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Winter climate change in plant–soil systems: summary of recent findings and future perspectives

Received: 30 June 2013 / Accepted: 2 December 2013 / Published online: 31 December 2013
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Abstract The winter climate is changing in many parts of the world, and it is predicted that winter climate change will modify the structure and function of plant–soil systems. An understanding of these changes and their consequences in terrestrial ecosystems requires knowledge of the linkage between above- and below-ground components as well as the species interactions found in plant–soil systems, which have important implications for biogeochemical cycles. However, winter climate-change studies have focused on only a part of the eco-

system or ecological process. We summarize here recent findings related to the effects of winter climate and its changes on soil nitrogen (N) dynamics, greenhouse gas (N₂O) emissions from the soil, N use by individual plants, vegetation development, and interactions between vegetation and pollinators to generate an integrative understanding of the response of the plant–soil system to winter climate change. This review indicates that the net effects on plants, soil microbes, pollinators, and the associated biogeochemical cycles are balanced among several processes and are highly variable depending on the context, such as the target species/functional group, original winter condition of the habitat, and type of climate change. The consequences of winter climate change for species interactions among plants, associated animals, and biogeochemical cycles are largely unknown. For further research, a large-scale comparative study to measure ecosystem-level functions is important, especially in less-cold ecosystems.

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Keywords Nitrogen · Species interaction · Context
dependence · Comparative study design ·
Winter–summer relationship · Ecosystem service

Introduction

Winter and its associated processes are important in many terrestrial ecosystems. More than 55 % of the land surface is exposed to annual freeze–thaw cycles, and approximately 47 % of that surface is estimated to experience snow cover (Zhang et al. 1999). However, the winter climate has been changing drastically in recent decades. These changes include continuous changes such as increasing temperature, and an increase in variability. In the northern hemisphere, the snow-covered area has decreased by approximately 3 % from 1930 to 2005 on average, which is mainly because of spring starting earlier (Serreze et al. 2000; IPCC 2007) but also because of a decrease in snow in some regions (Park et al. 2010). Furthermore, in many areas, there has been a continuous

decline in the proportion of annual precipitation that falls as snow rather than rain (Feng and Hu 2007; Ye 2008; Karl et al. 2009). The frequency and magnitude of extreme thaw events briefly interrupting winter frost can increase at higher latitudes (Bokhorst et al. 2012) along with increased variability of weather events in general (Augsburger 2009). On the other hand, an increase in the duration of the snow-cover season has also been observed in some regions (Choi et al. 2010), demonstrating the spatially heterogeneous effects of snow regime change.

Why should we study “winter” climate change in the plant–soil system? Soil freezing, snow coverage, and chilling temperature significantly affect the organisms that inhabit the plant–soil systems, including plants (Chapin 1983; Sakai and Larcher 1987; Körner 2003), soil microbes (Drotz et al. 2010; Jefferies et al. 2010; Haei et al. 2011; Ushio et al. 2013), and soil animals (Fujiyama 1996; Sulkava and Huhta 2003). These organisms play important roles in ecosystem functions, such as carbon (C) and nutrient cycling. Therefore, winter climate change is predicted to modify the functions of terrestrial ecosystems. However, compared with those on summer-time climate changes (e.g., Elmendorf et al. 2012), the limited numbers of studies available in the literature do not suffice to predict the precise consequences of highly region-specific winter climate change and to perform a meta-analytical survey with a large dataset [but see the examples by Wipf and Rixen (2010) for vegetation in the arctic and alpine tundra and by Blankinship and Hart (2012) for soil N dynamics and greenhouse gas emissions]. The limited understanding of winter-specific processes, e.g. snow root development for nitrogen (N) uptake (Onipchenko et al. 2009), make it difficult to estimate the annual budget of biogeochemical cycles accurately.

Moreover, while extreme summer drought and summer warming increase cold hardiness of plants during winter (Kreyling et al. 2012), winter climate also affects plant behavior (Tierney et al. 2001) and the soil biogeochemical cycle (Haei et al. 2013) during the summer, so summertime researchers should not ignore winter climate change in the study site. While the importance of above- and below-ground linkages and species interactions for ecosystem function (e.g., nutrient and greenhouse gas dynamics) under climate change have been addressed (Bardgett et al. 2013; van der Putten et al. 2013), winter climate change studies have primarily focused on only one part of the ecosystem (but see an example by Campbell et al. 2005).

To help advance an integrative understanding of the consequence of winter climate change in plant–soil systems, the symposium titled “Winter climate change: its significance in the plant–soil system” was held at the 60th Annual Meeting of the Ecological Society of Japan in 2013. In this review, we broadly summarize the recent findings of the effects of winter climate and its changes on (1) soil N dynamics, (2) greenhouse gas (N₂O) emission from soil, (3) N use by individual plants, (4)

