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REVIEW ARTICLE

Dynamics of alpine plant litter decomposition in a changing climate

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Abstract Climatic changes resulting from anthropogenic activities over the passed century are repeatedly reported to alter the functioning of pristine ecosystems worldwide, and especially those in cold biomes. Available literature on the process of plant leaf litter decomposition in the temperate Alpine zone is reviewed here, with emphasis on both direct and indirect effects of climate change phenomena on rates of litter decay. Weighing the impact of biotic and abiotic processes governing litter mass loss, it appears that an immediate intensification of decomposition rates due to temperature rise can be retarded by decreased soil moisture, insufficient snow cover insulation, and shrub expansion in the Alpine zone. This tentative conclusion, remains speculative unless empirically tested, but it has profound implications for understanding the biogeochemical cycling in the Alpine vegetation belt, and its potential role as a buffering mechanism to climate change.

Keywords Climate change · Snow · Alpine · Biogeochemistry · Plant litter · Plant growth form · Soil fauna

Introduction

Global warming and associated environmental changes are predicted to have a strong impact on high altitude ecosystems this century (IPCC 2007) and this change has been reported to be of much greater magnitude than former Holocene variability (Parry 2000). Hydrological and cryospheric systems will be affected by shifts in precipitation regimes and soil warming, thus altering snowline, soil moisture, soil disturbance regime and ultimately ecosystem distribution and function. Plant tissues will undergo various physiological changes in response to elevated CO_2 concentrations and altered temperature regimes. Overall, organisms close to the limits of their physiological tolerances may be particularly responsive to environmental change. Most vulnerable will be ecosystems lying around the snowmelt isotherm, where for every degree increase in temperature the snowline will rise by about 150 m (OECD 2007;

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Parry 2000). Furthermore, changes in precipitation regimes will influence the snowpack thickness and consequently the timing of snowmelt and duration of plant growing season. There is a growing awareness that this would lead to climatic space contraction and fragmentation of plant populations living in the alpine and nival belts, since those will be subjected to competition pressure from lower altitude vegetation, and rare and endemic species could become extinct (Grabherr et al. 1994). Nevertheless, besides by upward migration or extinction, alpine plants may respond to climatic change by persistence in the modified climate. This can be achieved by different means: long plant lifespan, gradual genetic adaptation of populations, phenotypic plasticity, or ecological buffering (Theurillat and Guisan 2001). The latter could be mediated by bio-edaphic processes, such as litter decomposition, that essentially control nutrient availability, productivity and hence the stage of ecosystem succession (Swift et al. 1979). This control may, as well, partly be indirect, through effects of surface litter amount and type on the microclimate. In this review current knowledge on the subject of litter decomposition in the temperate Alpine zone is compiled with emphasis on the direct and indirect effects of climate change on its functioning and role in those high altitude ecosystems. To this end, characteristics of the alpine physical environment are linked to biological and physicochemical processes governing plant litter decomposition and nutrient cycling. In a few instances, parallels are drawn between the Alpine and Arctic climatic zones as to enrich this text with additional experimental and observational knowledge. At last, predictions about future scenarios are evaluated based on the hierarchical importance of factors controlling litter production, quality and decomposition. There are four objectives of this review and they serve as a structuring backbone for the arguments put forth. They state that (1) biological plant litter decomposition does not exhibit a stereotyped kinetically-driven temperature sensitivity (Q_{10} coefficient) to atmospheric warming and is indeed retarded by other direct climate change effects, such as decreased soil moisture, and duration and thickness of snow cover. Furthermore, (2) indirect climate change effects, mediated through changes in plant tissues, alpine vegetation communities and soil fauna communities, can locally override the direct climatic controls. (3) Physical litter breakdown may exceed biological decay processes in unfavourable alpine habitats and potentially benefit from stochastic extreme climate events. Overall, (4) decomposition in the Alpine environment tends to be internally buffered to observed changes in the climate. Before addressing these statements, a general introduction is given to the forthcoming major climate change-induced disturbances in the temperate Alpine zone, as well as to the principles governing carbon and nutrient cycling in the soil.

The changing alpine climate

Observational climate data for the 20th century from a region with a wealth of climate station records—the Alps, provides evidence for a 1.5 K increase in average annual temperature (Beniston et al. 1997) and for a parallel increase in instances of persistent high pressure systems over the region (Beniston 2009). Worldwide meteorological data collected during the last several decades from high elevation sites conforms with this pattern, although western European mountains have been shown to exhibit the strongest change (Diaz and Bradley 1997; Diaz et al. 2003). Precipitation anomalies in the Alps show no trend in their distribution of occurrences, but nevertheless had dry conditions not been as frequent as they were, atmospheric temperatures in these mountains would have been on average 1 K cooler than observed (Beniston 2009), based on the positive feedback of dry soils (Seneviratne et al. 2006). These phenomena are complemented during the last 30 years by a consistent reduction in annual, but even more so, spring snow cover and depth over the Northern Hemisphere (Serreze et al. 2000), and locally in the Swiss Alps (Beniston 1997). A characteristic feature of the recent mountain climate is the elevation dependency of surface temperature warming, i.e. enhanced warming at higher altitudes (Beniston and Rebetez 1996; Diaz et al. 2003; Liu et al. 2009). This arises from positive feedbacks through snow albedo and cloud radiation to temperature rise, and is typically pronounced during winter and spring seasons.

