Effects of permafrost degradation on ecosystems

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A R T I C L E   I N F O

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A B S T R A C T

Permafrost, covering approximately 25% of the land area in the Northern Hemisphere, is one of the key components of terrestrial ecosystem in cold regions. As a product of cold climate, permafrost is extremely sensitive to climate change. Climate warming over past decades has caused degradation in permafrost widely and quickly. Permafrost degradation has the potential to significantly change soil moisture content, alter soil nutrients availability and influence on species composition. In lowland ecosystems the loss of ice-rich permafrost has caused the conversion of terrestrial ecosystem to aquatic ecosystem or wetland. In upland ecosystems permafrost thaw has resulted in replacement of hygrophilous community by xeromorphic community or shrub. Permafrost degradation resulting from climate warming may dramatically change the productivity and carbon dynamics of alpine ecosystems. This paper reviewed the effects of permafrost degradation on ecosystem structure and function. At the same time, we put forward critical questions about the effects of permafrost degradation on ecosystems on Qinghai–Tibetan Plateau, included: (1) carry out research about the effects of permafrost degradation on grassland ecosystem and the response of alpine ecosystem to global change; (2) construct long-term and located field observations and research system, based on which predict ecosystem dynamic in permafrost degradation; (3) pay extensive attention to the dynamic of greenhouse gas in permafrost region on Qinghai–Tibetan Plateau and the feedback of greenhouse gas to climate change; (4) quantitative study on the change of water-heat transport in permafrost degradation and the effects of soil moisture and heat change on vegetation growth.

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0. Introduction

Permafrost, defined as subsurface earth materials remaining below 0 °C for two consecutive years [1,2], is a geological entity that results from the exchange of material and energy between the earth and the atmosphere under the multiple impacts of regional geographic condition, geological structure, lithologic characters, hydrology and topographical features, and is more sensitive to the change of environments [3]. Permafrost is widespread in the Arctic and boreal regions of the Northern Hemisphere, where permafrost regions occupy 25% of the exposed land surface area [4]. Permafrost also occurs on the continental shelf of the Arctic Ocean and in mountainous regions [2]. In the Southern Hemisphere, permafrost occurs in mountains, in subantarctic islands, and in the Antarctic continent [2]. Russia [5], Canada [6], China [7,8], Alaska [9] and high mountains and subalpine [10] were countries and regions that underlain by permafrost widespread. Permafrost in china is mainly distributed on the Qinghai–Tibetan Plateau, in northeastern China and in the mountains in northwestern and central China. Permafrost bodies on the Qinghai–Tibetan Plateau is the largest permafrost region in the mid and low-latitude, which is estimated at about 1.5 × 106 km2 and account for 69.77% the total permafrost area in china [11]. Permafrost controlled by air temperature in the thickness, presence and geographic extent reacts sensitively to changes in atmospheric temperature and permafrost is identified as one of the key cryospheric indicators of global climate change [10,12,13]. Global average surface temperatures have increased by about 0.74 ± 0.18 °C over the past hundred years [14]. Global climate models project the strongest future warming in the high–latitudes, with some models predicting a 7–8 °C warming over land in these regions by the end of the 21st century [14]. Global circulation models project pronounced future warming in areas where discontinuous and continuous permafrost is currently present [15] and despite the many uncertainties associated with climate predictions there is a general agreement that this climatic warming will have serious impacts on high-latitude permafrost [16]. Increases in regional temperatures have led to widespread
degradation of permafrost, increase of thaw depths and disappearance of permafrost in local area, especially in the discontinuous and sporadic permafrost zones [17,18]. Widespread increases in active layer thickness can cause great changes in hydrological processes, distribution of vegetation, soil organic carbon and can also affect the infrastructure and economy of permafrost region [19–22]. This paper reviewed the effects of permafrost degradation on ecosystem structure and function and put forward critical questions about the effects of permafrost degradation on alpine ecosystems on Qinghai–Tibetan Plateau to promote research on permafrost ecosystem developing further.

