changes in SOC stocks.	Urgent
Disturbance	Poor	Microbial biomass, community and activity. Geomorphology, permafrost dynamics, fire, disease. Herbivory.	Microbial effects and response to global warming. Potential changes in geomorphological processes. Increase of fire and disease outbreaks. Herbivory effects of different species in various environments.	Urgent

balance. According to an expert assessment of the most important processes in the changing Arctic environment (Abbott et al. 2016), these sensitive processes include vegetation shifts, permafrost thaw as well as hydrological changes. The effect of permafrost thaw has received increasing attention, but it is still unclear how other geomorphological disturbance, fire events, shrubification, or disease and herbivory outbreaks influence CO₂ fluxes and the tundra carbon balance. It is thus crucial to deepen the understanding of these processes. A better conceptual framework and understanding of CO₂ fluxes will provide more information on the carbon cycling in the tundra.

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ORCID iD

Anna-Maria Virkkala  <http://orcid.org/0000-0003-4877-2918>

Supplemental material

Supplementary material for this article is available online.

References

- Aalto J, Le Roux PC and Luoto M (2013) Vegetation mediates soil temperature and moisture in Arctic-Alpine environments. *Arctic, Antarctic, and Alpine Research* 45(4): 429–439.
- Aalto J, Venäläinen A, Heikkinen RK, et al. (2014) Potential for extreme loss in high-latitude Earth surface processes due to climate change. *Geophysical Research Letters* 41(11): 3914–3924.
- Abbott BW, Jones JB, G Schuur EA, et al. (2016) Biomass offsets little or none of permafrost carbon release from soils, streams, and wildfire: an expert assessment. *Environmental Research Letters* 11(3): 1–13.
- Anderson K and Gaston KJ (2013) Lightweight unmanned aerial vehicles will revolutionize spatial ecology. *Frontiers in Ecology and the Environment* 11(3): 138–146.
- Arens SJT, Sullivan PF and Welker JM (2008) Nonlinear responses to nitrogen and strong interactions with nitrogen and phosphorus additions drastically alter the structure and function of a high arctic ecosystem. *Journal of Geophysical Research: Biogeosciences* 113(G3): 10.
- Amdal MF, Illeris L, Michelsen A, et al. (2009) Seasonal variation in gross ecosystem production, plant biomass, and carbon and nitrogen pools in five High Arctic vegetation types. *Arctic, Antarctic, and Alpine Research* 41(2): 164–173.
- Arnesen G, Bech PSA and Engelskjøn T (2007) Soil acidity, content of carbonates, and available phosphorus are the soil factors best correlated with alpine vegetation: evidence from Troms, north Norway. *Arctic, Antarctic, and Alpine Research* 39(2): 189–199.
- Asner GP, Scurlock JMO and Hicke JA (2003) Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. *Global Ecology and Biogeography* 12(3): 191–205.
- Aurela M, Laurila T and Tuovinen J-P (2004) The timing of snow melt controls the annual CO₂ balance in a subarctic fen. *Geophysical Research Letters* 31: 1–4.
- Baldocchi D, Falge E, Gu L, et al. (2001) FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society* 82(11): 2415–2434.
- Bardgett RD and Wardle DA (2010) *Aboveground–Belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change*. Oxford: Oxford University Press.
- Belshe EF, Schuur EAG and Bolker BM (2013) Tundra ecosystems observed to be CO₂ sources due to differential amplification of the carbon cycle. *Ecology Letters* 16(10): 1307–1315.
- Biasi C, Meyer H, Rusalimova O, et al. (2008) Initial effects of experimental warming on carbon exchange rates, plant growth and microbial dynamics of a lichen-rich dwarf shrub tundra in Siberia. *Plant and Soil* 307(1–2): 191–205.
- Billings WD (1973) Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. *BioScience* 23(12): 697–704.
- Billings WD and Mooney HA (1968) The ecology of arctic and alpine plants. *Biological Reviews* 43(4): 481–529.