In terms of predictions for the current century, a worldwide study of the main mountain systems (Nogues-Bravo et al. 2007) reveals that temperate Alpine and high latitude zones will experience the most intensive temperature rise with a rate of warming typically two to three times higher than that recorded over the 20th century. Alongside, hot spells coupled to a 30 % diminishing precipitation in Europe set for a profound increase in intensive dry periods (Beniston et al. 2007). Snow depth and duration in a projected warmer climate will further decrease in the subalpine and alpine zones (altitude range: 1000–2939 m asl) (Uhlmann et al. 2009).

The general pattern of decomposition

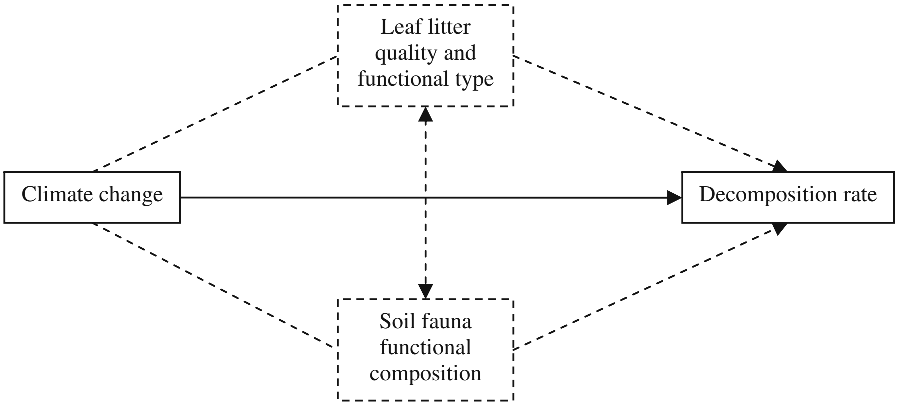
Decomposition is the breakdown of dead organic matter through the action of leaching, fragmentation and chemical reduction into CO_2 and inorganic nutrients (Chapin et al. 2002). Leaching removes soluble materials from decomposing organic matter. Fragmentation by large soil fauna (comminuters) and/or abiotic agents produces a fresh substrate for microbial colonization and a food source for smaller soil animals. Chemical alteration of dead organic matter is primarily due to the catabolic activity of bacteria and fungi, although some reactions occur spontaneously in the soil without a biotic mediation, i.e. photodegradation. Remains from the decomposition process are homogenised with the soil to form the soil organic matter (SOM) pool. Depending on the ecosystem type, SOM can form a major part of the ecosystem carbon and nutrient pools, especially in cold environments. This is due to the accumulation of undecomposed organic material in the soil, caused by certain constraints on decomposition. Three main factors control the decay rate of plant litter: the physical environment, the quantity and quality of substrate available to decomposers, and the characteristics of the soil biota community (Swift et al. 1979). To illustrate the differential importance of these factors and the extent to which they control decomposition, consider the case of disproportionate carbon pools in the Alpine—of the total ecosystem carbon, only 3–5% are found in live biomass, 2–3% in standing dead plant mass and litter, and the remaining part of >92% is contained in the SOM fraction (Körner 2003). This imbalance stems from the short leaf tissue lifespan (i.e., 1 season, or approx. 60–90 days) relative to the time it takes for the full structural decomposition of its remains. Seastedt et al. (2001) showed that the latter process may take 2 years in high alpine forbs, 5 years in sedge leaves, and 10 or more years in evergreen dwarf shrubs. Hence, on the one hand, adverse climate promotes a high retention time of organic matter in the soil, restricting the activities and the composition of the soil biota (Aerts 2006; Chapin et al. 2002). On the other hand, SOM accumulation, with specific rates dependent on the litter quality and quantity, constrains decomposition even further through soil acidification (Chapin et al. 2002). As a result, nutrient sequestration in SOM leads to a nutrient limited ecosystem, where the small contribution of biological nitrogen fixation to the annual nitrogen demand of alpine vegetation (Körner 2003) leaves plants heavily dependent on nutrient recycling. The higher the elevation, the more striking this pattern becomes with progressively lower temperatures reducing the rates of both ecosystem nitrogen accumulation and turnover. This results in decreasing amounts of total soil N and plant available N with altitude at the alpine-nival ecotone, paralleled by increasing soil pH (Huber et al. 2007).