1. Importance of permafrost for alpine ecosystem

Under the assemblage of permafrost molded by freeze–thaw action, cryogenic ecosystems and related processes of water and heat variations in the high-cold environment (alpine cold area and high-latitude cold area) are called permafrost ecosystem [23–25]. The permafrost plays an active role on vegetation growth and production in the alpine grassland ecosystem [26]. Permafrost degradation alter the water–heat process of soil, which lead to changes in species composition [27] and give rise to community succession [28] and ecosystem degradation [29] further. Therefore, development and protection well of permafrost is the material foundation that permafrost ecosystem keep ecological balance.

There is strong interdependence between vegetation and permafrost in permafrost region. The relationship of vegetation and permafrost is complex, which mainly embodies the interaction between vegetation and permafrost. Low ground temperature of permafrost restrict roots grow deeply and is beneficial to accumulation of organic materials. Permafrost is regarded as widely distributing semi-permeable which could prevent surface water and soil moisture infiltrating and migrating downward. In the meanwhile, soil nutrients leached from surface soil are apt to accumulate at the bottom of active layer [31]. Permafrost plays an important role of supplying soil moisture and nutrient to vegetation. Permafrost environment is essential to maintain stable climate and keep the balance of alpine ecosystem. On the other hand, the vegetation which can reduce sunlight and shed soil surface, lowered surface temperature and transpiration rate [30] is vital for thermal insulating and cooling permafrost [29]. Moreover, vegetation play an important role in soil water conservation, climate regulation, erosion prevention, sand fixation and keeping water balance between vegetation and soil. Permafrost and vegetation mutual restricting, interacting and complementing each other are key complements to maintain the balance of alpine ecosystem in permafrost region.

2. Effects of permafrost degradation on ecosystem structure

2.1. Effects of permafrost degradation on species composition

Environmental condition such as high elevation, low temperature, large temperature difference between day and night, low air pressure, strong solar radiation in permafrost region on QTP is harsh for plant growth [32,33]. Frost, snow, hail and gale are prevailing in growth season [32,33]. Plant has narrow ecological niche as a result of living in harsh habitat for a long time and extremely sensitively to environment change. Widespread degradation of permafrost and the concomitant expansion of thermokarst-related landforms have the potential to significantly affect the composition, distribution and extent of plant communities in the arctic and subarctic [34]. The collapsed areas caused by rich-ice permafrost degradation in central Alaska are rapidly colonized by aquatic herbaceous plants, leading to the development of a thick, floating organic mat (Table 1) [35]. The studies about effects of permafrost degradation on woody vegetation at Arctic treeline on the Seward Peninsula, Alaska show that improved soil drainage was the most important factor controlling the growth and distribution of vegetation and the second factor was the depth of active layer. Plant communities in steep pond banks were distinct from those found on surrounding level tundra. Thaw pond banks supported a significantly higher density of trees and large shrub species and shrubs were significantly taller on banks than elsewhere (Table 1) [34]. Permafrost degradation resulted in improving soil drainage might influence species composition considerably.

Permafrost degradation on QTP decrease species number of graminae and sedge suitable to live in the environment of low temperature and high soil moisture and increase the weeds (e.g. Potentilla nivia, Oxytropis) in the plant communities which caused the Economic value of plants decreased [27,28]. Accompanying by permafrost degradation, wet plant species like Kobresia tibetica and Kobresia humilis in communities decreased gradually and drought plants such as Stipe purpurea, Poa annua and Agropyron cristatum expanded rapidly. With the permafrost degradation further, soil moisture decreased and soil environment extremely drought which caused mesophyte in alpine meadow disappear, drought enduring plant expanded fully and alpine meadow change into alpine desert steppe gradually [37]. The response of species composition to permafrost degradation is significantly correlated with permafrost environment. In rich-ice permafrost region with thin active layer, permafrost degradation increased soil moisture, and aquatic plants or hygrophytes expanded gradually [35]. Permafrost degradation in regions with thick active layer and well drainage soil lowered soil moisture which increased the number of xerophytes or mesophytes and decreased the number of aquatic plants and hygrophytes (Table 1) [38].

