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Litter decomposition above the treeline in alpine regions: A mini review

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ABSTRACT

Litter decomposition is a key driver of ecosystem processes and carbon cycling. Decomposition rate is influenced by numerous factors, such as temperature, humidity, litter properties, soil properties, and properties of soil fauna/microbial communities. The aim of this review was to summarize current knowledge on litter decomposition above the treeline in alpine regions worldwide and identify: I) factors that have been studied in great detail, II) factors that have been less intensively investigated, III) geographical regions that have been less well studied, and IV) factors with consistent or inconsistent effects on decomposition. The review showed inconsistent results for all factors covered by two or more studies regarding their effect on decomposition rate (positive, negative, no effect), usually a result of interactions between factors. Studies examining one or several factors in the physical environment (i.e., altitude, experimental warming, microclimate, snow cover and soil moisture) were most common, while studies on different aspects of resource quality were the second most common. The impacts of trophic interactions on soil microbes and fauna were less frequently studied. Europe and Asia were the best-represented regions, in terms of number of studies and geographical distribution, while there were no studies from Africa and very few from South America and Australia. North American studies were all from Colorado, and those from Asia were all from China. In order to obtain better global representation, there is a need for studies in Africa, South America, and Australia. There is also a need for more studies to explain the large variation in responses of litter decomposition rates to different influencing factors in alpine environments. Future research should focus on interactions between different factors and on experiments testing specific relationships, such as the potential interaction between temperature and soil moisture and its effect on litter decomposition above the treeline in alpine regions.

1. Introduction

Litter decomposition is an important ecological process for determining nutrient cycling and ecosystem functioning (Bryant et al., 1998; Gavazov, 2010). It is mainly influenced by three important factors: resource quality (e.g. plant spp composition), the physical environment (e.g. humidity, soil structure) and soil organisms (e.g. fungus, worms) (Hartig, 1878; Krishna and Mohan, 2017; Lindquist, 1941; Swift et al., 1979; Waksman et al., 1928). During the decomposition process, organic matter is broken down through leaching, fragmentation and chemical reduction (Chapin et al., 2011) building up soil organic matter (SOM) content (Gavazov, 2010) and regulate air carbon dioxide (CO2) (Novara et al., 2015). As a result, litter decomposition is a major source for the return of organic matter and nutrients release to the soil. This process enhances soil functions, control microenvironment conditions and influence microbial communities and its growth, mainly in the litter influenced upper soil horizon (Freschet et al., 2013; Zheng et al., 2018).

In alpine regions, it is estimated that more than 90% of the total carbon pool is found in SOM, and that live biomass contains only 3–5% of total carbon (Körner, 1999). This is due to the short life span of leaves (often one season) compared with the time needed for decomposition of leaves, which may take 2–10 years, depending on plant functional group (forbs, sedges, or evergreen shrubs), with forbs decomposing faster than evergreens (Seastedt et al., 2001). In addition, the decomposition process tends to be slower in colder conditions and this can cause nutrient limitation (Aerts, 2006). Thus, both total soil nitrogen (N) and

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plant-available N decrease with altitude (Huber et al., 2007). A previous global study with data from 33 experimental warming experiments in cold biomes found that direct climate effects and plant growth forms were the main contributors to litter decomposition rate, while within-species variation made a much smaller contribution (Cornelissen et al., 2007). Climate change could therefore affect decomposition indirectly, through causing changes in species composition in plant communities (Cornelissen et al., 2007; Mori et al., 2020). Similar conclusions were reached in a meta-study on data from 336 sites using the Teabag Index (Keuskamp et al., 2013), which found that litter quality and climate were the main controlling factors for initial decomposition rate (Djukic et al., 2018). Multiple other factors can also influence decomposition. These include e.g., grazing (Sun et al., 2018), soil fauna (Lindquist, 1941; Wang et al., 2009), animal dung deposition (Liang et al., 2019), soil fertilization (Song et al., 2019; Soudzilovskaia et al., 2007), soil microbial communities (Hartig, 1878; Lipson et al., 2000; Štursová et al., 2020; Waksman et al., 1928), snow cover (Baptist et al., 2010), soil moisture (Soudzilovskaia et al., 2007) and metal concentrations in soil (Sarneel et al., 2020).

High-alpine regions (above the treeline) are sensitive to environmental changes (Alatalo et al., 2017a), so it is likely that climate change in coming decades will have an impact on alpine vegetation above the treeline (Schwager and Berg, 2019). This may have significant consequences for the decomposition process and for carbon and nutrient cycling in high-alpine regions.