Considering the complexity of the litter decomposition process, it is evident that observed and predicted climate change effects can operate on it at various levels. It has been postulated that the hierarchical control exerted by the main factors driving decomposition in cold biomes is in the order: climate (temperature and moisture) > plant litter quality > soil community composition (Aerts 2006), although a recent global meta-study rather prioritises the effect of litter quality over that of climate (Cornwell et al. 2008). These factors affect the decomposition process (1) directly, through changes in soil temperature and moisture that govern decomposers abundance and activity and thereby rates of litter mass loss; (2) directly, through physical (abiotic) degradation of leaf litter; (3) indirectly, through the effects of warming on plant litter quality of extant species; (4) indirectly, through warming and/or herbivory impacts on plant community structure and subsequent changes in plant litter quality; and (5) indirectly, through soil fauna community composition (Austin and Vivanco 2006; Cornelissen et al. 2007; Hobbie and Chapin 1996; Shaver et al. 2000) (see also Fig. 1).

Decomposition in the alpine climate

To properly infer the possible direction of a climate-driven change in rates of litter decomposition in the

Fig. 1 Schematic representation of direct (solid arrows) and indirect (dashed arrows) effects of climate change on plant litter decomposition rate in the Alpine



Alpine zone, the biome's characteristic environment should be considered, rather than typified as "cold". Distinct microclimate patterns, for instance, are present at high altitude, resulting from a topography-climate interaction. Snowdrift and snowmelt timing are important features of the alpine landscape, since they form vegetation patterns with distinct species community composition (Körner 2003), which in turn could spatially track their niche during long-term experimental manipulations of snowpack (Walker et al. 1999). These natural plant assemblages bear characteristic plant functional traits (Choler 2005), hence the latter possibly exert control on biogeochemistry and decomposition rates (*sensu* Cornelissen et al. 1999; Quested et al. 2007) (see also section "Species Control over Litter Decomposibility" in this text). Seastedt et al. (2001) summarised that the snowpack gradient in the alpine generates a temperature and moisture gradient that in turn controls organic matter decomposition. In their review, moisture appeared to be the strongest source of landscape variation in rates of decomposition and mineralization, seconded by temperature. Wet habitats exhibited the highest surface decay rates. Drier habitats, even though experiencing a longer snow-free season and higher surface temperatures, had a substantially lower decay rates than wet areas (see also Shaw and Harte 2001). Furthermore, since most biotic activities cease in frozen soils, decomposition remains limited to the fraction of the year when water exists in liquid phase. Oxygen limitation occurs at soil moisture levels close to or above field capacity, although this remains spatially limited to snowbeds and does not occur in the well drained alpine slopes. These characteristic responses of decomposition rates to the micro-scale climate support the concept of a curvilinear response of decomposition rates to soil moisture (Hodkinson et al. 1999) and grant only a secondary role to temperature. Furthermore, O'Lear and Seastedt (1994) provided experimental evidence for overwinter high decay rates under an intermediately thick snow cover, lower ones under an extensive snowpack, and the lowest under only a thin snow blanket. The explanation for the observed phenomenon was that while snow acted as insulation from sub-zero air temperatures, extensive snow insulated the soil from late spring heating that would otherwise stimulate decomposition. Most pronounced mass losses of the common leaf litter substrate were observed during late winter—early spring of the first year, when soil surface temperatures beneath snow approached or equalled 0°C. Similar seasonal dynamics of litter decomposition were reported by Baptist et al. (2009), who found evidence for predominant litter mass loss and high decay rates during the first winter of field incubation. This general trend was, however, not consistent across litter types, since poor quality litter decayed the most during the following summer (see also section "Species Control over Litter Decomposibility" in this text). Important mass losses over winter were reported also for "pre-treated" plant leaf litter. Hobbie and Chapin (1996) placed litter bags in the field in spring (as opposed to autumn) and after a pronounced mass loss during the first short growing season (probably due to leaching of water soluble substances), litter steadily decayed over the two following winters, but not during the next growing seasons. In another experiment, Sjögersten and Wookey (2004) looked directly at the seasonality during the second and third years of decomposition by using a standard substrate of one year old leaf litter collected from the field. Again winter decomposition was an important component of the overall mass loss.

