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Transport and decomposition of allochthonous litter in Icelandic headwater streams:

Effects of forest cover

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Hér með lýsi ég því yfir að ég samdi þessa ritgerð og vann að gagnasöfnun og úrvinnslu gagna sjálf með aðstoð leiðbeinenda. Ritgerðin hefur hvorki að hluta til né í heild sinni verið lögð fram áður til hærri prófgráðu.

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Abstract

The present study was a part of a larger research project entitled ForStreams. Changes in catchment vegetation can have large impacts on stream ecosystems, especially through transport of terrestrial organic matter into them. The objectives of the present study were to compare non-forested and forested catchments in Iceland in terms of litter transport into streams and litter decomposition within them. This was the first study made in Iceland on the terrestrial-aquatic interactions in forested ecosystems.

The main study consisted of nine run-off fed headwater streams in Fljótsdalshérað in eastern Iceland (N 65°01'–N 65°10' and W 14°28'–W 14°48'). The streams either ran through treeless heathlands, birch forests (*Betula pubescens* Ehrh.) or conifer plantations (mainly *Larix sibirica* Ledeb.). The transport of terrestrial organic matter was measured with litter traps inserted into the stream banks. Decomposition of litter was measured with the litter bag method, using fine and coarse mesh litter bags to evaluate the effects on microorganism and invertebrate activity in the decomposition processes. The invertebrate fauna found within the coarse bags was also studied.

Litter transport into the birch and conifer forest streams was 30–33 times higher than into the heathland streams. Hence, the litter transport increased the amount of energy available in the forest streams. Decomposition rate of birch leaves, larch needles and grass litter was 0.0033, 0.0040 and 0.0044 g g⁻¹ DM day⁻¹, respectively. This was low compared to measured decomposition rates in comparable studies elsewhere. Grass litter had the fastest decomposition rate in the forested streams, whereas there was no difference in decomposition rate of different litter types in the heathland streams. The decomposition rate was positively correlated with the concentration of phosphorous in the water across all catchment types. It was also negatively correlated with the number of Plecoptera (shredders) found in the litter bags. This could indicate a different feeding activity of the group in Iceland and needs to be studied further.

The number of taxonomic groups found in the litter bags was higher in birch than in conifer forest streams. There was no difference in the number of invertebrates found in the litter bags in different catchment types; on average 247 individuals per litter bag. The largest functional feeding groups in the litter bags were gathering collectors (44–57%) and scraping collectors (36–43%), but shredders were only 3–4% of the total number. There was no difference in the decomposition rate of litter within fine and coarse mesh bags, which was probably linked to lack of shredders in the streams. This indicated that invertebrates did not play a significant role in the decomposition process in the run-off streams, which is different from what has generally been found in forest streams elsewhere.

An additional study was done on eight spring-fed headwater streams located near Mt. Hekla in southern Iceland (N 63°57'–N 64°00' and W 19°53'–W 19°59'). There the streams ran either through birch forests or sparsely-vegetated eroded areas. There the decomposition rate of birch litter was higher in the coarse mesh litter bags than in the run-off fed streams in eastern Iceland. This shows how important it is to include different stream types when terrestrial-aquatic interactions are studied. In southern Iceland, the decomposition rate was also higher in the coarse mesh bags than in the fine mesh bags, which indicated a more important role of invertebrates in the decomposition process in the spring-fed streams. The decomposition rate in fine mesh bags did, however, not differ between southern and eastern Iceland which indicated that microbial decomposition was similar in the two stream types.

Ágrip (Icelandic Abstract)

[Flutningur og niðurbrot lífræns efnis í lækjum á skóglausum og skógi klæddum vatnasviðum]

Verulegar breytingar hafa orðið á gróðri á Íslandi á sögulegum tíma og svo á síðustu áratugum með aukinni landgræðslu og skógrækt. Í þessari rannsókn voru áhrif landrænna gróðurfars-breytinga á vistkerfi straumvatna skoðuð og leitað svara við því hvaða áhrif endurheimt birkiskóga og skógrækt með barrtrjám hefur á flutning lífræns efnis í lækjum og á niðurbrot efnisins í þeim. Þessi rannsókn var hluti af verkefninu SkógVatn, sem er fyrsta rannsóknin á Íslandi á tengslum skóga og straumvatns.