In November 2019 we searched six literature databases (Web of Science, Pub Med, Science Direct, Pro-Quest, Scopus, and Google scholar), for “alpine” and “decomposition” in titles, abstracts and keywords. In addition, we checked reference lists and recent citations to find additional papers not identified by our initial search. Our selection criteria included: (i) articles published in peer-reviewed journals, and (ii) conducted above the treeline in alpine regions. The literature review was restricted to studies published in English.

The aim of this review was to summarize current knowledge on litter decomposition above the treeline in alpine regions worldwide. The focus was on broader factors that may affect litter decomposition and potential evidence of their influence on litter decomposition. In addition to study location, we analyzed the direction (positive, negative, or no effect) of responses to the factors studied and the number of studies on different factors. We grouped relevant studies into the categories “physical environment” (altitude, snow cover, soil moisture, soil pH, temperature, etc.), “resource quality” (litter quality, lignin/N content, organic content, vegetation type, etc.), and “trophic interactions” (soil fauna, microorganisms, grazing). Specific objectives of the review were to identify: I) factors affecting litter decomposition that have been studied in great detail; II) factors that have been less intensively investigated, III) geographical regions that have been less well studied, and where future studies should be conducted to verify large-scale patterns; and IV) factors for which consistent or inconsistent effects on litter decomposition are reported in different studies. The overall objective was to identify factors and regions that should be prioritized in future research.

2. Factors studied and their impact on litter decomposition

2.1. Physical environment

2.1.1. Altitude

Conflicting effects of altitude on litter decomposition have been reported (Fig. 1). Three studies have found negative effects of altitude on decomposition rate (Andreyashkina, 2008; Coûteaux et al., 2002; Schinner, 1982). Two have found positive effects (Andreyashkina and Peshkova, 2003; Wood, 1970) or different patterns (positive and no effect) of effect between two mountain ranges (Withington and Sanford,