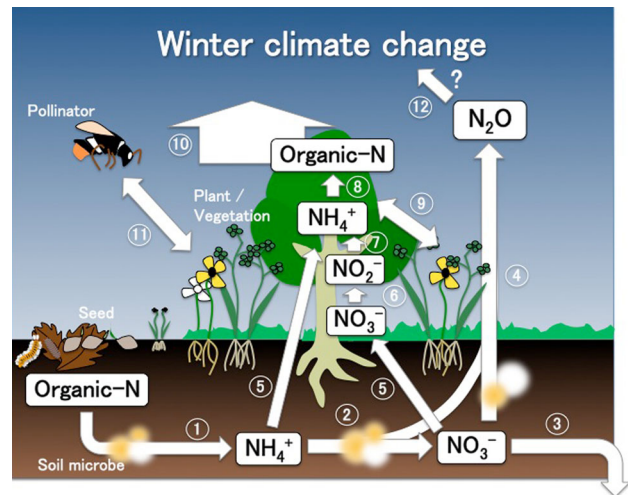


Fig. 1 Ecosystem processes described in this review. Numbers in the figure indicate 1 nitrogen mineralization, 2 nitrification, 3 nitrogen leaching, 4 denitrification, 5 nitrogen absorption, 6 nitrate reduction, 7 nitrite reduction, 8 nitrogen organization, 9 species interaction within vegetation, 10 plant (vegetation) growth, 11 pollination, 12 possible feedback via N₂O (see the details in “Future perspectives”)

vegetation development, and (5) interactions between vegetation and pollinators (Fig. 1). Here, the effects of winter climate change on soil C dynamics in permafrost soil are not covered. In the end, we suggest some future directions for winter climate-change studies.

Soil N dynamics

Snow cover functions as a heat insulator because of its porous properties. Thus, soil temperature is maintained warmer under enough snow compared to below a snow-free surface (Harada et al. 2009). When the snow cover does not insulate the ground, soil temperature responds well to changes in air temperature, which causes frequent freeze–thaw cycles of the surface soil, especially during the early winter and spring (Christopher et al. 2008; Shibata et al. 2013). Low temperature generally suppresses soil microbial activity and their N processing (mineralization and nitrification). Specifically at or just below 0 °C, microbes are known to shift the substrate necessary for their activity from N-poor detritus to N-rich microbial products (Schimel and Mikan 2005). Soil freeze–thaw events disrupt microbial tissue and induce the mineralization of microbial N and subsequent nitrification (DeLuca et al. 1992). Climate simulations and field observations suggest recent alteration in the snowfall and snow cover regimes in cool-temperate and boreal regions (Mote et al. 2005; Hosaka et al. 2005; and see the decadal examples in Uryu Experimental Forest, northern Japan, Fig. 2; Park et al. 2010). The altered heat and water regimes affect soil processes and functions related with N, an important limiting nutrient for primary production in most part of boreal and temper-

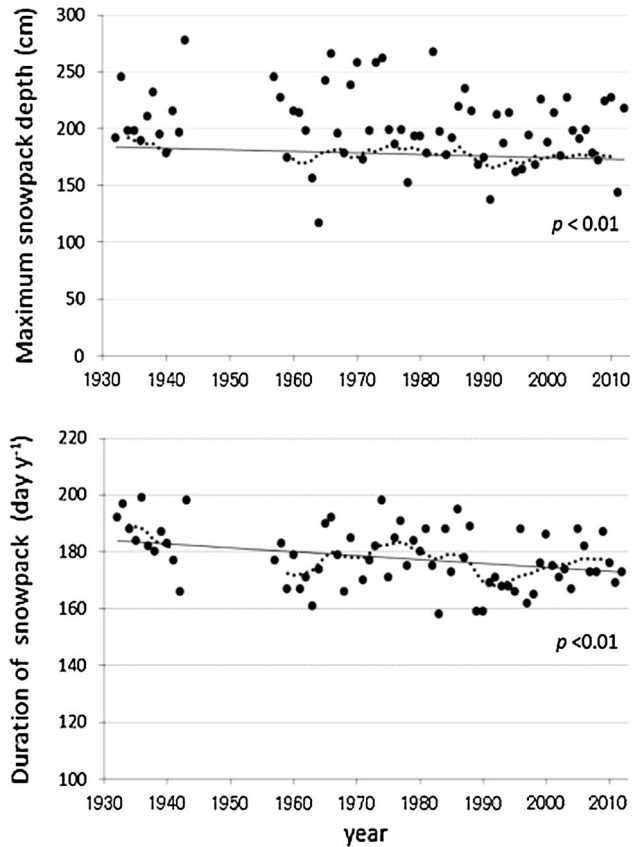


Fig. 2 Long-term observation of maximum snowpack depth and duration of snowpack at Uryu Experimental Forest (core site of the Japan Long-term Ecological Research Network) of Hokkaido University. The *closed circles*, *dashed lines*, and *solid lines* indicate observed data, 5-year averages, and linear correlation of the 5-year's average, respectively. The p value indicates significant temporal decrease of the 5-year averages in the maximum snowpack depth and the snowpack duration. The data of maximum snowpack depth are partly published in Park et al. 2010. There are no observed data between the years 1942 to 1958

ate forests (Vitousek and Howarth 1991). The predicted increase in freeze–thaw cycles in soil causes various responses and alters N dynamics in soil–vegetation–microbe systems (Groffman et al. 2011; Brooks et al. 2011; Matzner and Borken 2008; Templer 2012; Fig. 3). The soil freeze–thaw regime is determined directly by air temperature and the amount/form of precipitation, and indirectly by snow cover via its roles as water supplier and heat insulator (Fig. 3). Their changes modify soil freeze–thaw cycles leading to the change of soil N dynamics directly via substrate (soil and litter) properties, and indirectly via soil organisms (microbes and probably detritivores) and plants.