The above studies demonstrate that what is considered as a hostile environment for plant growth seems to provide a favourable habitat for the decomposers. Despite a short growing season in the Alpine, the period for decomposition is extended under the snowpack. Early autumn snowfall, for instance, can delay and even prevent the freezing of the alpine soils, and spring soil temperatures under snow exhibit a gradual increase which peaks at the time of snowmelt (Seastedt et al. 2001). In fact, alpine soils lying under the snowpack exhibit a distinct microclimate with circum zero temperatures. It allows microscopic films of unfrozen water to form at the surface of soil particles, and thus support large and diverse cold-adapted microbial communities to proliferate, decoupled from the atmospheric climate (Ley et al. 2004). Typically, these communities exhibit high sensitivity to temperature changes, with reported Q_{10} coefficients varying by one to two magnitudes around the freezing point of the soil solution (Brooks et al. 1996; Kato et al. 2005; Mikan et al. 2002). This phenomenon could not be accounted for by the direct kinetic effect of temperature on respiration/growth rate alone, but more likely reflects a physical constraint (i.e. the availability of water in liquid phase) on biological processes (Mikan et al. 2002). Nevertheless, high microbial activity has repeatedly been reported to occur in snow-covered soils below 0°C, where addition of a labile substrate could even further stimulate it (Brooks et al. 2005). In fact, permafrost soils, at least in the Arctic, host extremophile microorganisms showing detectable catabolic activity even at −39°C (Panikov et al. 2006), although decomposition rates at such temperatures should be considered negligible. Furthermore, soil microbial biomass reaches its annual peak under snow, with fungi accounting for the majority of it (Schadt et al. 2003). Microarthropodes also remain active under the snowpack and this activity is correlated with soil surface temperatures and hence thickness of the snowpack (Addington and Seastedt 1999). Schmidt and Lipson (2004) reviewed tundra ecosystem studies to define microbial communities as winter and summer ones, each characterised by a distinct composition, substrate, and population dynamics. They found that in late autumn, plant litter fuels microbial growth, resulting in a large increase of microbial biomass under the snow pack. This winter-adapted microbial community, dominated by fungi, can grow at low temperatures (−5 to 3°C) decomposing litter and immobilizing nitrogen. During and after snowmelt there is a die-off of this winter community, due to starvation and intolerance to higher soil temperature (Lipson et al. 2000), resulting in a release of nitrogen that can be utilized by plants and the summer microbial community. The summer microbial community, characterized by fast growing bacteria, can tolerate higher temperatures (5 to 20°C) and utilizes mostly plant root exudates for growth. Such recurring temporal shifts in microbial community structure exceed spatial heterogeneity across different soil and vegetation types in the alpine tundra at a given season, suggesting a smaller role for vegetation, snow cover and nitrogen turnover (Björk et al. 2008). This yearly cycle emphasises yet again the insulating capacity of snow and the fact that winter microbiological decomposition forms a substantial part of litter mass loss.

It appears that at least in winter alpine soils, lying covered under an extensive snowpack, are resilient to atmospheric temperature changes. Furthermore, exposed dry soils cool down and warm up quickly, whereas equivalent wet soils are thermally buffered, gaining and loosing heat more slowly (Hodkinson et al. 1999). Yet another consequence of soil moisture status is that mineralization rates, but also denitrification rates, are enhanced by alternate wetting and drying of the soil through stimulated microbial activity (Hodkinson et al. 1999). Given the importance of soil moisture status on biogeochmical processes, it is plausible that altered summer precipitation patterns and especially extreme events, such as intensive droughts or floods, could shape the summer decomposition process. Indeed, decreased soil water availability as a consequence of atmospheric warming has lead to decreased rates of decomposition (Bryant et al. 1998). This evidence for moisture-limited decomposition rates has been corroborated both by natural gradient studies and experimentally in artificial warming treatments (see Aerts 2006). Hence, it is likely that even though decoposition rates intensify under warmer climate with ample availability of soil moisture (Cornelissen et al. 2007), they would be indeed retarded if moisture limitation occurs, due to its vital role for soil fauna and microbial communities.