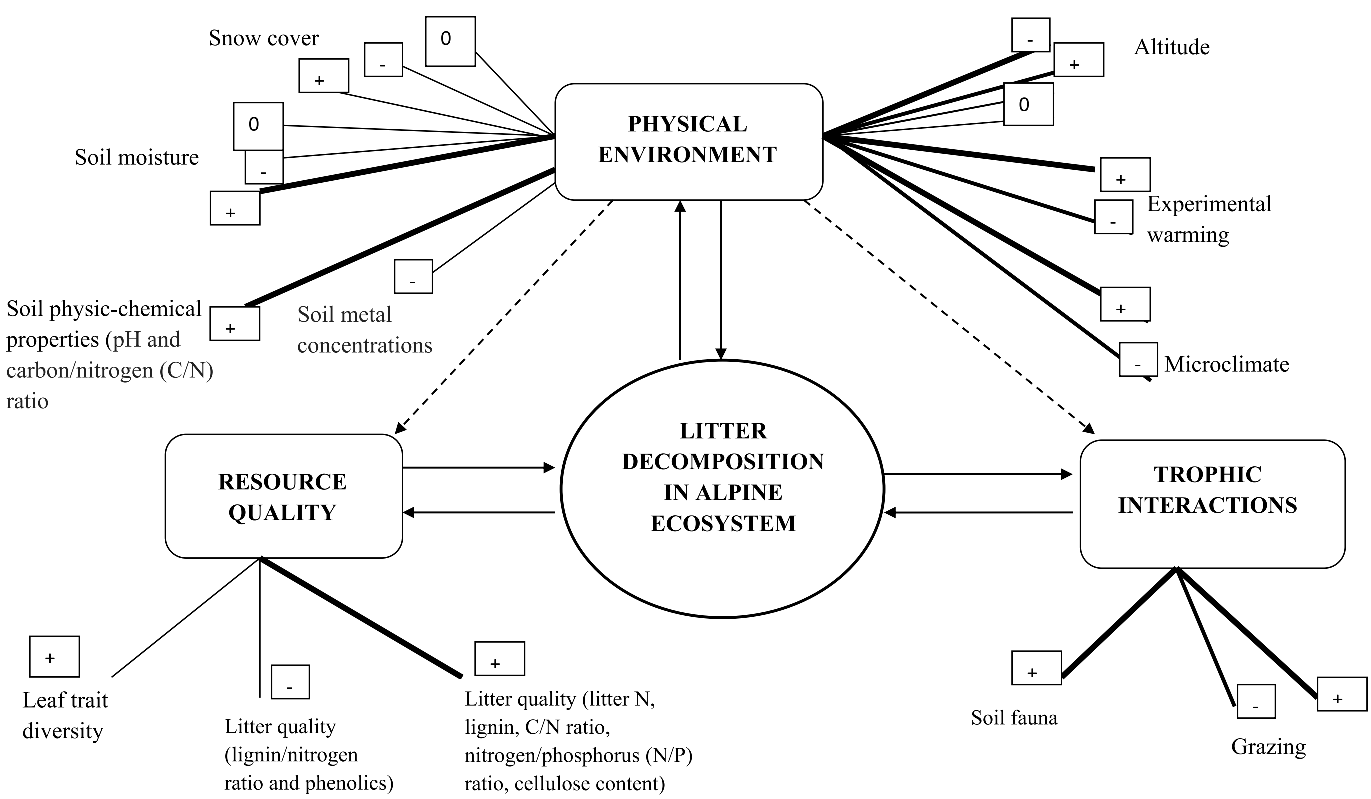

Fig. 1. Network diagram showing the linkages between litter decomposition with physical environment, resource quality and trophic interactions in alpine ecosystems. The width of the lines reflects the number of papers showing that linkage. The direction of the effect is indicated positive (+), negative (−), no relationships (0) when the result from the study is unclear. Arrows indicating direct effects and indirect effects.

2007), while one has found no effect (Duboc et al., 2012). Several indirect explanations have been suggested for the positive effects of altitude. These include increased soil moisture content (Withington and Sanford, 2007; Wood, 1970), soil organisms (Wood, 1970), better aeration, higher warming of soils, and higher proportion of herbaceous plants (Andreyashkina and Peshkova, 2003). The negative effect of altitude on decomposition has been suggested to be caused indirectly by decreasing microbial activity with altitude (Schinner, 1982), and e.g., a decrease in temperature with altitude in the tropical Andes (Coûteaux et al., 2002).

2.1.2. Experimental warming, microclimate, snow cover, and soil moisture

Experimental warming in alpine ecosystems has been found to result in positive effects on litter decomposition (Aerts, 2006; Carbognani et al., 2014; Gavazov, 2010; Luo et al., 2010; Lv et al., 2020; Sjögersten and Wookey, 2004), or negative effects (Cornelissen et al., 2007; Hong et al., 2021; Liu et al., 2021; Sarneel et al., 2020) (Fig. 1). Microclimate has also been found to have positive effects (Chen et al., 2018; Shaw and Harte, 2001) or negative effects linked to the interaction with grazing pressure, soil moisture content, and changes in vegetation structure (Vaieretti et al., 2018) (Fig. 1). Similarly, studies on snow cover have found negative (Baptist et al., 2010), positive (O'Lear and Seastedt, 1994), or no effect (Coûteaux et al., 2002; Huang et al., 2016; Zeidler et al., 2014) on litter decomposition (Fig. 1). Snow cover also affects soil moisture. Drought is reported to have a negative influence on decomposition (Schinner, 1983).

The majority of studies on soil moisture (78%, or seven out nine studies) have found a positive effect on decomposition (Bryant et al., 1998; Liu et al., 2021; Lv et al., 2020; Sarneel et al., 2020; Sjögersten and Wookey, 2004; Withington and Sanford, 2007; Wood, 1970) (Fig. 1). However, one study has reported a negative impact (Schinner, 1983) and one no effect (Coûteaux et al., 2002). The positive effect of soil moisture on litter decomposition is hypothesized to be caused by a water deficit in upper soil and litter layers in mesic/dry tundra (Sjögersten and Wookey, 2004), and large mass loss due to leaching in the early stage of decomposition (Bryant et al., 1998). In fact, it has been suggested that decomposition is primarily constrained by soil moisture and secondarily by temperature (Prescott, 2010). Thus, warming can be expected to have contrasting effects on decomposition of litter on drier and wetter alpine soils, with drier soils being more negatively affected by warming accompanied by drying of soils, while higher temperature might have a greater effect at wetter sites (Liu et al., 2021; Sarneel et al., 2020). However, the negative effect reported for both drought and excess water suggests that too much or too little water can impair the decomposition process (Schinner, 1983).