- Boelman NT, Stieglitz M, Rueth HM, et al. (2003) Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. *Oecologia* 135(3): 414–421.
- Bokhorst S, Bjerke JW, Melillo J, et al. (2010) Impacts of extreme winter warming events on litter decomposition in a sub-Arctic heathland. *Soil Biology and Biochemistry* 42(4): 611–617.
- Bret-Harte MS, Mack MC, Shaver GR, et al. (2013) The response of Arctic vegetation and soils following an unusually severe tundra fire. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 368(1624): 1–15.
- Brummell ME, Farrell RE and Siciliano SD (2012) Greenhouse gas soil production and surface fluxes at a high arctic polar oasis. *Soil Biology and Biochemistry* 52: 1–12.
- Buchmann N (2000) Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. *Soil Biology & Biochemistry* 32(11–12): 1625–1635.
- Bäckstrand K, Crill PM, Jackowicz-Korcz Nski M, et al. (2010) Annual carbon gas budget for a sub-arctic peatland, Northern Sweden. *Biogeosciences* 7(1): 95–108.
- Bäckstrand K, Crill PM, Mastepanov M, et al. (2008) Non-methane volatile organic compound flux from a subarctic mire in Northern Sweden. *Tellus B: Chemical and Physical Meteorology* 60(2): 226–237.
- Cahoon SMP, Sullivan PF, Post E, et al. (2012a) Large herbivores limit CO₂ uptake and suppress carbon cycle

- responses to warming in West Greenland. *Global Change Biology* 18(2): 469–479.
- Cahoon SMP, Sullivan PF, Shaver GR, et al. (2012b) Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. *Ecology Letters* 15(12): 1415–1422.
- Cahoon SP, Sullivan P and Post E (2016) Greater abundance of *Betula nana* and early onset of the growing season increase ecosystem CO₂ uptake in West Greenland. *Ecosystems* 19(7): 1149–1163.
- Callaghan TV, Björn LO, Chernov Y, et al. (2004) Effects on the function of Arctic ecosystems in the short-and long-term perspectives. *AMBIO* 33(7): 448–458.
- Christensen TR, Friborg T, Sommerkorn M, et al. (2000) Trace gas exchange in a high-Arctic valley 1. Variations in CO₂ and CH₄ flux between tundra vegetation types. *Global Biogeochemical Cycles* 14(3): 701–713.
- Chu H, Baldocchi DD, John R, et al. (2017) Fluxes all of the time? A primer on the temporal representativeness of FLUXNET. *Journal of Geophysical Research: Biogeosciences* 122(2): 289–307.
- Cornelissen JHC, Lavorel S, Garnier E, et al. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51(4): 335–380.
- Curasi SR, Loranty MM and Natali SM (2016) Water track distribution and effects on carbon dioxide flux in an eastern Siberian upland tundra landscape. *Environmental Research Letters* 11(4): 045002.
- Dagg J and Lafleur P (2010) An application of plot-scale NDVI in predicting carbon dioxide exchange and leaf area index in heterogeneous subarctic tundra. *Canadian Journal of Remote Sensing* 36: S111–S123.
- Dagg J and Lafleur P (2011) Vegetation community, foliar nitrogen, and temperature effects on tundra CO₂ exchange across a soil moisture gradient. *Arctic, Antarctic, and Alpine Research* 43(2): 189–197.
- Dahl MB, Prieme A, Brejnrow A, et al (2017) Warming, shading and a moth outbreak reduce tundra carbon sink strength dramatically by changing plant cover and soil microbial activity. *Scientific Reports* 7(1): 1–13.
- De Deyn GB, Cornelissen JHC and Bardgett RD (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters* 11(5): 516–531.
- Dinerstein E, Olson D, Joshi A, et al. (2017) An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* 67(6): 534–545.
- Doetterl S, Stevens A, Six J, et al. (2015) Soil carbon storage controlled by interactions between geochemistry and climate. *Nature Geoscience* 8(10): 780–783.