Meginhluti rannsóknarinnar var gerður á níu vatnasviðum með dragalækjum á Austurlandi (Fljótshálfhéraði) þar sem valin voru þrjú skóglaus vatnasvið með rýru mólendi, þrjú vaxin birkiskógum og þrjú vaxin miðaldra barrskógum. Flutningur sinu, laufs og barrs út í lækina var mældur með laufgildrum sem grafnar voru niður í lækjarkakkana. Hraði niðurbrots í lækjunum var metinn með finum og grófum niðurbrotspokum. Mismunandi möskvastærðir pokanna gerðu kleift að greina mikilvægi örvera og hryggleysingja við niðurbrotið. Fjöldi og samsetning hryggleysingja sem fundust í grófum pokum var ákvarðaður með talningu og greiningu í hópum undir víðsjá.

Um 30–33 sinnum meira magn lífræns efnis barst út í lækjum sem runnu um birkiskóga ($36,4 \text{ g m}^{-1}$) og barrskóga ($40,2 \text{ g m}^{-1}$) miðað við lækjum sem runnu um mólendi ($1,2 \text{ g m}^{-1}$). Niðurbrotshraði birkilaufs, lerkinála og sinu var $0.0033\text{--}0.0044 \text{ g}$ á hvert g þurrvigtar á dag. Almenn var þetta hægur niðurbrotshraði miðað við það sem fundist hefur í löndum sem við getum borið okkur saman við. Enginn munur var á niðurbrotshraða laufs, barrs eða sinu í finum og grófum niðurbrotspokum sem bendir til þess að niðurbrot í dragalækjum sé nánast eingöngu knúið áfram af örverum, ekki smádyrum eins og þekkist í öðrum löndum. Jákvætt samband var á milli niðurbrotshraða og magns fosförs (P) í vatni allra lækjanna á Austurlandi. Neikvætt samband fannst hinsvegar við fjölda steinflugnagryða (Plecoptera) sem teljast til tættara (þ.e. lífvera sem nærast beint á dauðu lífrænu efni). Þetta kom á óvart þar sem vel er þekkt að tættarar auka almennt niðurbrotshraða og væri því ástæða til frekari rannsókna á fæðuvejum steinflugna. Ekki var munur á fjölda smádyra sem fundust í grófum niðurbrotspokum í dragalækjum mismunandi gróðurlenda, en marktækt fleiri tegundahópar smádyra voru í birkiskógarlækjum en í barrskógarlækjum. Stærstur hluti smádyranna í niðurbrotspokunum tilheyrði síurum (36–43%) eða skröpurum (44–57%), en aðeins 3–4% tilheyrðu hópum tættara.

Önnur rannsókn var gerð á átta vatnasviðum lindarlækja á Suðurlandi, í nágrenni Heklu. Fjögur þeirra voru vaxin birkiskógi en fjögur voru skóglausir, uppblásnir melar. Þar var niðurbrotshraði í grófum pokum marktækt hærri en á Austurlandi. Hins vegar var hraði örveruknúins niðurbrots ekki marktækt frábrugðinn milli landshluta. Smádyr virðast því þjóna mikilvægu hlutverki í niðurbroti lífræns efnis í lindarlækjum á Suðurlandi og þau því á þann hátt líkari lækjavistkerfum nágrannalandanna.

Rannsóknin sýndi fram á ýmsa þætti í niðurbrotsferli lífræns efnis í íslenskum skógarlækjum sem voru frábrugðnir því sem fundist hefur í öðrum löndum. Þær óvæntu niðurstöður sýna hversu varasamt það er að heimfæra erlendar niðurstöður beint upp á íslensk vistkerfi án frekari rannsókna. Það er því mikilvægt að rannsaka frekar hvernig breytingar á landnotkun, s.s. skógrækt, hefur áhrif á lífríki og efnafræði straumvatna.