Impacts of carbon and nitrogen fertilisation on litter decomposability

It is generally considered that the increase of atmospheric CO_2 concentrations produce a ‘nitrogen dilution effect’ in living plant tissue. Global meta-analysis pinpoints a weakened dilution effect in senesced leaf litter, and only a marginal effect on its rate of decomposition (Norby et al. 2001). Nevertheless, significant decrease in naturally-senesced leaf litter N-concentration under elevated CO_2, coupled to significantly reduced decomposition rates, has been reported for a sedge-dominated alpine grassland (Hirschel et al. 1997). In a nutrient manipulation study at a high alpine ecosystem Soudzilovskaia et al. (2007) examined a possible scenario of increased nutrient availability due to an intensified airborne deposition. The authors found that nutrient addition had a profound effect on the quality of the produced litter, with increased leaf litter nitrogen and phosphorus concentrations due to increased fresh leaf concentrations and unchanged resorption efficiency. Litter decomposability, however, was not affected via the effects of nutrient amendments on litter quality of given species, but was indeed restrained due to enhanced production and accumulation of recalcitrant graminoid litter. Their results revealed a community level negative feedback to increased nutrient availability. Furthermore, artificial warming treatments have been reported to exert idiosyncratic effects on the quality of plant litter in the Alpine, with no clear pattern of increased or decreased quality parameters across plant functional types (PFTs) (Shaw and Harte 2001). In general, the effects of warming on leaf litter decomposition rates via phenotypic responses of leaves and, thereby, litter derived from them, are small, as was shown in a recent circum-arctic-alpine study (Cornelissen et al. 2007). Based on this information, it remains questionable to what extent climate change will be paralleled by an intraspecific change in leaf litter quality in the Alpine biome and how much this would contribute to a change in decomposability. Former studies have revealed that litter quality characteristics are essential in determining decomposition rates exclusively in environments where climatic and edaphic variables are held relatively constant (Swift et al. 1979). Hence, it is conceivable that litter quality variables exert only a secondary control on litter decay rates in ecosystems characterised by particularly extreme environments, such as the Alpine. Indeed, interspecific differences in litter quality and decomposability may be substantially larger than warming-induced phenotypic responses within species (Aerts 2006). Thus, changes in species composition and structure of plant communities are prone to a considerably greater impact on ecosystem litter decomposition than phenotypic responses.

Species control over litter decomposability

Vascular plant functional types have repeatedly been shown to decompose at distinct rates, due to their specific leaf litter quality. A classification based on growth forms revealed a decreasing order of decay rates across groups: forbs > graminoids ≥ deciduous shrubs > evergreen shrubs (Cornelissen 1996). This might be especially true for high alpine vegetation where herbaceous plants’ short leaf lifespan has been shown to coincide with very low carbon investment per unit leaf area and high leaf nitrogen concentration (Körner 1989; Kudo 1996). Across-ecotone altitudinal gradient studies on decomposition of standard cellulose substrates corroborate this, providing counterintuitive information for higher annual decomposition rates at higher altitudes (Drewnik 2006; Withington and Sanford 2007). In a montane-alpine ecotone cellulose decomposition rates within a given vegetation zone decreased with altitude due to progressively lower temperatures, but nevertheless were higher in the alpine than in the subalpine (Drewnik 2006), indicating the effect of specific zonal vegetation on the nutrient availability in the soil and hence on the potential for carbon cycling. Withington and Sanford (2007) also found higher cellulose decomposition rates in their alpine plots as compared to forest and krummholz plots, but their findings were idiosyncratic with respect to spatial variation across altitudinal transects, possibly due to differences in soil moisture.

Recent global model scenarios have predicted major upward ecotonal shifts. For the Swiss Alps, an increase of 3.3 degrees in mean air temperature, corresponding to an altitudinal shift of 600 m, would reduce on average the area of alpine vegetation belt by 63 % to the benefit of lower altitude vegetation (Theurillat and Guisan 2001). Diminishing winter snow cover and earlier snowmelt will play an important role in determining the floristic composition along the snowmelt gradient. In that respect, snowbed communities may be particularly vulnerable to invasions from neighbouring plants under warmer climate (Björk and Molau 2007). Extended growing season length may stimulate opportunistic alpine flora to advance their phenology, but simultaneously pose a hazard on them through early growing season frosts (Inouye 2000, 2008). Plant physiological alterations, arising from elevated levels of CO_2 and warming, are equally so detrimental to newly formed tissues exposed to freezing temperatures (Martin et al. 2010). However, as stated in Körner's (2003) discussion about treelines, montane vegetation may not shift by more than 100–200 m upwards in response to a 1–2 degree mean annual temperature increase. This leaves open the question which plants from the treeline ecotone would be the ones to pose pressure on the alpine vegetation. Grime (1973) came up with certain criteria for competitive species in the European alpine landscapes, indicating the following beneficial features: (1) a relatively tall stature, (2) a growth form which allows extensive and intensive exploration of the environment above and below ground, (3) a high maximum potential relative growth rate and (4) a tendency to deposit a dense layer of litter on the ground surface. These plant growth form features remarkably resemble prostrate deciduous dwarf shrubs, and attributes them a keystone role in a warmer alpine climate. A trend for a shrub expansion in the alpine zone was, indeed, observed in the last 50 years, paralleled to the increase in average temperatures (Cannone et al. 2007; Sanz-Elorza et al. 2003). This has also been the case in Subarctic mountainsides over the past 20 years (Wilson and Nilsson 2009). Shrub cover increase was also recorded for subalpine meadows in response to infrared heating (Harte and Shaw 1995). A meta-analisis of results from warming experiments across the Arctic tundra also supports the notion for expansion of shrubs at the expense of other growth forms (Walker et al. 2006). This phenomenon could be ascribed to the fact that specific vegetation canopy structure determines the surface heat exchange with the atmosphere, and could play a beneficial role for certain growth forms, i.e. prostrate dwarf shrubs, in cold biomes (Körner 2003). In spring, emerging dark wood above the snow surface absorbs more radiation than the highly reflective snow, leading to a significant increase in net radiation input and ultimately to more rapid snowmelt and a prolonged plant growing season (Chapin et al. 2005; Sturm et al. 2005).