During summer, warm temperature increase N mineralization rate in soil (Rustad et al. 2001). Increased soil N availability results in high plant productivity, which causes feedback regulation of air temperature via the decrease of CO_2 concentration. On the other hand, the increasing N mineralization increases the risk of leaching of N from soil, which may interfere with the feedback regulation between soil and plants over the long term

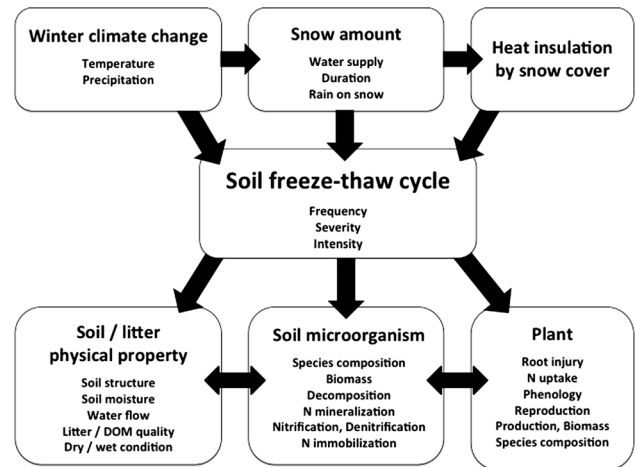


Fig. 3 Impacts of increased freeze–thaw cycle in soil on N biogeochemistry and the related processes in soil–microbe–plant systems (based on Groffman et al. 2011; Brooks et al. 2011; Matzner and Borken 2008; Templer 2012)

(Wu et al. 2012). Winter climate change is known to affect N leaching. In cold and snowy ecosystems, less snow is often coincident with increased soil freeze–thaw cycles. Consequently, less snow often results in more N mineralization and inorganic N in the soil (Christopher et al. 2008; Groffman et al. 2011; Shibata et al. 2013). As a mechanism of increased N mineralization, Shibata et al. (2013) found that the dissolved organic carbon (DOC) and DOC/dissolved organic nitrogen (DON) ratio in soil increased with a decrease in snowpack during the snow melt period, which suggests that the change in substrate quality by physical disruption along with the increase in freeze–thaw cycles caused the significant enhancement of microbial ammonium production in the soil. Snow manipulation experiments in the Hubbard Brook Experimental Forest in the north-eastern USA showed that winter climate changes that result in less snow and more soil freezing will increase N losses (nitrate leaching) (Groffman et al. 2011). Soil frost induces the increase of nitrate flushing during the snow-melt periods in some forested streams (Mitchell et al. 1996). Critical factors triggering increasing N loss from the soil include the increased lability of C by the soil freeze–thaw cycle (Brooks et al. 2011) as well as the degree of soil aggregation, soil water content at freezing, size of the labile C and N pools, and temperatures below freezing (Matzner and Borken 2008).

On the other hand, such relationships among snow cover, soil freeze–thaw frequency, and N dynamics vary depending on the absolute amount of snow accumulation in ecosystem. In cold but snow-poor ecosystems, in which the freeze–thaw cycle has been less studied than in snow-rich systems, an increase of winter temperature decreases the soil freeze–thaw frequency and the DON and NH_4^+ pool in the soil (Ueda et al. 2013), although the response of N leaching from the soil has not been investigated.

The soil freeze–thaw cycle changes the biomass and composition of soil microbes (Lipson et al. 2002; Gilliam et al. 2010), which are the main players in N dynamics. Schadt et al. (2003) showed that the microbial biomass in tundra soil reaches its annual peak under snow and that fungi account for most of the biomass, which was determined using microbiological and molecular techniques. However, the responses and patterns in soil N dynamics vary among regions and have not been consistently explained. Experiments combining the manipulation of microbial communities, substrate quality, freeze–thaw regimes, and snow cover at different location in situ or in laboratory can be helpful for a comprehensive understanding of these responses.

Nitrous oxide emissions from soil

How climate change affects greenhouse gas emissions is a central question in ecology. N₂O is an important greenhouse gas that contributes 6 % to global warming (Solomon et al. 2007). The atmospheric N₂O concentration has increased from 280 ppb in the pre-industrial era to 320 ppb in 2006, showing linear increase at a rate of 0.26 % per year. Because N₂O is also a dominant substance related to the depletion of the stratospheric ozone layer (Ravishankara et al. 2009) and the dominant source of N₂O is microbial production which is stimulated by the use of N fertilizers in agriculture, plenty of monitoring studies have been conducted for quantitative estimates of the amounts of N₂O derived from soil. Unlike the soil-derived emissions of the other important greenhouse gases CO₂ and CH₄, which are strongly correlated with temperature, soil-derived N₂O emissions are largely affected by precipitation (soil moisture conditions and/or soil O₂ level) and substrate availability (Davidson 2009). In addition, snowmelt in early spring also is well known as an important event causing N₂O emissions from soil in some cases as described later or in Yanai et al. (submitted to *Ecological Research*). As a result, there is no clear relationship between N₂O emission from soil and temperature, which makes it difficult to estimate N₂O flux of the terrestrial ecosystems in a global scale. On the other hand, the atmospheric N₂O concentration shows three distinct dynamics: (1) a clear north–south gradient with higher values in the northern hemisphere, (2) a seasonal cycle at high latitudes in the northern hemisphere and (3) the highest value in the spring and lowest value in the summer (Ishijima et al. 2009). Possible reasons for the seasonal dynamics are the intrusion of N₂O-poor stratospheric air into the troposphere and significant local N₂O emissions from soil (Ishijima et al. 2009). Therefore, studies to elucidate the responsible processes for N₂O production in soil and the factors that determine the regional heterogeneity of N₂O emissions are critical to understand the global N₂O budget.