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1. Introduction

Vegetation cover has decreased in Iceland through the centuries and more recently there has been a relatively large effort on reclaiming lost vegetation. These schemes in re-establishing vegetation have also led to an extensive research on their environmental effects (Ágústsdóttir, 2004; Elmarsdóttir & Magnusson, 2005; Eyjólfsdóttir, 2005; Jónsson et al., 2006). It is important to gather knowledge about how changes in land-use affect the existing ecosystems. An important question related to this is how large-scale changes in vegetation cover and composition may affect aquatic ecosystems.

The effects of large-scale changes in vegetation cover within whole catchment areas on the aquatic production, the biodiversity and the biogeochemistry has not been much studied in Iceland. In autumn 2007, an interdisciplinary research project, FORSTREAMS (SKÓGVATN; www.forstreams.is), was launched with the main goal to study if large-scale changes in vegetation cover and ecosystem productivity may affect water quality and aquatic ecosystems. The project was collaboration between Agricultural University of Iceland, University of Iceland, Institute of Freshwater Fisheries, Iceland Forest Service, Soil Conservation Service of Iceland, the regional afforestation project Hekluslógar and Icelandic Food Research.

The part of the FORSTREAMS research project that is presented in this thesis, as a MSc project, aimed to answer questions related to terrestrial litter transport to first-order streams and its decomposition processes within the streams.

1.1. Historic changes in vegetation cover in Iceland

The fact that Iceland is an island in the North Atlantic Ocean, just south of the Arctic Circle and in a fair distance from other landmasses, results in a limited migration and colonization of species to the country (Bradshaw, 1995; Ministry for the Environment and the Icelandic Institute of Natural History, 2001; Steindórrson, 1964). Pollen analysis has shown that most of the present terrestrial flora has colonised the island during last 10 thousand years (Hallsdóttir, 1995), after the last major deglaciation. The vegetation that could become established in Iceland was probably affected by colonization abilities and climatic conditions (Hallsdóttir, 1995; Wöll, 2008). The Gulf stream reaches the SW-S coast of

Iceland and therefore the mean annual temperature is higher than might be expected at this latitude (Einarsson, 1976). The winters are relatively mild and the summers are generally cool. The climate in Iceland is mostly maritime where the lowlands are cold-temperate but the highlands are considered low arctic (Einarsson, 1976). A typical vegetation for cold-temperate areas (the Boreal Zone) in Scandinavia are coniferous forests (Taiga), but low-arctic areas are generally covered by downy birch (*Betula pubescens* Ehrh.) woodlands or treeless heath or wetland vegetation (Aas & Faarlund, 2001). Since the main part of the Icelandic lowlands (below 400 m a.s.l.) have an average July temperature above 10°C and mean January temperature around 0°C (Einarsson, 1976), Iceland should belong to the Boreal Zone according to Köppen's climate classification (Köppen, 1931). However, since the only native conifer species is the common juniper (*Juniperus communis* L.) Iceland is rarely included within that zone but defined as sub-arctic (Sigurgeirsson & Kristjánsdóttir, 1995) or arctic (The Times Atlas of the World, 1986).

The international definition of a forest has a minimum height of 5m (FAO, 2005). However, the Icelandic definition of a birch forest is based on a mean tree-height of 2m and areas with tree-height <2m are termed woodlands (Sigurðsson, 2002). Downy birch woodlands and forests became the dominant terrestrial vegetation at lower altitudes after ca. 8,000 BP, while higher altitudes were probably to large extent treeless heaths (Hallsdóttir, 1995). This is different from what prevailed in Scandinavia, where conifer trees were dominating. In Scandinavia the downy birch trees cannot compete with the taller conifers in the lowlands, but they can grow at higher altitudes and latitudes than the conifers (Wöll, 2008). Therefore the downy birch forms continuous forests above the conifer tree-line in the Scandinavian alps (Aas & Faarlund, 2001).