It is conceivable that such widely occurring expansion of shrub cover in the Alpine will counteract the warming-induced increase in decomposition rates, through the feedback of litter with worse quality. Experimental evidence (Shaw and Harte 2001) showed that differences in litter mass loss among litter types (PFTs: graminoids, deciduous shrubs, forbs) were much greater than the differences in litter mass loss between heating treatments. This opinion was seconded by Cornelissen et al. (2007) who showed an increase in decomposition rates resulting from warmer temperatures for a wide range of PFTs, but concluded that warming-induced shifts in plant growth-form composition might counteract this pattern. Indeed, a structural change in an alpine plant community towards a shrub dominated one has the potential to increase the storage of carbon and nitrogen in the soil. This would arise from (1) an increase in the turnover time of these elements because shrubs are long lived and allocate a large proportion of their biomass to woody perennial tissues, and from (2) a much slower decay rate of their leaf litter in comparison to the one from forbs, and somewhat slower than that from graminoids. A similar negative feedback on decomposition rates would arise from expansion of graminoids to the expense of alpine forb-dominated vegetation in response to warming (Zhang and Welker 1996), reduction in snowbed habitat area (Schob et al. 2009), or nitrogen deposition (Bowman et al. 2006; Soudzilovskaia et al. 2007). Nitrogen immobilization in recalcitrant litter with high phenolic content has been shown to contribute significantly to ecosystem nitrogen retention in the Alpine over winter and prevent dissolved organic matter (DOM) runoff during the snowmelt (Steltzer and Bowman 2005). Parallel to this process, however, experimental increase in CO_2 concentrations has lead to an increased abundance of hemiparasites in the Alpine (Hättenschwiler and Zumbrunn 2006) which in turn had the potential to transfer nutrients locked up in perennial vascular plant tissues underground into a high-quality forb litter. Consequently, hemiparasitic forbs ultimately enhance decomposition and nutrient cycling in nutrient-poor environments (Quested et al.

2005), although it is hard to estimate their quantitative significance at the ecosystem scale.

A climate-driven shift in the floristic composition of the Alpine zone has also the potential for influencing belowground processes, and litter decomposition in particular, through trophic interactions with foraging wild herbivores. Different mechanisms have been proposed for herbivores regulation of within plant species quality and quantity of organic matter and litter production, as well as for the functional composition of vegetation communities (Bardgett and Wardle 2003). On the one hand, plant species which produce high amounts of defence compounds are selectively avoided by browsing herbivores as compared to more palatable plants; hence at a community level these species are favoured and increase in cover (Bardgett et al. 1998). Considering that the litter of these plants is also highly recalcitrant, this exerts a negative feedback to the belowground system and ultimately impedes decomposition rates (Grime et al. 1996). On the other hand, intense grazing in the long term favours palatable nutrient rich species with high re-growth potential, which also stimulates their litter decomposition rates (Olofsson and Oksanen 2002; Olofsson et al. 2004). It could be speculated that the intensity of grazing pressure is essential to the plant community structure and function, and this has been corroborated by studies on the effects of steady natural increase in numbers of free browsing red deer in nature protected subalpine grasslands (Schutz et al. 2003). On a global scale, large vertebrates herbivory has been shown to regulate the frequency of a set of functional traits in plant communities (Diaz et al. 2007), but it remains hard to predict the potential trophic cascades resulting from its interactions with climate change-induced shifts in vegetation or in herbivores habitat ranges (Wookey et al. 2009).

The example provided above of prostate shrubs as a successful plant growth form in the Alpine vegetation zone, can be further elaborated with other growth forms which modify their immediate microclimate in order to withstand the harsh environmental conditions and benefit in terms of nutrient recycling. Cushion plants, cryptogams, as well as specialist forbs and graminoids accumulate “litter compost” within their dense branchwork or as standing dead tussocks and thus partly decouple themselves from the substrate, recovering essential elements from their own senesced tissues (Körner 2003). Such a litter trap life strategy seems especially beneficial in an environment characterised by extremely strong winds. It has been shown that, at least in the arctic, redistribution of plant litter by wind and snow during winter is an important mechanism of nutrient transfer across the arctic landscape. In the tundra litter transportation from exposed hills and ridges by wind and snowdrift has lead to a tenfold increase in litter biomass accumulation in areas of high deposition such as snowbed depressions, krummholz islands or dwarf shrub stands (Fahnestock et al. 2000). Possibly, there is a positive synergistic effect of allochtonous fine quality litter on decay rates of litter mixtures (Hättenschwiler et al. 2005), although recent studies demonstrate large context dependency and only minor strength of these non-additive mixing effects (Hoorens et al. 2010; Jonsson and Wardle 2008). Moreover, to date, observations in the Alpine on wind scouring surface litter from fellfields and glacier forefields are numerous, but have remained unquantified (Seastedt et al. 2001).