- Dorrepaal E (2007) Are plant growth-form-based classifications useful in predicting northern ecosystem carbon cycling feedbacks to climate change? *Journal of Ecology* 95(6): 1167–1180.
- Douma JC, Van Wijk MT, Lang SI, et al. (2007) The contribution of mosses to the carbon and water exchange of arctic ecosystems: quantification and relationships with system properties. *Plant Cell and Environment* 30(10): 1205–1215.
- Elmendorf SC, Henry GHR, Hollister RD, et al. (2012) Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2(6): 453–457.
- Falk JM, Schmidt NM, Christensen TR, et al. (2015) Large herbivore grazing affects the vegetation structure and greenhouse gas balance in a high arctic mire. *Environmental Research Letters* 10(4): 045001.
- Flessa H, Rodionov A, Guggenberger G, et al. (2008) Landscape controls of CH₄ fluxes in a catchment of the forest tundra ecotone in northern Siberia. *Global Change Biology* 14(9): 1–17.
- Fletcher BJ, Gornall JL, Poyatos R, et al. (2012) Photosynthesis and productivity in heterogeneous arctic tundra: Consequences for ecosystem function of mixing vegetation types at stand edges. *Journal of Ecology* 100(2): 441–451.
- Forbes BC, Fauria MM and Zetterberg P (2010) Russian Arctic warming and ‘greening’ are closely tracked by tundra shrub willows. *Global Change Biology* 16(5): 1542–1554.
- Fox AM, Huntley B, Lloyd CR, et al (2008) Net ecosystem exchange over heterogeneous Arctic tundra: Scaling between chamber and eddy covariance measurements. *Global Biogeochemical Cycles* 22(2): 1–15.
- Fraser RH, Olthof I, Lantz TC, et al. (2016) UAV photogrammetry for mapping vegetation in the low-Arctic. *Arctic Science* 2(3): 79–102.
- Giblin AE, Nadelhoffer KJ, Shaver GR, et al. (1991) Biogeochemical diversity along a riverside toposequence in Arctic Alaska. *Ecological Monographs* 61(4): 415–435.
- Gil J, Pérez T, Boering K, et al. (2017) Mechanisms responsible for high N₂O emissions from subarctic permafrost peatlands studied via stable isotope techniques. *Global Biogeochemical Cycles* 31(1): 172–189.

- Grand S, Rubin A, Verrecchia EP, et al. (2016) Variation in soil respiration across soil and vegetation types in an alpine valley. *PLoS One* 11(9): e0163968.
- Griffis TJ, Rouse WR and Waddington JM (2000) Scaling net ecosystem CO₂ exchange from the community to landscape-level at a subarctic fen. *Global Change Biology* 6(4): 459–473.
- Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86(6): 902–910.
- Grogan P and Chapin FS (2000) Initial effects of experimental warming on above- and belowground components of net ecosystem CO₂ exchange in arctic tundra. *Oecologia* 125(4): 512–520.
- Grogan P and Jonasson S (2005) Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types. *Global Change Biology* 11(3): 465–475.
- Hartley IP, Garnett MH, Sommerkorn M, et al. (2012) A potential loss of carbon associated with greater plant growth in the European Arctic. *Nature Climate Change* 2(12): 875–870.
- Heikkinen JEP, Maljanen M, Aurela M, et al. (2002) Carbon dioxide and methane dynamics in a sub-Arctic peatland in northern Finland. *Polar Research* 21(1): 49–62.
- Hinzman LD, Bettez ND, Bolton WR, et al. (2005) Evidence and implications of recent climate change in northern Alaska and other Arctic regions. *Climatic Change* 72(3): 251–298.
- Hinzman LD, Deal CJ, McGuire AD, et al. (2013) Trajectory of the Arctic as an integrated system. *Ecological Applications* 23(8): 1837–1868.
- Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs* 66(664): 503–522.