In winter to spring, spike-like rate changes in soil N₂O emissions have been observed since the 1970s (Duxbury et al. 1982). Because such N₂O emissions

during the cold half of the year can account for more than 50 % of the annual N₂O emissions (Flessa et al. 1995; Maljanen et al. 2007; Wagner-Riddle et al. 2007; Virkajärvi et al. 2010), various experiments based on field manipulation and/or laboratory incubation have been performed to verify the responsible processes for N₂O production using both agricultural and forest soils (e.g., Röver et al. 1998; Ludwig et al. 2004, 2006; Öquist et al. 2004; Koponen et al. 2006; Mørkved et al. 2006; Phillips 2008). With a few tracer experiments, the large contribution of denitrification under freeze–thaw conditions, including N₂O reduction to N₂ was revealed (Müller et al. 2002; Wagner-Riddle et al. 2008). Furthermore, by observing natural abundance of ¹⁵N and ¹⁸O of N₂O in soil, Goldberg et al. (2010) found the high N₂O concentration (26–50 ppm) in all soil horizons when the surface soil was subjected to seasonal freeze–thaw cycles. They also found denitrification-derived N₂O production in the deep soil layer around the groundwater table, based on the analysis of $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$ of soil gas N₂O. On the other hand, Yanai et al. (2011) conducted snow cover manipulation experiments in two agricultural fields in Japan and observed a decrease in O₂ concentrations with increasing N₂O concentrations at a depth of 10 cm of soil during a snowmelt period, suggesting denitrification in the frozen surface soil layer. These results indicate that (1) soil freezing triggers microbial denitrification in soil, (2) a large part of the accumulated N₂O may not be reduced to N₂ and (3) the accumulated N₂O is released after snowmelt or soil-thawing (Katayanagi and Hatano 2012). In other words, the amount of residual NO₃[−] in the soil (Koga 2013) and enhanced availability of labile organic C (Pelster et al. 2013), including the partial sterilization effect (Yanai et al. 2004, 2007), can be stimulus factors for N₂O production in soil and subsequent emissions from soil in the winter-to-spring period.

Because soil freezing is controlled both by air temperature and thickness of snow cover on the ground, changing regional winter climate conditions because of global warming can influence regional, and further global N₂O flux. Groffman et al. (2001) suggested that an increase in the ground affected by seasonal freezing was due to decreasing snowfall leading to “colder soils in a warmer world”, which was based on long-term field observations at the Hubbard Brook Experimental Forest. However, Kreyling and Henry (2011) analyzed the data from 177 German weather stations from 1950 to 2000 and found that the number of days with snow on the ground tended to decrease but that the minimum soil temperature tended to increase. Thus, there is no evidence for an increased occurrence of soil freezing. On the other hand, Hirota et al. (2006) found a trend of decreasing annual maximum soil frost depth in eastern Hokkaido in northern Japan (a cold but snowless region) since the late 1980s. This was not because of an increasing air temperature but because of an intensified snowfall in early winter due to the changing pressure

pattern in the atmosphere. Evaluating the effect of changing soil frost dynamics on N₂O emissions from soil is one of the important issues to validate our current understanding related to the winter climate change.

To quantify the impact of changing winter climate and soil freeze–thaw dynamics on the N₂O flux of terrestrial ecosystems, further snow cover manipulation experiments and numerical simulation techniques are necessary, in addition to field observations with a secure hypothesis. Blankinship and Hart (2012) conducted a meta-analysis of snow-cover manipulation experiments. Although the dataset was limited, the authors concluded that decreasing snow cover depth caused larger increases in spring N₂O flux at sites with greater mean annual precipitation, and where snow cover manipulation caused less extreme soil-cooling. This result partially agrees with the estimation by Ishijima et al. (2009), in which the annual rate of increase in atmospheric N₂O concentration was positively correlated with soil water content and negatively with soil temperature in the global scale. In contrast, several simulation studies using “ecosys” (Grant and Pattey 1999) and “DNDC” (Norman et al. 2008; de Bruijn et al. 2009; Kariyapperuma et al. 2011), which are process-based models of soil biochemical reaction with water and heat movements, show the difficulty in predicting the spike-like rate changes in N₂O emissions from soil in the winter-to-spring period. Presumably, expressing the presence of a micro-anaerobic environment in soil under freeze–thaw conditions (Teepe et al. 2004; Yanai et al. 2011) is a key point for an advanced numerical simulation of N₂O emissions from soil.

Plant N use

Winter may not be a completely dormant season for plants, even in the ecosystems with harsh winter such as arctic, alpine, or boreal regions. Many plants in areas with short growing season preform flower buds and leaves, some of whose activity probably takes place in the winter (e.g., Kimball et al. 1973; Forbis and Diggle 2001). Recently the Caucasian snow bed species *Corydalis conorhiza* was shown to take up substantial amounts of N from snow through specialized snow roots, which grow upward into snow packs (Onipchenko et al. 2009). Thus, we should take into account winter when discussing the annual N budget. Soil N availability for plants increases from late winter to early spring (Grogan and Jonasson 2003; Kielland et al. 2006; Larsen et al. 2012), and plants actively acquire N in the early spring (Högberg et al. 1986, 1992; Stadler and Gebauer 1992; Ohlson and Högbom 1993; Pearson and Ji 1994; Troelstra et al. 1995; Koyama et al. 2008). However, the research regarding plant N uptake before the snowmelt period is limited, and these results are not consistent.

Several studies have shown N acquisition and enzyme activity during the winter. In temperate regions, Ueda et al. (2010) investigated the uptake and assimilation of

NO₃[−] by a deciduous oak species and detected a substantial uptake and assimilation during winter. Another temperate oak species, the evergreen *Quercus glauca*, showed the highest nitrate reductase activity (NRA) in the leaf-expansion period followed by lower steady-state enzyme activity that continued through the mid-winter (Koyama et al. 2008). Moreover, it was demonstrated that a citrus species (*Citrus unshu*) assimilated the absorbed NO₃[−] into amino acids immediately after uptake in winter (Kato and Kubota 1982).