Vegetation changes following settlement

When the Nordic settlers colonised Iceland in the late 8th century, they found a country covered with birch woodlands and forests from mountains to seashore, as described in the Landnáma saga which was written in the 11th century (Hið íslenska bókmenntafélag, 1968). Recent studies of birch pollen in sediments from these times (Hallsdóttir, 1995), by modelling the climate thresholds for the present downy birch treelines (Wöll, 2008), and sites protected from livestock grazing by natural barriers (Þorgeirsson, 1982), have shown that this statement is generally correct. On the other hand scholars do not agree on how

much of Iceland was covered by woodlands. Recent estimations range from 8% (Ólafsdóttir et al., 2001) to 40% (Bjarnason, 1974). However, it is generally believed that about 25–40% was covered with downy birch in the 9th century (Arnalds, 1992; Hallsdóttir, 1995; Kristinsson, 1995). In a recent study, which was based on detailed modelling of climate thresholds for existing downy birch in Iceland it was revealed that the climate condition at ca. 40% of Iceland's surface area could have maintained downy birch forests and woodlands of low stature and ca. 25% could have sustained birch taller than 2 m (Wöll, 2008). It is therefore a general consensus that vegetation cover of Iceland has changed much during the past 1100 years.

Soon after the humans settled in Iceland, a severe deforestation began (Hallsdóttir, 1995). Today downy birch covers only 1.2% of the total surface area of Iceland (Traustason & Snorrason, 2008). Large-scale soil erosion and loss of vegetation cover followed the deforestation and these changes are believed to have occurred due to many combined factors, e.g. overgrazing, land-clearing for agricultural use and wood cut for house heating and charcoal making (Arnalds, 1987). Ólafsdóttir and coworkers (2001) suggested that the forests and woodlands were already decreasing at the time of settlement due to cooling climate, and the deforestation was only reinforced by arrival of humans. However, they suggest that if only climatic variation was the main explanation for change in vegetation cover, then the cover should be about twice more than it is today.

Soil conservation and afforestation

Land degradation and soil erosion are common problems in Iceland (Aradóttir & Arnalds, 2001; Arnalds et al., 1987). The total historical degradation is considered about 40,000km² since settlement, or ca. 40% of Iceland's total surface area (Þorsteinsson, 1978). Such large-scale changes have, without a doubt, affected the biological diversity and possibly caused extinction of many species through loss of their habitats (Aradóttir, 2008). Organized soil conservation, revegetation and afforestation have been practiced by the Icelandic authorities and the public for past century. This action has stopped and reversed erosion in many of the most severely affected areas (Ministry for the Environment and the Icelandic Institute of Natural History, 2001).

Considering the afforestation, two most planted tree species are the native downy birch and the exotic conifer, Siberian larch (*Larix sibirica* Ledeb.). Together these two tree species account for about half of the total amount of trees planted annually in Iceland at present, or 22% and 24%, respectively (Gunnarsson, 2006). The long-term official goal of state-supported afforestation schemes in Iceland is to cover 5% of land below 400m elevation before 2040 (Stjórnarráð Íslands, 2007). The total cover of forests and woodlands today is 1.5% of the total land surface and 3.6% of land below 400 m a.s.l. (Traustason & Snorrason, 2008). In total afforested and revegetated areas in Iceland between 1990–1999 was about 36,400ha (Sigurdsson & Snorrason, 2000). Such large-scale schemes to re-establish different vegetation types is bound to fundamentally change the ecosystem structure and function, which is of course their main goal.