- Hu FS, Higuera PE, Walsh JE, et al. (2010) Tundra burning in Alaska: linkages to climatic change and sea ice retreat. *Journal of Geophysical Research: Biogeosciences* 115(G4): 1–8.
- Hudson JMG and Henry GHR (2009) Increased plant biomass in a high arctic heath community from 1981 to 2008. *Ecology* 90(10): 2657–2663.
- Hugelius G, Strauss J, Zubrzycki S, et al. (2014) Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. *Biogeosciences* 11(23): 6573–6593.
- Hultman J, Waldrop MP, Mackelprang R, et al. (2015) Multi-omics of permafrost, active layer and thermokarst bog soil microbiomes. *Nature* 521(7551): 208–212.
- Hutchinson GL and Livingston GP (2001) Vents and seals in non-steady-state chambers used for measuring gas exchange between soil and the atmosphere. *European Journal of Soil Science* 52(4): 675–682.
- Illeris L, Michelsen A and Jonasson S (2003) Soil plus root respiration and microbial biomass following water, nitrogen, and phosphorus application at a high arctic semi desert. *Biogeochemistry* 65(1): 15–29.
- Illeris L, König SM, Grogan P, et al. (2004) Growing-season carbon dioxide flux in a dry subarctic heath: Responses to long-term manipulations. *Arctic, Antarctic, and Alpine Research* 36(4): 456–463.
- Johnson LC, Shaver GR, Cades DH, et al. (2000) Plant carbon-nutrient interactions control CO₂ exchange in Alaskan wet sedge tundra ecosystems. *Ecology* 81(2): 453–469.
- Jones A, Stolbovoy V, Tarnocai C, et al. (2010) *Soil Atlas of the Northern Circumpolar Region*. Publications Office of the European Union, Luxembourg.
- Kade A, Bret-Harte MS, Euskirchen ES, et al. (2012) Upscaling of CO₂ fluxes from heterogeneous tundra plant communities in Arctic Alaska. *Journal of Geophysical Research: Biogeosciences* 117(G4): G04007.
- Karelin DV, Zanolodchikov DG, Zukert NV, et al. (2013) Interannual changes in PAR and soil moisture during the warm season may be more important for directing of annual carbon balance in tundra than temperature fluctuations. *Zhurnal Obshchei Biologii* 74(1): 3–22.
- Kasischke ES and Turetsky MR (2006) Recent changes in the fire regime across the North American boreal region: spatial and temporal patterns of burning across Canada and Alaska. *Geophysical Research Letters* 33(9): 1–5.
- Kelsey KC, Leffler AJ, Beard KH, et al. (2016) Interactions among climate, topography and herbivory control greenhouse gas (CO₂, CH₄, and N₂O) fluxes in a subarctic coastal wetland. *Journal of Geophysical Research: Biogeosciences* 121(12): 2960–2975.
- Knowles JF, Blanken PD and Williams MW (2016) Wet meadow ecosystems contribute the majority of over-winter soil respiration from snow-scoured alpine tundra. *Journal of Geophysical Research: Biogeosciences* 121(4): 1118–1130.
- Köster K, Köster E, Orumaa A, et al. (2016) How time since forest fire affects stand structure, soil physical-

- chemical properties and soil CO₂ efflux in hemiboreal scots pine forest fire chronosequence? *Forests* 7(9): 1–12.
- Koven CD, Ringeval B, Friedlingstein P, et al. (2011) Permafrost carbon-climate feedbacks accelerate global warming. *PNAS* 108(36): 14769–14774.
- Krawchuk MA, Moritz MA, Parisien M-A, et al. (2009) Global pyrogeography: the current and future distribution of wildfire. *PLoS One* 4(4): e5102.
- Kuhry P, Dorrepaal E, Hugelius G, et al. (2010) Potential remobilization of belowground permafrost carbon under future global warming. *Permafrost and Periglacial Processes* 21(2): 208–214.
- Kutzbach L, Schneider J, Sachs T, et al. (2007) CO₂ flux determination by closed-chamber methods can be seriously biased by inappropriate application of linear regression. *Biogeosciences* 4(6): 1005–1025.