While the absorption of N in winter is less than that in summer, it makes a substantial contribution to the annual budget. Kato et al. (1982) demonstrated that *C. unshu* absorbed N in winter, and the amount was approximately a tenth of the summer uptake. Grogan and Jonasson (2003) investigated the seasonal changes of NH₄⁺ uptake of understory heath species in northern Sweden, and found that one of the dominant species, *Empetrum hermaphroditum*, showed substantial N uptake in early winter.

Furthermore, the activity during winter appears to be related to the lifespan of the leaves and growth form. Among the Mediterranean species, semi-deciduous plants keep assimilating NO₃[−] in the winter, whereas evergreens show a drastic decrease in NO₃[−] assimilation during the winter (Dias et al. 2011). In sub-arctic heathland, evergreen dwarf shrubs acquire N before early May but not in earlier seasons, whilst other functional groups, such as deciduous shrubs and graminoids, absorbed N later in the season (Larsen et al. 2012).

Leaf N is mainly used for photosynthetic activity (Field and Mooney 1986). Winter is not necessarily a dormant season for certain species. In temperate regions, the photosynthetic capacity in saplings of six species was investigated throughout the year, and *Camellia japonica* retained high capacity in winter (Miyazawa and Kikuzawa 2005). The optimum temperature for photosynthesis differed depending on the species origin. The optimum temperatures for arctic species were 15–20 °C lower than those for temperate species (Chapin 1983), which allows northern species to photosynthesize during cold periods (Lundell et al. 2008 for *Vaccinium vitis-idaea*).

A possible problem with winter climate change, namely a warmer and shorter winter in general, for plant physiological ecology and associated biogeochemistry is caused by the disharmony or change in the association of light conditions and temperature (Bascañán-Godoy et al. 2012; Fig. 4). Especially for the wintergreen plants light intensity will not change with climate change while temperature rises. Most enzyme activities have optimum temperatures at which the enzyme shows the highest activity. If the optimum temperature is higher than the current temperature, the warming should increase the activity of the enzyme. However, some ecophysiological properties, such as leaf anatomy and N and RubisCo contents (Muller et al. 2005, 2009), are influenced by the light conditions, which will not change with climate change. The sunlight serves as an energy source or

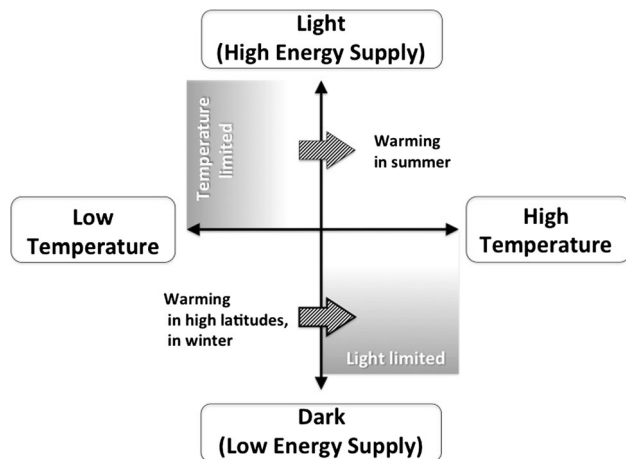


Fig. 4 Schematic diagram that shows the balances between the energy supply and demand changing with warming. In high latitudes and winter, warming may cause plant growth to be limited by light (energy)

inhibitor for such physiological processes. For example, in relation to N metabolism in plants, nitrate reductase is an enzyme that catalyzes the first step of NO_3^- assimilation in plants, and its activity in leaves is regulated by the light conditions, as reviewed in Kaiser and Huber (2001). The effects of light on this enzyme regulate gene transcription, protein synthesis, and enzyme activity (Lillo 1994). Thus, it is possible that the regulating factor for plant NO_3^- assimilation may be changed from temperature to light with climate change.

Vegetation development

Changing climate during winter affects vegetation structure indirectly via soil N availability. In arctic tundra, increase of snow depth results in expansion of a certain functional group (shrubs) via the increasing N mineralization under deepening snow (Sturm et al. 2005). Because shrubs catch more snow than other small-stature vegetation in tundra, positive feedback occurs between plant and soil via increasing N availability by winter climate change (Sturm et al. 2005). In addition to N availability, the changes in winter-specific processes (freezing temperature and snow cover) logically affect each stage of vegetation development directly: seed germination, seedling establishment, growth, and reproduction of plants.

The change in winter-specific processes influences vegetation positively and negatively depending on how the processes affect different plants in their habitats. In cold biomes, winter (cold stratification) generally improves seed germination performance (Reynolds 1984; Densmore 1997; Körner 2003; Shimono and Kudo 2005). The consequences of winter climate change on seed germination, however, are not consistent across species (Baskin et al. 2000, 2002). The responses vary depending on the origin of the species (harshness of

winter, Milbau et al. 2009), seed dispersal strategy (Drescher and Thomas 2013), and growth forms (Wesche et al. 2006). The indirect effect of changes of the snow regime on seed germination through plant-associated organisms is predictable, but has not been investigated in detail. In northern Japan, dark snow blight (*Racodium therryanum*) is a major pathogen that infects the seeds of coniferous species (Igarashi and Cheng 1988). Dark snow blight infects conifer seeds mainly under snow cover (Igarashi and Cheng 1988). Therefore, snow decrease and coincidental exposure of the pathogen to freezing might enhance seed germination.