1.2. Effects of vegetation change on stream ecosystems

When considering the possible impact from a change of land use on streams, it is usually assumed that those changes mainly affect the structure of stream ecosystems but they can also impact the stream ecosystem functions, such as leaf litter processing which is frequently neglected in this context (Paul et al., 2006). Freshwater ecosystems are an important resource for living organisms and a vital link for wetland and terrestrial ecosystem functioning. Therefore it is important to know which abiotic and biotic factors are affected in the streams following land use change like afforestation and soil conservation. This is for instance important to retain biological diversity as well as the protection of the water quality itself. An increased emphasis has been on implementing conservation and restoration programmes in Europe which focuses on retaining and improving the ecological health of running waters (e.g. European Rivers Network, European Water Association, Freshwater Biological Association). The European Water Framework Directive (EWFD; Steyaert & Ollivier, 2007) focuses on the ecological status of freshwaters with the main objectives to prevent further deterioration and increase its ecological condition. The EWFD will probably be integrated into the Icelandic legislation later this year (in 2010).

Changes in land use

Alterations in land use can affect aquatic ecosystems for many years after land use change occurred (Goodale & Aber, 2001). All changes that occur within catchment areas, such as changes in vegetation composition or cover, usually affect stream ecosystems and may change the faunal assemblages (Kedzierski & Smock, 2001) or productivity (Quinn et al., 1997). Most of the studies carried out on the change of leaf decomposition in relation to changes in land use, have focused on the urbanisation, forest clear cutting or change towards agriculture (Bird & Kaushik, 1992).

It has been shown that forest clear-cutting can affect the stream ecosystem in many ways. As consequences, reduced woody debris in the streams, increased sediment input and decreased shading on the streams may cause major changes for the stream community (Kedzierski & Smock, 2001). Benfield and others (1991) detected an increased litter decomposition rate in streams running through logged catchments and explained it with elevated nitrogen concentrations, seasonal temperature fluctuations, or the abundance of shredders among benthic stream invertebrates. Leaf breakdown has also been found to decrease in the streams where catchments have been logged, which was connected to sediment accumulation which partly buried the leaf litter (Webster & Waide, 1982). However, one year after the logging the decomposition within the streams was faster than it had been before the logging. The temperature and nutrient levels were higher after logging but Webster and Waide (1982) suggested that the increase in decomposition rate resulted from a lack of alternative food sources for the shredders in the stream. Another study focused on the difference in decomposition between an undisturbed hardwood catchment and a hardwood catchment subjected to an insect outbreak (Meyer & Johnson, 1983). There the decomposition rate was higher within the disturbed catchment, resulting from the elevated concentration of nitrogen in the stream water (Meyer & Johnson, 1983). Many studies have been made on the effect of deforestation on the decomposition processes in streams (Benfield et al., 1991; Cummins, 1979; Rounick & Winterbourn, 1983; Tuchman & King, 1993). It is suggested that the action of deforestation can lead to a lack of shredders within the streams due to a shortage of their prime food source (Dance & Hynes, 1980). This can lead to a great change within the food-web and ecosystem structure.

Effects of afforestation

Afforestation within a catchment area does not only reverse the process of deforestation, e.g. by increasing litter transport to streams, trees casting a shade on stream channels or a decrease of in-stream primary production. Afforestation could also decrease river flows and clog fish spawning areas (gravel) as well as lowering the pH of the water (Moss, 1998). Only few studies have been made focusing on the effect of afforestation on litter decomposition. A study was made by Abelho and Graça (1996) in Portugal to find out if afforestation by *Eucalyptus globules* (Labill.) affected the litter dynamics in streams and the structure of invertebrate communities within the streams. They found that the decomposition rates were higher in the streams running through a non-*Eucalyptus* forest and that the invertebrate communities were significantly different. A follow-up study, made by Pozo and others (1998), aimed to see if it was possible to reduce the negative effects of the afforestation with *E. globulus* on the leaf decomposition rate. They found that the presence of *E. globulus* had negative effects on the decomposition rate, but that this negative impact could be reduced with an addition of dissolved nutrients.