- Kuzyakov Y (2005) Sources of CO₂ efflux from soil and review of partitioning methods. *Soil Biology and Biochemistry* 38(3): 425–448.
- Larsen KS, Ibrom A, Jonasson S, et al. (2007) Significance of cold-season respiration and photosynthesis in a subarctic heath ecosystem in Northern Sweden. *Global Change Biology* 13(7): 1498–1508.
- Le Roux PC and Luoto M (2014) Earth surface processes drive the richness, composition and occurrence of plant species in an arctic-alpine environment. *Journal of Vegetation Science* 25(1): 45–54.
- Leffler AJ, Klein ES, Oberbauer SF, et al. (2016) Coupled long-term summer warming and deeper snow alters species composition and stimulates gross primary productivity in tussock tundra. *Oecologia* 181(1): 287–297.
- López-Blanco E, Lund M, Williams M, et al. (2017) Exchange of CO₂ in Arctic tundra: impacts of meteorological variations and biological disturbance. *Biogeosciences* 14(19): 4467.
- Lund M, Raundrup K, Westergaard-Nielsen A, et al. (2017) Larval outbreaks in West Greenland: instant and subsequent effects on tundra ecosystem productivity and CO₂ exchange. *AMBIO* 46: 26–38.
- Luo Y, Ahlström A, Allison SD, et al. (2016) Toward more realistic projections of soil carbon dynamics by Earth system models. *Global Biogeochemical Cycles* 30(1): 40–56.
- Maanaviija L, Riutta T, Aurela M, et al. (2011) Spatial variation in CO₂ exchange at a northern aapa mire. *Biogeochemistry* 104(1–3): 325–345.
- Mack MC, Synderbret-Harte M, Hollingsworth T, et al. (2011) Carbon loss from an unprecedented Arctic tundra wildfire. *Nature* 475(7357): 489–492.
- Marushchak ME, Kiepe I, Biasi C, et al. (2013) Carbon dioxide balance of subarctic tundra from plot to regional scales. *Biogeosciences* 10(1): 437–452.
- Marushchak ME, Pitkämäki A, Koponen H, et al. (2011) Hot spots for nitrous oxide emissions found in different types of permafrost peatlands. *Global Change Biology* 17(8): 2601–2614.
- McGuire AD, Anderson LG, Christensen TR, et al. (2009) Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs* 79(4): 523–555.
- McGuire AD, Christensen TR, Hayes D, et al. (2012) An assessment of the carbon balance of Arctic tundra: comparisons among observations, process models, and atmospheric inversions. *Biogeosciences* 9(8): 3185–3204.
- McGuire AD, Hayes DJ, Kicklighter DW, et al. (2010a) An analysis of the carbon balance of the Arctic Basin from 1997 to 2006. *Tellus, Series B: Chemical and Physical Meteorology* 62(5): 455–474.
- McGuire AD, Macdonald RW, Schuur EAG, et al. (2010b) The carbon budget of the northern cryosphere region. *Current Opinion in Environmental Sustainability* 2(4): 231–236.
- Mernild SH, Liston GE, Mernild SH, et al. (2012) Greenland freshwater runoff. Part II. Distribution and trends, 1960–2010. *Journal of Climate* 25(17): 6015–6035.
- Metcalf DB and Olofsson J (2015) Distinct impacts of different mammalian herbivore assemblages on arctic tundra CO₂ exchange during the peak of the growing season. *Oikos* 124(12): 1632–1638.
- Mucina L, Bültmann H, Dierßen K, et al. (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science* 19(S1): 3–264.
- Myklebust MC, Hipps LE and Ryel RJ (2008) Comparison of eddy covariance, chamber, and gradient methods of measuring soil CO₂ efflux in an annual semi-arid grass, *Bromus tectorum*. *Agricultural and Forest Meteorology* 148(11): 1894–1907.