Relative contribution of soil biotic processes to decomposition

Soil animals influence decomposition by fragmenting and metabolizing litter, grazing on populations of bacteria and fungi surfacing the litter, and altering soil structure (Wardle 2002). Larger animals (macrofauna) often serve as ecosystem engineers and alter the resource availability by modifying the physical properties of soils and litter. Those play a central role in litter fragmentation and in mixing the organic and mineral soil layers. By doing so, they provide a fine food source for smaller soil animals as well as an increased soil aeration and water infiltration (Chapin et al. 2002). A characteristic feature of alpine soils, however, is the absence of macrofauna comminuters, such as earthworms and large arthropods (Hodkinson and Wookey 1999), although reported activity of burrowing mammals (marmots, susliks, voles, etc.) may party take up their function as modifiers of microrelief and soil properties (Semenov et al. 2001). Moreover, Schinner (1982), using a range of litter bag mesh sizes (25–1000 µm), found no effect of micro- and mesofauna on seasonal and annual decomposition rates in contrasting alpine habitats. This study provided evidence for a primary microbial decomposition, possibly facilitated through abiotic mechanical or chemical plant tissue degradation. Similarly, repelling with naphthalene of microarthropodes from decaying basidiocarp fruiting bodies during the alpine growing season had no effect in dry sites, but slowed down decomposition rates in wet habitats where, however, mass loss was attributed mainly to the feeding activity of diptera larvae which do not necessarily affect leaf litter decay (O'Lear and Seastedt 1994). The same authors demonstrated also that total microarthropod densities at the top 5 cm of soil do not follow the landscape-related patterns of plant leaf litter decomposition rates and do not differ among habitats, although the soil biota communities change with the change in habitat moisture characteristics. An interesting remark made by Seastedt et al. (2001) was that there was an autocorrelation between soil microclimate characteristics and substrate quality on the one hand, and the soil biota on the other hand. The first two predictors of decomposition were found sufficient to explain most of the variation in decomposition studies, without even acknowledging the real agents of the decay process. At a mesocosm scale, it has been shown that experimental addition of earthworms to subalpine soils greatly increases rates of litter breakdown (Seeber et al. 2006). Hence, it is conceivable that a significant increase in litter decomposition rates could be expected if temperature-driven upwards migration of large comminuters into cold-adapted soil fauna communities occurred (Aerts 2006). Nevertheless, the scarcity of available data on functional species redundancy and species' dispersal abilities (Aerts 2006) obscures how far-reaching would be the consequences of changes in soil community composition and structure for litter decomposition.

Relative contribution of physical processes to decomposition

Soil microbial communities, however, are not the only agents of plant litter decay, and abiotic degradation has often been reported for various extreme environments with poor conditions for soil organism life. Decomposition in the Alpine could, indeed, benefit from the adverse climate, and there is evidence for physical breakdown of leaf litter (Hobbie and Chapin 1996) and enhanced soil carbon and nitrogen turnover (Matzner and Borken 2008) caused by freeze-thaw events in cold biomes. Most precipitation in the Alpine is in the form of snow, which is distributed heterogeneously across the landscape by strong winds. When certain microrelief sites (such as ridges) remain primarily snow-free and thus exposed to direct atmospheric influence, soils experience large diurnal swings in temperature. These affect soils to a depth of 10 cm diurnally during the snow-free season and up to a meter during seasonal cycles, depending on the snow cover thickness (Körner 2003). Freeze-thaw events thus promote the physical breakdown of organic matter, rupturing leaf tissues while still permitting active microbial decomposition. The latter takes place because alpine microbial communities (Lipson and Monson 1998) as well as springtail and mite communities, at least in the Subarctic (Sjursen et al. 2005), are highly resistant to freeze-thaw events. Yet another soil frost event occurring during the snow-free season in the Alpine is the “needle-ice” formation. This phenomenon causes soil heaving to a depth of 30 cm, and a subsequent mixing of the soil horizons (Körner 2003). It could be assumed that such a force promotes the homogenisation of the H_0 horizon with the mineral horizon and to some extent resembles the soil regeneration process that is typically carried out by earthworms at lower altitudes.