The role of litter in stream ecosystems

The River Continuum Concept (RCC) is a framework to describe the function and structure of a stream ecosystem (Vannote et al., 1980). According to the concept, shredders are important in low order forested streams due to the fact that their in-stream primary production is often low due to shading. In such streams, the allochthonous energy, usually as leaf litter, is an important energy input to the stream food chain. The coarse particulate organic matter (CPOM) is used and parts of it converted to fine particulate organic matter (FPOM) which floats downstream and is used in higher order streams. This suggests that shredders are most likely to be abundant in low order forest streams but collectors are likely become more prevalent group further downstream although they may also occur upstream.

The RCC has had much support and most stream systems seem to fit into this concept. However, Winterbourn and others (1981) showed that streams in New Zealand do not seem to fit the RCC. New Zealand is similar to Iceland in the way that it has diverse landscape with a low timber line and short river continua compared to the rivers studied by e.g. Vannote and co-workers (1980). Within the streams in New Zealand, representation of functional feeding groups did not seem to change downstream, and in general, shredders are

poorly represented in streams or even absent from the forested headwater streams (Winterbourn et al., 1981). The lack of CPOM in these streams may explain a low abundance of shredders and they point out that many New Zealand stream invertebrates are opportunists (Winterbourn et al., 1985).

A sudden or gradual decline in vegetation within catchments which could be due to over grazing or climate change can lead to changes in stream morphology and stream temperature regimes. Such changes in the habitat can easily affect the stream biota, such as invertebrates and fish (Moss, 1998). Deforestation can also affect the temperature regime of streams due to decrease in shading. A removal or decline of woody debris from a stream may alter the stream current and retention of litter and other organic material floating downstream, which means that nutrients may become lost to the stream ecosystem (Gurnell et al., 1995). The nutrients that are released during the decomposition process may be used by organisms within the stream ecosystem. The litter/shredder system is therefore an important part of the food-webs of streams (Gurnell et al., 1995; Moss, 1998). When vegetation cover increases, as in the present study, it could be assumed that these published negative changes of deforestation could be reversed.

1.3. Transport and decomposition of leaf litter in stream ecosystems

Litter fall from catchment vegetation is the main part of the allochthonous organic matter which can be used as an energy source for the aquatic food web (e.g. Giller & Malmqvist, 1998). Litter may consist of leaves, needles, bark, wood, floral parts and fruits from the catchment vegetation. In temperate deciduous forests, the main amount of litter fall occurs in the autumn or between 70 and 80% (Abelho & Graça, 1998), but the lateral transport of litter continues all year round (Benfield, 1997). The litter may reach the streams by vertical litter fall or lateral transport by wind or sliding down the stream banks (Benfield, 1997). In temperate deciduous forests, 73% of annual litter input transports in the autumn (Abelho & Graça, 1998). The litter fall inputs to streams do not only depend on the amount of litter produced in the adjacent canopy but also physical attributes of the streams, such as stream order but usually the litter input is higher as the stream order is lower (Benfield, 1997). Since the streams used in this study were all headwater streams (order 1–3), it was expected

that the amount would be similar to what has been found in other countries in similar latitude.

Like all ecosystems, streams are dependent on a continual input of energy to be able to function. This energy can be obtained from autochthonous pathways i.e. solar radiation for primary production of in-stream vegetation or algae, or by allochthonous pathways, i.e. organic material that is produced in terrestrial ecosystems and transported to the streams (Giller & Malmqvist, 1998). The organic material is usually in the form of nonliving organic carbon such as leaves, fruits, twigs or logs, referred to as CPOM, which is defined as organic matter larger than 1 mm in size (Cushing & Allan, 2001). The organic matter is chemically very different from living matter since plants absorb reusable substances, prior to defoliation, and what is left is largely cellulose and lignin (Moss, 1998). Autumn shed leaves, of terrestrial origin, are the major energy input for many forested, low order streams (Allan & Castillo, 2007).