- Nadelhoffer KJ, Giblin AE, Shaver GR, et al. (1991) Effects of temperature and substrate quality on element mineralization in six Arctic soils. *Ecology* 72(1): 242–253.
- Natali SM, Schuur EAG, Trucco C, et al. (2011) Effects of experimental warming of air, soil and permafrost on

- carbon balance in Alaskan tundra. *Global Change Biology* 17(3): 1394–1407.
- Nobrega S and Grogan P (2008) Landscape and ecosystem-level controls on net carbon dioxide exchange along a natural moisture gradient in Canadian low arctic tundra. *Ecosystems* 11(3): 377–396.
- Nykänen H, Heikkinen JEP, Pirinen L, et al. (2003) Annual CO₂ exchange and CH₄ fluxes on a subarctic palsamire during climatically different years. *Global Biogeochemical Cycles* 17(1): 18.
- O'Rourke SM, Angers DA, Holden NM, et al. (2015) Soil organic carbon across scales. *Global Change Biology* 21(10): 3561–3574.
- Oberbauer SF, Tweedie CE, Welker JM, et al. (2007) Tundra CO₂ fluxes in response to experimental warming across latitudinal and moisture gradients. *Ecological Monographs* 77(2): 221–238.
- Oechel WC, Hastings SJ, Vourlitis G, et al. (1993) Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature* 361(6412): 520–523.
- Oechel WC, Vourlitis G, Hastings SJ, et al. (2000) Acclimation of ecosystem CO₂ exchange in the Alaskan Arctic in response to decadal climate warming. *Nature* 406(6799): 978–981.
- Olivas PC, Oberbauer SF, Tweedie CE, et al. (2010) Responses of CO₂ flux components of Alaskan coastal plain tundra to shifts in water table. *Journal of Geophysical Research: Biogeosciences* 115(G4): 1–13.
- Olofsson J, Ericson L, Torp M, et al. (2011) Carbon balance of Arctic tundra under increased snow cover mediated by a plant pathogen. *Nature Climate Change* 1(4): 220–223.
- Osterkamp TE and Romanovsky VE (1999) Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost and Periglacial Processes* 10(1): 17–37.
- Otieno DO, Wartinger M, Nishiwaki A, et al. (2009) Responses of CO₂ exchange and primary production of the ecosystem components to environmental changes in a mountain peatland. *Ecosystems* 12(4): 590–603.
- Overeem I and Syvitski JPM (2010) Shifting discharge peaks in Arctic rivers, 1977–2007. *Geografiska Annaler Series A: Physical Geography* 92(2): 285–296.
- Pare MC and Bedard-Haughn A (2012) Landscape-scale N mineralization and greenhouse gas emissions in Canadian cryosols. *Geoderma* 189: 469–479.
- Parker TC, Subke JA and Wookey PA (2015) Rapid carbon turnover beneath shrub and tree vegetation is associated with low soil carbon stocks at a subarctic treeline. *Global Change Biology* 21(5): 2070–2081.
- Parmentier F-JW, Christensen TR, Rysgaard S, et al. (2017) A synthesis of the arctic terrestrial and marine carbon cycles under pressure from a dwindling cryosphere. *AMBIO* 46: 53–69.
- Pearson RG, Phillips SJ, Lorant MM, et al. (2013) Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change* 3(7): 673–677.
- Ping CL, Jastrow JD, Jorgenson MT, et al. (2015) Permafrost soils and carbon cycling. *Soil* 1(1): 147–171.
- Post E, Forchhammer MC, Bret-Harte MS, et al. (2009) Ecological dynamics across the Arctic associated with recent climate change. *Science* 325(5946): 1355–1358.
- Poyatos R, Heinemeyer A, Ineson P, et al. (2014) Environmental and vegetation drivers of seasonal CO₂ fluxes in a sub-Arctic forest-mire ecotone. *Ecosystems* 17(3): 377–393.
- Raynolds MK, Comiso JC, Walker DA, et al. (2008) Relationship between satellite-derived land surface temperatures, arctic vegetation types, and NDVI. *Remote Sensing of Environment* 112(4): 1884–1894.