Soil physic-chemical properties (pH and carbon/nitrogen (C/N) ratio) have been found to have positive effects on litter decomposition at high-alpine sites (Duboc et al., 2012; Schinner, 1983; Sjögersten and Wookey, 2004; Wang et al., 2020) (Fig. 1). The cause for this positive relationship has been hypothesized to be due to adaptation of microbial populations to low quality litter with increasing soil C:N ratio (Duboc et al., 2012). One study found a negative effect of soil metal concentrations and moisture on decomposition rate (Sarneel et al., 2020) (Fig. 1). In another study, soil C/N ratio had a positive effect during the first year of decomposition, while soil pH was important during the second year (Duboc et al., 2012). This might have been caused by indirect effects of soil properties on microbial communities. Experimental soil acidification, lowering the pH, has been found to have a negative effect on root decomposition in Tibet, causing an increase in belowground biomass (Wang et al., 2020). In addition, other properties of the soil have been studied, e.g., it has been found that soil structural stability is increased by the presence of earthworms (Seeber et al., 2006).

The physical environment broadly influences litter decomposition in the global carbon and nutrient cycles (Murphy et al., 1998). Climate factors such as temperature, precipitation, and evapotranspiration control decomposition mechanisms to a large extent and have a significant impact on carbon and nutrient cycling (Giweta, 2020; Zhang et al., 2008; Zhou et al., 2008). Thus, an improved understanding of how physical factors control/affect decomposition processes could lead to better predictions on how global warming may affect nutrient cycling and ecosystem functioning in the future (Song et al., 2014).

2.2. Resource quality

Studies on resource quality in alpine regions report contrasting effects on litter decomposition (Fig. 1). Positive responses of litter quality, i.e., litter N, lignin, C/N ratio, nitrogen/phosphorus (N/P) ratio, cellulose content, have been found (Carbognani et al., 2014; Drewnik, 2006; Hong et al., 2021; Wang et al., 2021). Negative responses (e.g., of lignin/nitrogen ratio and phenolics) (Shaw and Harte, 2001; Steltzer and Bowman, 2005; Wang et al., 2021) and negligible effects of litter chemistry (Soudzilovskaia et al., 2007) have also been reported. Leaf trait diversity can have a positive effect (Song et al., 2019). Species and vegetation type specific litter quality parameters have been found to influence decomposition in different ways (Andreyashkina, 2008; Andreyashkina and Peshkova, 2003; Carbognani et al., 2014; Sarneel et al., 2020; Soudzilovskaia et al., 2007; Wood, 1970; Zeidler et al., 2014; Zheng et al., 2020), with forbs decomposing at a faster rate than graminoids (Soudzilovskaia et al., 2007). In a study that included four species (three *Eucalyptus* spp., one *Poa* sp.), but no chemical analysis of the plant material, it was found that *Eucalyptus* litter decomposed faster than *Poa* litter at higher altitude, where *Eucalyptus* does not naturally occur (Wood, 1970). Experimental fertilization has also been found to result in contrasting responses, e.g., in one study fertilization significantly increased N and P concentrations in plant litter, but had no effect on decomposition (Soudzilovskaia et al., 2007). Similarly, no effect of fertilization was found in a study in the Rocky Mountains, Colorado (Bryant et al., 1998). However, a study in Switzerland found that soil fertilization increased decomposition rate (Arnone and Hirschel, 1997). A study in Tibet found that dung deposition had a positive effect on litter decomposition (Liang et al., 2019). In general, higher N and P concentrations are believed to have a positive effect on decomposition (Cornwell et al., 2008). However, it has also been suggested that other traits, such as toughness, lignin concentration, or cellulose concentration, might be of greater importance for decomposability than high N or P concentrations in litter (Soudzilovskaia et al., 2007).

Decomposition is strongly influenced by the physical environment, but litter quality aspects such as nitrogen, lignin, polyphenol, C/N ratio, and lignin/nitrogen ratio can also play an important role in influencing the decomposition process (Giweta, 2020; Krishna and Mohan, 2017; Zheng et al., 2020). Decomposing plant material passes through three different stages, i.e., nutrient release, net immobilization, and net release (Wang et al., 2021), which control the functioning of the forest ecosystem (Zhou et al., 2008). Thus, litter quality can serve as a predictor of decay rate and is an important component of the biogeochemical cycle (Giweta, 2020).

2.3. Trophic interactions

Studies on the effect of trophic interactions on decomposition have also reported conflicting results (Fig. 1). Most studies have found that soil fauna have a positive effect on decomposition (Kitz et al., 2015; Ma et al., 2019; O'Lear and Seastedt, 1994; Wang et al., 2018). One study found contrasting results for different species of macro-decomposers, with primary decomposers increasing decomposition and secondary composers having no or negative effects (Seeber et al., 2006). Contrary to expectations, that study also found that decomposers preferred to feed on low-quality litter with high lignin and tannin content (Seeber et al., 2006). Grazing has been found to have both positive (Luo et al., 2010; Sun et al., 2018) and negative (Vaieretti et al., 2018) effects on litter decomposition on alpine soils. The negative effect is reported to be caused by grazing interacting with vegetation, microclimate, and soil moisture, with reduced grazing leading to taller vegetation, higher soil moisture content, and ultimately increased decomposition rates (Vaieretti et al., 2018).