Alpine ecosystem is extremely sensitive to permafrost degradation and species composition responds permafrost degradation in two different ways. For plant community in lowland on flat with rich-ice soil (e.g. Tanana Flats in central Alaska), permafrost degradation cause drought habitat moistening gradually. Accompanying by permafrost degradation, soil moisture increased and the xerophytes were substituted by hygrophytes. Permafrost on QTP and upland in arctic degraded resulted in improved soil drainage and drought soil environment which caused the xerophytes expand gradually. Permafrost degradation affected species composition through altering soil water conditions that increased or decreased soil moisture.

2.2. Effects of permafrost degradation on succession

Permafrost degradation increased permafrost table, thickened active layer, and altered water conditions of vegetation growth environment, which caused the changes of floristic composition and community structure, and arouse the community succession [36,39–41]. For forests on ice-rich permafrost, the loss of ice-rich permafrost can caused the wholesale conversion of ecosystems from terrestrial to aquatic or wetland systems [42–45]. Studies on the thermokarst in the Mentasta Pass area in Alaska showed that wet sedge meadows, bogs, thermokarst ponds, and lakes are replacing forests [45]. Permafrost on the Tanana Flats in central Alaska degradation is widespread and rapid, causing large shifts in ecosystems from birch forests to fens and bogs which birch forest have decreased 35% and fens have increased 29% from 1949 to 1995 (Table 1) [35]. In lowland ecosystems and hillside of Alaska, permafrost degradation improved soil drainage which provided a microsite that favours tall woody vegetation and caused the shift of communities from tussock-tundra communities to shrub-tundra communities (Table 1) [34] and shrub expanded widespread in arctic tundra was a typical example [39].
Wang Genxu et al. studied the permafrost ecosystems on QTP and presented the primary succession mode of alpine vegetation during the permafrost degradation: alpine marsh meadow changed into alpine meadow with the permafrost degradation, then meso-phyle community, and then drought community (Table 1) [37]. The study on the relation between permafrost degradation and Kobresia meadow change on the southern piedmont of the Tangula Range showed accompanying by permafrost degradation, species occurred in cold–wet habitat disappear gradually and the species suitable to live in cold–drought habitat invaded community, and K. tibetica meadow changed into Kobresia pygmaea meadow gradually (Table 1) [27].

The response of alpine ecosystem to permafrost degradation showed two different trends which was complex due to the variability of vegetation, content of ground ice and thaw settlement. In general, the degradation of permafrost with ice-rich soil would result in the conversion of terrestrial ecosystem to aquatic or wetland systems. However, drought community or shrub community might become dominant community of alpine ecosystem in regions that permafrost degradation caused improved soil drainage (e.g. QTP or upland in Arctic).