Snow cover shortens the growing season. Therefore, advancing snowmelt has the potential to improve the growth and mortality of plants because of increased carbon fixation (Griffith and Loik 2010; Wipf et al. 2009; Wipf and Rixen 2010). However, freezing events, which occur in the absence of insulation by snow cover, limit seedling survival and growth (Johnson et al. 2004; Coop and Givnish 2008) by damaging the aboveground (especially winter buds: Sakai and Larcher 1987) and belowground organs (by frost damage to the root cells and cutting of roots by soil cryoturbation, Tierney et al. 2001; Cleavitt et al. 2008; Schaberg et al. 2008; Drescher and Thomas 2013). Therefore, where the negative effects of freezing stress exceed those of the short growing season for the plant, the benefits of a longer non-frozen season for vegetation growth under a warm winter may be cancelled out by frost damage (Wipf et al. 2009; Kim et al. 2012). On the other hand, the delayed snowmelt keeps water availability high for plants during the growing season, which is beneficial for plant growth (Hättenschwiler and Smith 1999). Moreover, some studies demonstrate a change not in the survival rate but in the driver of the mortality of plants with decreased snow in winter (Scherff et al. 1994; Holdo 2007), which implicates the presence of a complex mechanism that makes it difficult to extract the determinant of net changes of winter of vegetation growth by winter climate changes.

Species- or functional group-dependent effects of winter climate change modify the composition of vegetation. Broadly, in arctic and alpine systems, more snow accumulation and delayed snowmelt increase the abundance of forbs and dwarf shrubs, whereas lichen and graminoids decrease (Wipf and Rixen 2010). In a manipulation study of boreal forests, a long-term increase in the number of soil freeze-thaw cycles during a warm winter increased the abundance of grasses and decreased dwarf shrubs (Kreyling et al. 2011). These functional group-specific responses were likely because of the original preference of each species for changing winter conditions and to the differential competitiveness among the species, such as the large production to biomass ratio in deciduous shrubs with plastic growth-related traits for changing environments (Scott and Rouse 1995; Wahren et al. 2005).

While summer-time warming generally decreases the species diversity and species evenness of the vegetation

(Walker et al. 2006), the changing snow regime was also reported to decrease the species diversity of vegetation in moist arctic tundra because of the increase in the cover of species most abundant at the beginning of the experiment, which resulted in decreased evenness in the vegetation (Wahren et al. 2005). However, such a snow regime-vegetation relationship can vary depending on the vegetation structure. Where snow-preferring species are rare, species diversity can be expected to increase through the increase of species evenness (as implicated by Wahren et al. 2005). Above-ground and below-ground freezing events act as a disturbance for vegetation structure to change the diversity. Intermediate freeze-thaw cycles create high species diversity in the plant community (Chen et al. 2011; Makoto and Klaminder 2012), although little is known about how the freezing disturbance/species diversity relationship is influenced by on-going rapid climate change.

As an indirect effect, the change of the snow regime influences vegetation structure through its effects on pathogens. In the sub-arctic tundra, evergreen plant species decreased their biomass with increasing snow cover because of an outbreak of the parasitic fungus *Arwidssonia empetri* (Olofsson et al. 2011). As in the case of seed germination, studies on pathogen-related effects of winter climate change on vegetation are greatly needed. The loss of plant species and functional diversity has large effects on ecosystem function, such as terrestrial carbon dynamics (Kaneko and Salamanca 1999; Fornara and Tilman 2008). Moreover, because the response to summer-time environmental change (e.g., summer drought, CO₂ concentration) differs depending on the species or functional diversity of vegetation (Tilman and Downing 1994; Reich et al. 2004), the relationship between changing vegetation diversity and its responses to winter climate change and its feedback to carbon cycling should be investigated.

For the reproductive stage of vegetation development, advancing snowmelt and a coincidental increase in the exposure of flower buds to spring frost has been observed (Inouye 2008). Reproductive organs are more susceptible to freezing than vegetative organs (Sakai and Larcher 1987). Thus, the increased exposure of plants to spring frost events appears to affect reproduction more than vegetative growth (Bokhorst et al. 2008). Manipulation of snow duration results in a change of reproductive traits, such as flowering time and duration, flowering number, seed production, and/or seed weight (Bell and Bliss 1979; Galen and Stanton 1993; Dunne et al. 2003; Wipf et al. 2006; Lambrecht et al. 2007).

Phenological shifts and plant-pollinator interactions

Vegetation structure is directly determined by abiotic conditions, such as soil N availability and temperature, and indirectly by biotic factors, such as plant-associated insects and mammals through herbivory (Sala 1988) and pollination (Ramirez 2010). Phenological shifts of plants

and associated animals are the most apparent ecological response to global warming in northern ecosystems (Fitter and Fitter 2002; Root et al. 2003; Parmesan 2007; Wielgolaski and Inouye 2013). Responses of phenological events of plants and associated animals to temperature are highly variable among species and populations. The inter-specific variation may reflect the species-specific minimum thermal threshold for growth initiation, whereas local climates may cause intra-specific variation among populations. Furthermore, differences in the overwintering habitat of insects and the location of overwintering meristems (dormant buds) of plants also cause variation in spring phenology among species.

Phenological variation may affect biological interactions, such as phenological mismatch between plants and associated animals. However, evidence of phenological mismatch in terrestrial ecosystems is restricted, and most observations of phenological mismatch are on plant-herbivore and prey-predator interactions (Yang and Rudolf 2010). In contrast, phenological mismatch in plant-pollinator interaction has scarcely been reported (e.g., McKinney et al. 2012; Kudo and Ida 2013), partly because long-term monitoring of flowering time and the seasonal activity of pollinators is rare.