Trophic interactions are crucial for decomposition processes in many ecosystems. Soil fauna in particular increase plant litter decomposition in ecosystems, but their distribution varies with climate conditions and habitats (Phillips et al., 2019). Furthermore, the results on earthworm global distribution tend to differ from what is normally found for aboveground taxa, suggesting that aboveground and belowground biodiversity may not follow the same broad distribution pattern (Phillips et al., 2019). Macrofauna, such as millipedes and earthworms, frequently act as detritivores, while soil microarthropods, such as collembolans and oribatid mites, impact litter decomposition by modifying the activity and composition of saprotrophic fungal communities (Schaefer et al., 2009; Zhou et al., 2020). How climate change will affect alpine soil fauna, and their contribution to alpine decomposition, is still unclear, as there are still only a few experimental climate change studies on soil fauna in alpine regions (Alatalo et al., 2015, 2017b; Høgvar and Klanderud, 2009; Roos et al., 2020).

2.4. Geographical distribution of studies

Regarding the geographical distribution of published studies on litter decomposition above the treeline included in this review, we found that the majority of the studies were carried out in Europe and Asia (Austria, Norway, Sweden, Italy, France, Russia, Switzerland, and China), and five studies were performed in North America (all USA) (Fig. 2). Two were from South America (Argentina and Venezuela) and one from Australia. The three global studies included compiled data from 18 sites with Arctic and Alpine climate change experiments. Of these, one study included data from 10 sites in Canada, China, Finland, Italy, Japan, Norway, Russia, Sweden, and USA (Cornelissen et al., 2007) and one included data from climate change experiments at one alpine site in the USA and three alpine tundra sites in Norway and Sweden (Aerts, 2006). The third meta-study was a conventional review paper on the potential impact of climate change on alpine plant litter decomposition (Gavazov, 2010). While it is likely that we overlooked some studies, it is unlikely that this would affect the general geographical pattern observed to any great degree.

3. Conclusions

This review showed that factors relating to the physical environment and resource quality have been the main focus in the majority of published studies on litter decomposition above the treeline in alpine areas, while the potential impacts of trophic interactions have received less attention. The review also revealed a severe lack of studies from Africa and South America. Surprisingly, all studies from North America were from Colorado, while all studies from Asia were from China. There is thus a need for studies in Africa and South America, and also in other regions of North America and Asia, to provide data across broader scales. Overall, Europe was well represented in terms of number of studies and different alpine regions. However, more recent studies have mainly originated from China. A noteworthy finding was that factors (altitude, experimental warming, litter quality, soil organisms, soil physic-chemical properties) covered by more than one study all showed inconsistent results regarding their effect on decomposition. Thus, there is a need for further studies on how different factors interact/influence the litter decomposition process at high-alpine sites. Future research should focus on interactions between different factors and conduct experiments to examine specific relationships, such as potential interactions between temperature and soil moisture and the effect on litter decomposition on soils with different moisture levels. There is also a need to evaluate the impact of trophic interactions between organisms and decomposition processes.

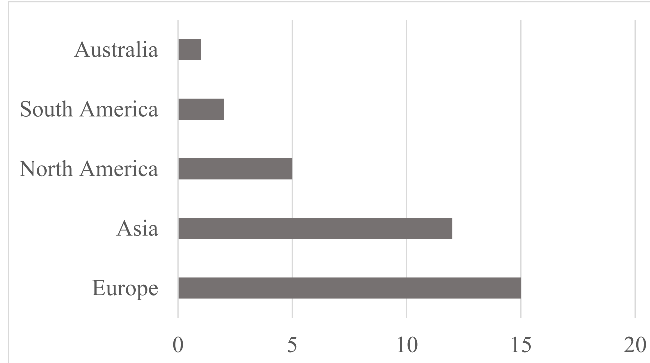

Fig. 2. Geographical distribution of studies on plant litter decomposition in alpine regions above treeline.

Author contributions

JMA conceived the study, MR and JMA conducted the literature review, MR and JMA were the main authors of the paper, AKJ and YB commented on the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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