Table 1

<table>
<thead>
<tr>
<th>Model of community succession</th>
<th>Succession stage</th>
<th>Dominant species</th>
<th>Associate species</th>
<th>Area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Swamp meadow–true meadow–steppe meadow–sandy meadow</td>
<td>Swamp meadow</td>
<td>Kobresia tibetica</td>
<td>Blysmus sinocom pressus, Polygonum macrophyllum, Pedicularis longiflora var tubiflris, Caltha scaposa, Carex atrofusca, Hippuris vulgaris</td>
<td>Xidatan-the southern hillside of tanggula mountain [38]</td>
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<td></td>
<td>Ture meadow</td>
<td>Kobresia humilis</td>
<td>K. capitillifolia, Poa pratensis, Stipa sp., Leontopodium nanum, Oxytropis anserinus</td>
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<tr>
<td></td>
<td>Steppe meadow</td>
<td>Kobresia pygmaea</td>
<td>Stipa aliena, Saussurea superba, Festuca rubra, Elymus nutans, Aster flaccidus, Gentiana sp.</td>
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<tr>
<td></td>
<td>Sandy meadow</td>
<td>Stipa purpurea + Carex sp.</td>
<td>Stipa subsecisflora, Festuca spp., Poa pratensis, Astragalus spp., Potentilla bifurca, Saussurea sp,M yricarap rastrata</td>
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<tr>
<td>Kobresia tibetica meadow–Kobresia pygmaea meadow</td>
<td>Kobresia tibetica, Kobresia pygmaea</td>
<td>Anemone sp., Gentiana leucum elena, Trollius put ilus, Cham aesium paradi oxum, Saussurea sp., Poo sp., Creem anthodium sp.</td>
<td>The southern hillside of tanggula mountain [27]</td>
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<td>Kobresia pygmaea meadow</td>
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<td></td>
<td>Kobresia pygmaea</td>
<td>Blysmus sinocom pressus, Potentilla nivia, Androsoace sp., Leontopodium nanum, Oxytropis kansuensis, Saussurea sp., Poo pratensis</td>
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<tr>
<td>Tussock-tundra–shrub-tundra</td>
<td>Tussock-tundra</td>
<td>Eriophorum vaginatum</td>
<td>C. bigelowii, Empetrum niigrum, Arctostaphylos spp., Rubus chamaenemor, Salix arctica, Vaccinium spp.</td>
<td>Seward Peninsula in western Alaska [34]</td>
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<td></td>
<td>Shrub-tundra</td>
<td>Salix glauca</td>
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<td>Forest–fen</td>
<td>Lowland birch forests</td>
<td>Betula papyrera</td>
<td>Picea glauca, Picea mariana, Rosa acicularis, Equisetum arvense, Calamagrostis anadensis, Lemna minor, Cala pallustris, Ledum groenlandicum</td>
<td>Tanana Flats [35]</td>
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<tr>
<td></td>
<td>Lowland fen meadows</td>
<td>Menyanthes trifoliata, Equisetum fluviatile</td>
<td>C. aquatilis, Potentilla palustris, Typha latifolia, Cicuta mackenziana, Galium trifidum, Myrica gale</td>
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</table>

2.3. Effects of permafrost degradation on vegetation coverage

Permafrost degradation lead to changes in soil hydrological properties [34] which influenced vegetation coverage eventually since soil moisture is the key ecological factor limiting vegetation distribution, plant growth and community structure and function. In the headwater area of the Yellow River, alpine marsh meadow commonly with exuberant Kobresia (K. tibetica, K. humilis, Kobresia prattii, etc.) occurred in the area where suprapermafrost water buried depth was between 0.1 m and 0.8 m and the coverage was about 85–95%. When the suprapermafrost water buried depth was between 0.8 m and 2 m the dominant vegetation type was cold–arid grassland with the coverage between 30–50% in which the dominant species were drought-tolerant plant like S. purpurea, A. cristatum, Elymus nutans and so on. Alpine desert steppe was the outstanding landscape type and the vegetation was composed of drought-tolerant weed (e.g. Artemisia arenaria, Leontopodium na num, Thermopsis lanceolata) with the coverage below 30% when the suprapermafrost water buried depth was larger than 2 m. In general, community type and vegetation zoning have the significant relation with the buried depth of suprapermafrost water in the permafrost region on QTP. In turn, the vegetation coverage is the important factor affecting the buried depth of suprapermafrost. In regions where alpine marsh meadow was with high vegetation coverage, the buried depth of suprapermafrost water was totally less than 1 m [46]. Permafrost table has a closely relation with vegetation coverage; low permafrost table always accompanied by high vegetation coverage. At the time of permafrost table being less than 2 m, soil moisture content and vegetation coverage are high, and permafrost table is negative relation with vegetation coverage. When permafrost table is larger than 2 m, most plant growth is limited and only few drought-tolerant species with developed root system are survival with low coverage being less than 35%, as a result of which the growth environment is drought dramatically due to low level of suprapermafrost water, little water recharge, few quantity of suprapermafrost water and rising height of capillary water being not reach the surface soil layer in which the root mainly distributed [36].