- Scherrer D and Körner C (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography* 38(2): 406–416.
- Schuur EAG, Bockheim J, Canadell JG, et al. (2008) Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. *BioScience* 58(8): 701–714.
- Schuur EAG, Vogel JG, Crummer KG, et al. (2009) The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature* 459(7246): 556–559.
- Segal AD and Sullivan PF (2014) Identifying the sources and uncertainties of ecosystem respiration in Arctic tussock tundra. *Biogeochemistry* 121(3): 489–503.
- Sharp ED, Sullivan PF, Steltzer H, et al. (2013) Complex carbon cycle responses to multi-level warming and supplemental summer rain in the high Arctic. *Global Change Biology* 19(6): 1780–1792.
- Shaver GR, Johnson LC, Cades DH, et al. (1998) Biomass and CO₂ flux in wet sedge tundras responses to nutrients, temperature and light. *Ecological Monographs* 68(1): 75–97.

- Shaver GR, Rastetter EB, Salmon V, et al. (2013) Pan-Arctic modelling of net ecosystem exchange of CO₂. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 368(1624): 1–13.
- Shaver GR, Street LE, Rastetter EB, et al. (2007) Functional convergence in regulation of net CO₂ flux in heterogeneous tundra landscapes in Alaska and Sweden. *Journal of Ecology* 95(4): 802–817.
- Sitch S, McGuire AD, Kimball J, et al. (2007) Assessing the carbon balance of circumpolar arctic tundra using remote sensing and process modeling. *Ecological Applications* 17(1): 213–234.
- Sjögersten S, van der Wal R, Loonen MJJE, et al. (2011) Recovery of ecosystem carbon fluxes and storage from herbivory. *Biogeochemistry* 106(3): 357–370.
- Smol JP and Douglas MS V (2007) Crossing the final ecological threshold in high Arctic ponds. *PNAS* 104(30): 12395–12397.
- Stewart KJ, Brummell ME, Coxson DS, et al. (2013) How is nitrogen fixation in the high arctic linked to greenhouse gas emissions? *Plant and Soil* 362(1–2): 215–229.
- Stocker TF, Qin D, Plattner G-K, et al. (2013) *Climate Change 2013: The Physical Science Basis*. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.
- Street LE, Shaver GR, Rastetter EB, et al. (2012a) Incident radiation and the allocation of nitrogen within Arctic plant canopies: implications for predicting gross primary productivity. *Global Change Biology* 18(9): 2838–2852.
- Street LE, Shaver GR, Williams M, et al. (2007) What is the relationship between changes in canopy leaf area and changes in photosynthetic CO₂ flux in Arctic ecosystems? *Journal of Ecology* 95(1): 139–150.
- Street LE, Stoy PC, Sommerkorn M, et al. (2012b) Seasonal bryophyte productivity in the sub-Arctic: a comparison with vascular plants. *Functional Ecology* 26(2): 365–378.
- Soegaard H, Nordstroem C, Friborg T, et al. (2000) Trace gas exchange in a high-Arctic valley: 3. Integrating and scaling CO₂ fluxes from canopy to landscape using flux data, footprint modeling, and remote sensing. *Global Biogeochemical Cycles* 14(3): 725–744.
- Susiluoto S, Rasilo T, Pumpanen J, et al. (2008) Effects of grazing on the vegetation structure and carbon dioxide exchange of a Fennoscandian fell ecosystem. *Arctic, Antarctic, and Alpine Research* 40(2): 422–431.
- Tape K, Sturm M and Racine C (2006) The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology* 12(4): 686–702.
- Tarnocai C, Canadell JG, Schuur EAG, et al. (2009) Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles* 23(2): 1–11.
- Thomazini A, Francelino MR, Pereira AB, et al. (2016) Geospatial variability of soil CO₂-C exchange in the main terrestrial ecosystems of Keller Peninsula, Maritime Antarctica. *Science of the Total Environment* 562: 802–811.