The flowering time of northern plants is strongly determined by the thermal requirements of individual species (Diekmann 1996; Hülber et al. 2010). In alpine and arctic ecosystems, snowmelt time is a major determinant of flowering phenology (Kudo 2006; Wipf 2010) because the thermal accumulation of plants with a lower stature starts after snowmelt. Snow distribution in the alpine region is highly varied, which reflects the microtopography and slope direction, and spatiotemporal variation in snowmelt patterns creates the diversity of the flowering structures in alpine ecosystems. Landscape structures of the flowering phenology influence the reproductive success and gene flow, which are mediated by pollinator availability and activity (Kudo 2006).

Advancing snowmelt time is evident in many alpine regions (Mote et al. 2005; Kudo and Hirao 2006). Early snowmelt, in addition to warm temperatures, accelerates the initiation and progress of flowering phenology in plant communities (Kudo and Hirao 2006; Hülber et al. 2010; Wipf 2010). Earlier flowering may increase the risk of frost damage in spring (Inouye 2008; Thomson 2010) and decrease pollination success because of reduced pollinator activity (Kudo 2006; Boggs and Inouye 2012). The shorter flowering season and higher flowering overlap may cause a genetic disturbance among local populations by pollen-mediated gene flow (Kudo 2006) and influence the temporal variation in floral resources for pollinators (Aldridge et al. 2011; Kudo 2013). The ecological impact of climate change on local ecosystems may be highly site-specific, because the extent and direction of phenological shifts are highly dependent on the species composition of communities.

Overwintering behaviour is linked to the phenology of pollinators. Photoperiod and temperature are major factors that determine the diapause schedule for many

insects (Tauber and Tauber 1976). Because most physiological studies on diapause have been conducted in the laboratory (Beekman et al. 1998; Amin et al. 2007; White et al. 2009; Sgolastra et al. 2011), it is difficult to predict the emergence time of pollinators in the field. In northern ecosystems, diapause breakdown usually occurs in the middle of winter when the ambient temperature is lower than the thermal threshold for activity and post-diapause development. Therefore, spring temperatures are the most important determinant of pollinator emergence (Høye and Forchhammer 2008; Gordo and Sanz 2006; Ellwood et al. 2012). Furthermore, local temperature varies greatly depending on snow depth and period. Thus, local snow conditions influence the emergence time of pollinators overwintering in the soil or soil surface (Alford 1969; Høye and Forchhammer 2008; Iler et al. 2013). Global warming may produce a shorter diapause duration and an earlier emergence of pollinators (Bale and Hayward 2010) and can also influence the phenology of migratory pollinators greatly at high latitude (McKinney et al. 2012).

Changes in climatic conditions also influence winter survival and fitness after the diapause. A delay of diapause induction due to a late onset of winter may increase the energetic expenditure and weight loss, which results in a higher winter mortality of pollinators (Sgolastra et al. 2011). Declining snow cover causes soil chilling and accelerates soil freeze–thaw cycles that may increase the winter mortality of insects (Bale and Hayward 2010). Furthermore, diapause duration and temperature influence the preoviposition period and colony development of bumblebees (Beekman et al. 1998; Amin et al. 2007). These empirical results indicate that the changes in winter climate may have serious impacts on the lifecycle and fitness of pollinator insects, although evidence in the field is incomplete.

When plants and pollinators respond differently to climate variation, phenological mismatch may occur. A simulation of phenological responses to a warming climate predicts that phenological shifts reduce the floral resource availability to 17–50 % of pollinator species because of the advancement of flowering season and the coincidental failure of pollinators to utilize floral resources as food during the season (Memmott et al. 2007). Several studies have detected different phenological sensitivities to a warming climate between plants and insects (Gordo and Sanz 2005; Parmesan 2007; Forrest and Thomson 2011; Kudo and Ida 2013). In general, phenological responses to climate variation are highly species-specific and most plant and pollinator species within communities are generalists in the pollination system, so plant–pollinator mutualism may be easily restored against the phenological mismatch in a pollination network (Hegland et al. 2009; Rafferty and Ives 2011). However, plant–pollinator interactions between specific species may be sensitive to climate change, especially early in the season (Thomson 2010; Kudo and Ida 2013).

Plant–pollinator interactions in the alpine ecosystem may be most sensitive to climate change because the

flowering season is extremely short and highly determined by snowmelt regime. Under such conditions, small differences in the thermal requirements may cause a significant mismatch. Although field surveys on the phenological synchrony between flowers and pollinators are limited, the results of these studies are not uniform. Temporal synchrony between pollinators and flowers was retained in syrphid flies, solitary bees and wasps in North America (Forrest and Thomson 2011; Iler et al. 2013), whereas a clear mismatch was detected between bumblebees and flowers in an extremely warm season in northern Japan (Kudo 2013). These differences indicate the importance of life cycles and microclimates in overwintering habitats of individual pollinator insects responding to climate variations.

For the next step, evaluation of fitness and population dynamics is crucial for understanding the ecological significance of phenological shifts (Miller-Rushing et al. 2010). Studies evaluating the effect of phenological mismatch on plant fitness are limited (Rafferty and Ives 2011; Kudo and Ida 2013), and there is only one study on pollinator fitness (Boggs and Inouye 2012). Because insect pollinators have an annual cycle, their population dynamics should be sensitive to temporal variations in floral resources (Inari et al. 2012). The population dynamics of major pollinators are susceptible to phenological mismatch and should influence the species composition of pollinators, resulting in the modification of pollination linkages as well as in a decrease in pollination services. In the cold and snowy alpine and arctic ecosystems, modification of snow and soil temperature regimes may be a major driving force causing phenological mismatch between plants and insects because the overwintering meristems of plants and the habitats of insects are near the ground. Moreover, soil N availability, which is influenced by snow and soil temperature, can affect plant–pollinator networks through the change of nectar chemistry, flower morphology and plant phenology as well as nectar consumption and longevity of pollinators (Hoover et al. 2012; but also see Burkle and Irwin 2009). Monitoring the temporal change of available N and its regulators such as soil temperature and moisture contents, in addition to the analysis of the aboveground climate, may be a key issue for understanding the biological dynamics under a changing winter.