2.4. Effects of permafrost degradation on biodiversity

Permafrost degradation changed habits and species composition which affected species richness. The result based on the quadrant investigating indicated that little difference existed between the different communities in successional series. However, the richness index was significantly different within the 100 m sampling zones in the degraded permafrost region on QTP, which species richness in alpine meadow and steppe meadow was significantly larger than that in marsh meadow and desert steppe. The difference of results obtained from two different sampling approaches indicated though the species richness in single quart had little difference, the role and importance of species in communities changed because the distribution and occurrence frequency of species was different. Species evenness indices were significantly different between communities in permafrost region on QTP that increased from marsh meadow to steppe meadow, and decreased
from steppe meadow to steppe grassland [38,47], α diversity was significantly different among the successional series and its change trend was in accord with the evenness index that increased from marsh meadow to steppe meadow, and then decreased from steppe meadow to steppe grassland. With the degradation of permafrost, marsh meadow was drained and changed into alpine meadow which brought about invasion and development of mesophytes. Species richness index in quadrat was almost no change between marsh meadow and alpine meadow because even distribution of species in communities, however, α diversity in alpine meadow increased compared with in marsh meadow. At the succession stage of steppe meadow, xerophytes replaced mesophytes and hygrophytes gradually and the proportion of meadow plant decreased. Although species composition in steppe meadow changed compared with in alpine meadow, α diversity was not significantly different. Xerophytes had high ecological dominance with disappearance of mesophytes because of extremely degraded permafrost environment and α diversity index decreased [38,47]. Yan et al. [27] carried out the study on the relation between permafrost degradation and Kobresia meadow change on the southern piedmont of the Tangula Range and the results showed that when the permafrost environment changed from permafrost island to seasonally frozen-ground area, ecological dominances and species diversities were increasing in a certain degree. The discrepancy between the results obtained by Yan et al. [27] and Guo et al. [38,47] demonstrated that it is not a universal law about the response of biodiversity and ecological dominance to permafrost degradation. The effect of permafrost degradation on biodiversity was complex which should be contingent on permafrost type, specific region and succession mode.

β Diversity is often used to analyze the difference of species composition between communities; it reflects species replacement along an environmental gradient. β Diversity is high when different communities had large number of common species [48]. At the stage of marsh meadow during permafrost degradation on QTP, the heterogeneity of habitat was low due to high soil moisture content and the rate of species replacement was small. Along with permafrost degradation on QTP, soil moisture decreased gradually and mesophytes invaded community that led to increase of the β diversity. The rate of species replacement increased further when the soil moisture decreased further resulting in the disappearance of hygrophytes and the invasion of xerophytes. Soil environment was greatly drought due to permafrost degraded extremely lowered the heterogeneity of habitat and steppe plant had high ecological dominance which decreased the rate of species replacement. The change trend of β diversity reflected the heterogeneity of microhabitat increased from marsh meadow to steppe meadow, and decreased from steppe meadow to steppe grassland; also reflected the change rate of species diversity of alpine grassland community during permafrost degradation on QTP [38,47].

3. Effects of permafrost degradation on ecosystem function

3.1. Effects of permafrost degradation on soil moisture

Under unique plateau climate environment, especially in permafrost region, variations in the process of soil moisture were the significant change of eco-environment on QTP. Soil moisture was important factor influencing vegetation growth which depended on vegetation type, soil characteristics and permafrost environment. Changes in freezing and thawing process caused by altered permafrost environment influenced soil moisture drastically. Soil moisture was the key factor linking the changes of permafrost environment and vegetation dynamics. The melting of permafrost impacted alpine ecosystem mainly through changes in soil moisture conditions. Thickened active layer and lowered level of suprapermfrost water caused by permafrost degradation on QTP were one of important reasons responsible for a dropping groundwater table. With the increase in the permafrost table, the thickness of active layer thickens. With the development of active layer during permafrost degradation, soil moisture converge at the permafrost table, in the meanwhile, vaporous water migrate toward and condense at permafrost table under the vapor pressure leading to decrease of moisture in surface soil which cause the loss of soil moisture in upper active layer and drought gradually [46].