- Van der Molen MK, van Huissteden J, Parmentier FJW, et al. (2007) The growing season greenhouse gas balance of a continental tundra site in the Indigirka lowlands, NE Siberia. *Biogeosciences* 4(6): 985–1003.
- Van Huissteden J and Dolman AJ (2012) Soil carbon in the Arctic and the permafrost carbon feedback. *Current Opinion in Environmental Sustainability* 4(5): 545–551.
- Virtanen R, Oksanen L, Oksanen T, et al. (2016) Where do the treeless tundra areas of northern highlands fit in the global biome system: toward an ecologically natural subdivision of the tundra biome. *Ecology and Evolution* 6(1): 143–158.
- Virtanen T and Ek M (2014) The fragmented nature of tundra landscape. *International Journal of Applied Earth Observation and Geoinformation* 27: 4–12.
- Vogel J, Schuur EAG, Trucco C, et al. (2009) Response of CO₂ exchange in a tussock tundra ecosystem to permafrost thaw and thermokarst development. *Journal of Geophysical Research: Biogeosciences* 114(G4): G04018.
- Voigt C, Marushchak ME, Lamprecht RE, et al. (2017) Increased nitrous oxide emissions from Arctic peatlands after permafrost thaw. *PNAS* 114(24): 6238–6243.
- Vourlitis GL, Oechel WC, Hope A, et al. (2000) Physiological models for scaling plot measurements of CO₂ flux across an arctic tundra landscape. *Ecological Applications* 10(1): 60–72.
- Walker DA, Daniëls FJA, Alsos I, et al. (2016) Circumpolar Arctic vegetation: a hierarchic review and roadmap toward an internationally consistent approach to survey, archive and classify tundra plot data. *Environmental Research Letters* 11(5): 055005.

- Walker DA, Raynolds MK, Daniels FJA, et al. (2005) The Circumpolar Arctic Vegetation Map. *Journal of Vegetation Science* 16: 267–282.
- Wang Y, Fu B, Lü Y, et al. (2010) Local-scale spatial variability of soil organic carbon and its stock in the hilly area of the Loess Plateau, China. *Quaternary Research* 73(1): 70–76.
- Welker JM, Fahnestock JT, Henry GHR, et al. (2004) CO₂ exchange in three Canadian High Arctic ecosystems: Response to long-term experimental warming. *Global Change Biology* 10(12): 1981–1995.
- Welker JM, Fahnestock JT and Jones MH (2000) Annual CO₂ flux in dry and moist arctic tundra: Field responses to increases in summer temperatures and winter snow depth. *Climatic Change* 44(1–2): 139–150.
- White DM, Garland DS, Ping CL, et al. (2004) Characterizing soil organic matter quality in arctic soil by cover type and depth. *Cold Regions Science and Technology* 38(1): 63–73.
- Williams M, Street LE, van Wijk MT, et al. (2006) Identifying differences in carbon exchange among arctic ecosystem types. *Ecosystems* 9(2): 288–304.
- Xue K, Yuan MM, Shi ZJ, et al. (2016) Tundra soil carbon is vulnerable to rapid microbial decomposition under climate warming. *Nature Climate Change* 6(6): 595–600.
- Ylänne H, Stark S, Tolvanen A, et al. (2015) Vegetation shift from deciduous to evergreen dwarf shrubs in response to selective herbivory offsets carbon losses: evidence from 19 years of warming and simulated herbivory in the subarctic tundra. *Global Change Biology* 21(10): 3696–3711.
- Zamolodchikov DG (2015) CO₂-exchange in tundra ecosystems of Vaygach Island during the unusually warm and dry vegetation season. *Zhurnal Obshchei Biologii* 76(2): 83–98.
- Zhu RB, Bao T, Wang Q, et al. (2014) Summertime CO₂ fluxes and ecosystem respiration from marine animal colony tundra in maritime Antarctica. *Atmospheric Environment* 98: 190–201.