Temperature fluctuations are not the only abiotic agent that could potentially cause organic breakdown. For example, total solar radiation has been shown to account for 60 % of leaf litter mass loss in low altitude semi-arid environments, and UV-B alone accounted for 50 % of this photodegradation (Austin and Vivanco 2006). This decay pattern may, or may not occur in the Alpine, but it is a fact that the alpine life zone is characterized by intensive solar radiation with increasing UV-B light hitting the ground surface at higher altitudes (Körner 2003). Clearly mountain ridges, which are exposed to a combined direct high solar radiation, diffuse light transmittance from thin (stratoccirius) clouds, and light reflection form adjacent snowbanks, could exhibit this ‘short-circuit’ in carbon cycling.

Conclusions

The main climate-induced disturbances in the alpine zone that will prevail under future climates are:

(1) increased air CO_2 concentration and mean atmospheric temperatures; (2) less snow cover; (3) changes in hydrology with pronounced drought episodes; and (4) increased risk of stochastic freeze events during the plant growing season (Parry 2000), however, one should bear in mind the considerable level of uncertainties associated with these climate scenarios due to the characteristic landscape-scale spatial heterogeneity in mountain regions (Barry 1992). On a plant community scale, the prevailing trend for invasion of thermophilic species into the higher Alpine is expected to continue and perhaps feedback positively to climate warming, thus posing a competitive pressure on the local flora. Consequently, since temperature affects virtually all biological processes, both direct and indirect effects are likely to have repercussions on the decomposition process as well (see Table 1 for overview). This analysis of current literature on decomposition dynamics in alpine ecosystems provides evidence that litter decay rates are substantially influenced by global warming, precipitation regimes, and nitrogen deposition and perhaps slightly by increased atmospheric CO_2 concentrations and intensive UV-B radiation. The direction and magnitude of the observed changes, however, are often hard to disentangle from one another and from the background temporal and spatial noise. With respect to the objectives of this study, the author provides arguments for (1) a substantial increase in litter decomposition rates due to atmospheric temperature rise, which is nevertheless directly retarded by other climate change effects such as reduced soil moisture availability in summer and reduced snowpack insulation efficiency in winter. Furthermore, (2) indirect climate change effects such as increased dwarf shrub abundance, but not intraspecies change in leaf litter quality, has the potential to locally counteract the warming effects on decay rates. Future soil fauna community composition is also a plausible agent of change, however, one hard to predict. (3) Physical litter breakdown may indeed provide a shortcut to carbon and nutrient cycling, but

Table 1 Directionality[a] and magnitude[b] in the response of alpine plant litter decomposition to climate change

	Direction	Magnitude	References
Direct effects			
Temperature rise	↑	strong	(Aerts 2006; Cornelissen et al. 2007; Cornwell et al. 2008; Shaw and Harte 2001)
Reduction in snow cover	↓	strong	(Baptist et al. 2009; Hobbie and Chapin 1996; Sjögersten and Wookey 2004)
Reduction in soil moisture availability	↓	strong	(Aerts 2006; Bryant et al. 1998; Shaw and Harte 2001)
CO_2 enrichment	↓	strong	(Hirschel et al. 1997)
Nutrient deposition	–	NA	(Soudzilovskaia et al. 2007)
Intensified UV-B radiation	↑	NA	(Austin and Vivanco 2006)
Intensified freeze-thaw cycles	↑	NA	(Matzner and Borken 2008)
Indirect effects			
Expansion of shrubs	↓	strong	(Aerts 2006; Cornelissen 1996; Cornelissen et al. 2007; Cornwell et al. 2008; Shaw and Harte 2001)
Expansion of graminoids	↓	strong	(Schob et al. 2009; Soudzilovskaia et al. 2007; Zhang and Welker 1996)
Expansion of hemiparasites	↑	weak	(Quested et al. 2005)
Phenotypic change in leaf chemistry	–	NA	(Cornelissen et al. 2007; Norby et al. 2001)
Herbivory	↕	weak	(Bardgett and Wardle 2003; Olofsson and Oksanen 2002)
Colonisation by soil macrofauna	↑	strong	(Aerts 2006; Seeber et al. 2006)
Extinction of soil fauna functional types	↓	strong	(O'Lear and Seastedt 1994)

[a] Arrows indicate (↑) increase, (↓) decrease, (↕) bidirectional, or (–) no change in decomposition rates

[b] Categories represent educated estimates based on the published literature. *NA* not available

Alpine-specific literature on the subject is missing to date. Provided the above aspects, one can tentatively assume that (4) plant litter decomposition in Alpine environments is internally buffered to observed and predicted changes in climate, however such conclusions can be deemed robust only when future studies emphasise on a quantitative approach which incorporates tests for both direct and indirect climate effects.

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