At community scale, surface soil moisture with decreasing trend changed dramatically and the difference between succession stages reached significant level. The difference of soil moisture during permafrost degradation on QTP was mainly because that permafrost could prevent soil moisture infiltrating and maintain high soil moisture content in root zone; however, increased active layer during permafrost degradation weakened the support action of permafrost to groundwater, decreased the level of groundwater, and brought about the drought trend of surface soil gradually [38]. Soil moisture distributed in vertical profile in different vegetation types (e.g. shrub grassland, Kobresia meadow, and black soil land) with the same trend that the content of soil moisture decreased with the increase of soil depth. However, there were apparent differences in the extent of soil moisture change in profile, which soil moisture distributed vertically in black soil land and Kobresia meadow changed much more dramatically than that in shrub grassland. The content of soil moisture in shrub grassland was highest and it had the lowest value in Kobresia meadow. Black soil land with more degraded permafrost environments had higher soil moisture content than Kobresia meadow due to compact soil structure of black soil land restricted infiltration maintaining high soil moisture [49]. At region scale, the melting of permafrost and the thickening of active layer were the crucial factors that caused a dropping groundwater table at the source areas of the Yangtze River and Yellow River, which in turn results in lowering lake water levels, drying swamps and shrinking grasslands [50].

3.2. Effects of permafrost degradation on soil nutrient

The main driving factor for soil organic material (SOM) storage is the thickness of the active layer [51]. The degradation of permafrost and the related deepening of the active layer make large amounts of previously frozen SOM may become bioavailable [54,55] and increase SOM mineralization [53,56] dramatically by improving soil drainage and oxygen availability [52,53]. The recent studies on permafrost on QTP showed that accompanying by the process of permafrost degradation, SOM reduced significantly. The content of SOM in alpine marsh meadow was five and seven times higher than that of in alpine steppe meadow and alpine desert steppe, respectively [11,38]. Additionally, the melting of permafrost decreased the content of the hydrolysable nitrogen, available potassium, and available phosphorous [49].

Permafrost degradation led to thermokarst formation that influenced the content of soil organic carbon and total nitrogen. Soil organic and total nitrogen in thermokarst caused by permafrost degradation was much less than in intact bogs [51]. Some study showed contradictory findings that total canopy N was significantly higher at thermokarst compared to Tussock [57] suggesting permafrost degradation increased soil temperature resulting in improved nitrogen mineralization and nitrogen availability, more soil nitrogen to be utilized in thermokarst which caused the increase of community productivity limited by soil nutrient currently [57,59–61]. Therefore, the effects of permafrost degradation and long-term development of thermokarst pond on carbon and nitrogen cycling are not insightful and it is a great challenge for the study about the
effect of permafrost degradation on the nutrient cycling in the future [58,61].

3.3. Effects of permafrost degradation on ecosystem productivity

Permafrost play a significant role on vegetation production in the alpine grassland ecosystem in permafrost region due to that permafrost as semi-permeable could prevent soil moisture infiltrating and supply an ample water resource for plant growth, in the meanwhile, permafrost is beneficial for plant survivor and organism remaining in soil and played an important role on nutrients cycling [26]. Therefore, the degradation of permafrost would alter vegetation pattern and change ecosystem productivity [62–64]. Guo et al. [38] revealed that primary productivity of grassland decreased gradually during permafrost degradation; plant biomass lowered 60% when alpine marsh meadow changed into alpine meadow and alpine desert steppe had the lowest plant biomass, only about 500 kg/hm². However, there were not significantly different in plant biomass between alpine meadow and alpine steppe meadow. Although the difference in plant biomass between some successional series was not significant, carrying capacity, quality of grassland decreased dramatically because the proportion of available forage decreased, and toxic and hazardous weeds in plant communities increased in the successional series, which was instanced in a fact that sedge decreased and the species richness of weeds such as P. nivius, Stellera chamaejasme, etc. increased as a result of shift in vegetation type from alpine steppe meadow to alpine desert steppe during permafrost degradation on QTP [38]. The main cause being responsible for permafrost degradation led to the decrease of ecosystem productivity was that ecological water level and groundwater level lowered due to increased depth of seasonal thawing layer, and soil moisture was not restricted in the surface soil reducing the available water to plant growth, causing the root withered and resulting in the decrease of primary productivity of alpine ecosystem [65,66]. In upland tundra in Alaskan, the development of thermokarst decreased the aboveground plant biomass which changed from being dominated by sedges, to becoming increasingly dominated by deciduous and evergreen shrubs. Tussock had the lowest shrub biomass and the highest graminoid biomass indicated permafrost degradation changed cold, dry microsites suitable for graminoids into warm, moist microsites associated with shrubs closely [57].