Future perspectives

We have reviewed recent studies of plant–soil interactions conducted mainly in cold biomes and focused on how the winter environments or events (e.g., low temperature, snow cover, and soil freeze–thaw cycles) are linked to biological processes at various levels during and after winter. Recent findings have been summarized from field observations and experimental studies, which might contribute to predicting the impact of on-going or expected future changes in the winter climate on plant–

soil interactions. However, such predictions are uncertain in many interactions. The winter-related biological processes that are discussed in this review vary in the scales of space and time, including those of relatively short-term individual plant responses (e.g., photosynthesis and N uptake) and long-lasting ecosystem-level functions (e.g., C- and N₂O-flux as well as N dynamics). In addition, there are biological processes (e.g., plant–pollinator interactions) in which seasonal reproductive schedules are independent but closely connected to one another indirectly by snow-melt time. Some processes (e.g., shorter- and smaller-scale phenomena) can be predicted more precisely than others (e.g., longer-term and larger-scale ones) because of less complexity in the factors involved. This may not be necessarily true, however. As seen in the case of the arctic tundra, for example, long-term studies with warming experiments have been conducted to predict vegetation responses at various levels against a possible scenario of winter climate change (less snow cover, frequent soil freeze–thaw cycles, and a prolonged growing season), indicating that the observed patterns were not simple even for a change in short-term, fine-scale phenomena (Walker et al. 1993, 1999, 2006; Phoenix and Lee 2004; Brooks et al. 2011; Elmendorf et al. 2012). Therefore, there are still many challenges in studies of winter climate change and its impact on biological and ecological processes.

Here we have identified several priorities for future field study and experiments as well as methodological improvements (see under each specific topic above). Nitrogen is the limiting factor of the performance of primary producers in most parts of cold terrestrial ecosystems (Vitousek and Howarth 1991). Therefore, the changing soil N dynamics under changing winter conditions can be the trigger for changes in vegetation composition and vegetation-related species interactions as well as their ecological functions and services. On the other hand, at global scale, the degrees of winter climate change (e.g., such as winter temperature) are influenced by N₂O concentration. This implicates the increasing/decreasing N₂O emission via the change of soil N dynamics can act as positive/negative feedback to ongoing winter climate change. By summarizing the topics in this paper, it is hypothesized that winter climate modify structure and function of plant–soil system both via soil N and atmospheric N in soil–vegetation–atmosphere linkage. Furthermore, large-scale comparative studies might be important, especially for ecosystem-level functions (C and nutrients dynamics). As previously stated, a worldwide network of studies on warming experiments has already been established for the comparison of originally cold biomes (i.e., arctic and alpine tundra, boreal forests) but not yet for the other biomes, or “less but cold ecosystems” (i.e., cool-temperate forests). The latter systems include larger areas that will experience the phase-shift from solid soil to soft soil (or vice versa) than the former ones under changing winter climate, which is expected to induce drastic change of organism activity together with their functions in plant–

soil system. Considering (1) high heterogeneity of winter condition within a landscape and that (2) there are differential responses of plant–soil systems to climate change under different snow and freezing regimes, it is likely more difficult to predict landscape-level consequences of winter climate change in cool temperate forests than in much cooler systems. Furthermore, as even within boreal biomes, individual tree growth, forest productivity and nutrient dynamics are likely to respond to warming in different manners by locations (e.g., northern limits vs. southern boundary). Northern range limits of plants are commonly well explained by isotherms such as minimum temperature or the mean temperature of the coldest month (Kreyling 2010). This fact implicates that, while the predicted change of winter temperature would directly modify plant performance at northern limits, the indirect pathways (e.g., changing soil N availability or phenological mismatch by winter climate change) might be critically influential for plants at southern boundaries. Comparisons of the plant–soil interactions between boreal forests in Europe and Siberia established in different soil conditions (i.e., seasonally frozen soil vs. permafrost) suggest that patterns of plant growth responses are largely varied, most likely because of interactions below the ground as opposed to interactions above the ground (Osawa et al. 2010). This fact implies that indirect effects of winter climate change via soil properties on forest system would be stronger than the direct effects in Siberia with permafrost soil and vice versa in Europe with seasonally frozen soil. Information from such a large-scale comparative study of plant–soil interactions should contribute to a greater understanding of and the ability to predict the impact of winter climate change on terrestrial ecosystems.

Acknowledgments We deeply acknowledge Prof. Inouye DW and two anonymous reviewers for their helpful comments on an early version of this manuscript. We thank all attendants to the symposium at the 60th Annual Meeting of the Ecological Society of Japan in 2013 in Shizuoka who contributed valuable comments on each talk. This symposium was partly supported by the travel fund from Ecological Research. We thank Prof. Nobuhiro Kaneko for his support for a part of this study and Uryu Experimental Forest, Hokkaido University for providing long-term observation data of snowpack. This reviewing work is partly supported by research funds (22248016 and 25252026 for HS, 24-3240 for KM) from the Japan Society for the Promotion of Science, and the Environmental research and technology development fund (S-9-3) of the Ministry of the Environment, Japan.

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