3.4. Effects of permafrost degradation on greenhouse gas emission

Large quantities of carbon are sequestered in the permafrost of boreal peatlands and tundra regions [67] and the near-surface layer of permafrost is a substantial proportion of the carbon pool in terrestrial ecosystems [68], which approximately 970 Gt of carbon are contained in permafrost [69]. Therefore, distribution of permafrost and composition and quantity of organic materials in permafrost are essential for understanding the response of ecosystems in high-latitude region to global warming [53,70]. That change permafrost C from the frozen to the thawed state rapidly increase the C pool size available for decomposition was crucial for determining C emission from permafrost to atmosphere. Under a warming climate, release rate and type of C from permafrost to the atmosphere were closely associated with thaw mechanisms of permafrost at landscape scale and the thaw mechanisms mainly included active layer thickening, talik formation, river and coastal erosion and thermokarst development [2]. However, the main causes controlled thaw rate and influence extent of permafrost were the content of ground ice and the characteristics of landscape such as terrain, slope, etc. [45]. The melting of permafrost improved release of C from permafrost to the atmosphere mainly through accelerated microbial decomposition of organic matter. Accompanying with the melting of permafrost, large quantities of CO₂ were emitted from frozen C pool to atmosphere due to increased soil temperature and improved soil drainage and oxygen availability [55]. The melting of permafrost in peatlands across western Canada led to 1.6- and 30-fold increased in CO₂ and CH₄ emissions, respectively and the function of high-latitude terrestrial ecosystems as an atmospheric CO₂ sink was weakened gradually or even reverse because of permafrost degradation [52,55]. The function of wetlands in permafrost regions on the QTP contribute significantly to the global budgets of greenhouse gases. However, the functions of these wetlands as an atmospheric CO₂ sink may change substantially because permafrost under these wetlands has been degrading [8]. Studies on the effects of the degradation of swamp and alpine meadows on CO₂ emission on the QTP showed that CO₂ emission flux of the swamp meadow gradually decreased with increasing degradation degree, while that of the alpine meadow gradually increased with increasing degradation degree [80]. Fire disturbance is an important abiotic mechanism for transferring C thawed from permafrost to the atmosphere that oxidizes organic C primarily to CO₂, but also releases smaller quantities of CH₄, carbon monoxide, and other volatile C compounds [2]. The size of C pool of permafrost, biological decomposition and fire disturbance were the important influencing factors that control the release of C from permafrost to atmosphere. Under a warming climate, increased biological decomposition and frequency of fire disturbance would cause large quantities of organic C stored in permafrost release to atmosphere in the form of greenhouse gas [81,82]. It is about 100 PgC in permafrost predicted to be lost by 2100 [83].

Permafrost degradation influenced climate change through complex mechanisms, both positive and negative feedbacks relating to CO₂ fluxes. Emission of greenhouse caused by permafrost degradation accelerated global warming through positive feedback mechanisms. However, increased photosynthetic rate and prolonged growth season could sequester C from atmosphere that restrained the climate warming to some extent through negative mechanism. One important offset of release C from permafrost was that increased soil temperature and improved nutrient availability during permafrost degradation promote plant growth limited by soil nutrients, cold temperature and extreme seasonality with a short growing season and sequestered more gaseous C in alpine ecosystems [84]. Studies have revealed that net ecosystem C uptake in growing season increased 1–6 g/m² caused by the increase of temperature [85,86]. Vegetation C in bogs caused by permafrost degradation increased [71] due to that accelerated mineralization of organic matter released ample available nutrients led to increase in net primary productivity of ecosystem [72]. Carbon sequestration in ecosystem at long-term scale could not offset the release of C from permafrost to atmosphere resulted from the melting of permafrost and the development of thermokarst [2]. Therefore, the response of ecosystem dynamics in permafrost region to global warming was not only carbon emission and it is actually great complex [73,74]. Long-term observation about the flux of CO₂, nutrient status, net primary productivity and thaw depth of permafrost was crucial for estimating the balance of C in permafrost region accurately in the future. The melting of permafrost may not only affect the CO₂ efflux but also the exchange of the greenhouse gases CH₄ [75]. The direction and the size of the net CH₄ exchange were mainly controlled by the degree of soil water saturation, the temperature, and the amount of bioavailable organic matter [76,77]. Little knowledge about N₂O release from permafrost soil was known due to low nitrogen turnover and availability and emission was considered to be low [70]. Large quantities of organic nitrogen accumulated in boreal peatlands [78] and permafrost degradation induced a lowering water tables or drainage of boreal peatlands might increase emission of...
N₂O. High N₂O emissions were found in permafrost soils rich in organic nitrogen where appeared to be a strong potential for denitrification [70,79].

4. Problems and perspectives on the effects of permafrost degradation on ecosystem on QTP

Compared with geocryology in other countries, permafrost study in China is closely related with economic construction and development of cold region and has obtained great achievements in engineering geocryology concerned exploitation of frozen-ground regions and geocryology physics (e.g. classification of permafrost, type of permafrost, temperature and thickness of permafrost). Unique high altitudinal permafrost on QTP attracted much attention in the context of global warming since the QTP is the sensitive and promoter region of climate change in China. However, investigation about the effects of permafrost degradation on ecosystem on QTP was not systematical.

At present, there is lack of long-term observations in studying succession dynamic of alpine ecosystem during permafrost degradation and space sequence instead of chronosequence approach or static analogy approach is mostly adopted. A hypothesis was based on by utilizing space sequence instead of chronosequence approach that swamp meadow degrade into true meadow, and then steppe meadow, desert steppe eventually during permafrost degradation. However, the hypothesis is not scientific sufficiently due to the fact that each vegetation type existed previously and changes of vegetation type is unnecessarily resulted from permafrost degradation. In the meanwhile, the true meadow changed into “black soil land” instead of steppe meadow under the influence of climate change and human activity. So, the hypothesis maybe weakens the actual effects of permafrost degradation on grassland ecosystem. To investigate the mechanism of alpine grassland degradation in permafrost region on QTP, the long-term and located field observations and research system should be constructed, based on which predict ecosystem dynamic in permafrost degradation.

Permafrost on QTP is a huge C pools since alpine grassland soils of the Qinghai–Tibetan Plateau’s permafrost region bear a total organic carbon content of 9.3–10.7 kg C/m². Organic carbon stored in permafrost is vulnerability to change under an increasingly warmer climate. Permafrost degradation has resulted in decreasing the content of soil organic carbon in alpine meadow and alpine steppe. Climate warming could increase the active layer depth in permafrost soils and subsequently release the carbon sequestered in the upper permafrost layers. This would drastically increase soil organic matter mineralization by improving soil drainage and oxygen availability which cause positive and negative feedback to climate change. In future, study should pay extensive attention to the dynamic of greenhouse gas in permafrost region on Qinghai–Tibetan Plateau and the feedback of greenhouse gas to climate change. Grassland ecosystem in cold region has close relation with permafrost and its water–heat process. Changes in freezing and thawing process resulted from permafrost degradation influence vegetation growth environment directly through altering soil moisture and indirectly through changing nutrient availability. Quantitative study on the mechanism of water–heat transport in permafrost degradation is the theoretical premises that discuss the response of grassland ecosystem in permafrost region on QTP to global climate change. Therefore how to quantitatively analyze changes in water–heat process during permafrost degradation and its effects on plant growth; reveal the relationship between alpine grassland ecosystem degradation and changes of soil moisture and temperature during permafrost degradation and predict further the trend of dynamics change of alpine grassland ecosystem under future climate change is a great challenge in the study about the effects of permafrost degradation on alpine grassland ecosystem on QTP.

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