The allochthonous leaf decomposition is very important for the stream ecosystem function, especially in forested streams (Kaushik & Hynes, 1971; Petersen & Cummins, 1974). When a leaf enters a stream, two things can happen, it can be transported down the stream or it can be broken down by a combination of chemical, physical and biological processes within the stream (Webster et al., 1999). The energy that is available to the stream organisms is the proportion of how much organic material remains in the stream systems and how fast it decomposes within the streams (e.g. Minshall et al., 1983). Leaf decomposition can also be used to measure the ecosystems responses to disturbance (e.g. Irons et al., 1994) or a stream integrity (e.g. Bergfur et al., 2007a).

Abiotic factors

Chemical leaching occurs as soon as a leaf enters a stream and gets wet. Then soluble chemicals are dissolved and leak from the leaf. The speed of leaching depends on the leaf type i.e. conifers are generally leached more slowly than the leaves of deciduous trees (Moss, 1988). Leaching can account for up to 30% of the initial weight loss from most leaf types, within a few days of the leaf exposure to water (Petersen & Cummins, 1974).

Various physical- and chemical factors, such as temperature, nutrient concentration, pH and hydrological fluctuations may affect the decomposition in different ways. Litter decomposition can occur with temperature down to zero (Short et al., 1980) since fungal and microbial respiration have been demonstrated at that temperature but decomposition rates are generally much faster in warm waters since bacterial and fungal production increases exponentially with temperature (Suberkropp & Weyers, 1996). Low pH also seems to slow down the decomposition process by inhibiting microbial and invertebrate growth and activity (Dangles et al., 2004; Hall et al., 1980; Winterbourn & Collier, 1987) and therefore slows down the decomposition process in an indirect way (Webster & Benfield, 1986). A supply of nitrate and phosphate is often limited in natural ecosystem but increased amount of these nutrients is thought to increase the decomposition rate (Rosset et al., 1982; Royer & Minshall, 2001; Sedell et al., 1975) when micro-organisms are nutrient limited (Royer & Minshall, 2001).

Biotic factors

Biological processes include decomposition of the litter by organisms such as fungi, bacteria and invertebrates. Studies have shown that invertebrates often only use litter as food source after it has been processed or colonised by microorganisms (Webster et al., 1999). Bacteria and fungi usually colonize litter shortly after it enters the stream. Experiments have shown that fungi seem to be more important in the decomposition processes than bacteria (Kaushik & Hynes, 1971). Fungi seem to dominate an early colonization of leaves but are gradually replaced by bacteria as the decomposition goes on (Webster & Benfield, 1986). Leaves only provide a small part of the nitrogen and phosphorus which the fungi needs so it has to obtain those nutrients from the water instead (Moss, 1998), which makes the nutrient concentration in the water quite important in the decomposition process. The microorganisms make the leaves more nutritious and soft for the shredding invertebrates. However, although bacteria and fungi can degrade the litter on their own, the presence of shredding invertebrates is known to speed up the process by at least 20–40% (Petersen & Cummins, 1974). Some studies have shown that the main factor in the litter decomposition process are the microorganisms and physical fragmentation but invertebrates play only a minimal role (Leff & McArthur, 1989; Stockley et al., 1998). Increased decomposition rate has, in several studies, been associated with fungal biomass (Ferreira et al., 2006; Gessner & Chauvet, 2002), while in others no relationship between

litter decomposition and fungal biomass has been found (Graça et al., 2001), which means that the decomposition process can be depended on different decomposition processes in various ecosystems.

Shredders only utilize about 40% of the material they ingest for their own benefit the rest is excreted and enters the stream as FPOM (Figure 1). The shredders usually prefer the soft tissue of the leaves and therefore eat between the leaf veins, leaving a leaf skeleton (Cummins, 1974). Animals that feed on the FPOM are referred to as collectors since they are adapted to filter particles from the water or the fine silt in the stream. The role of shredding invertebrates in the process of decomposition seems to be less important in large rivers and also in streams where the allochthonous inputs are relatively small (Chauvet, 1997; Short et al., 1980; Short et al., 1984).

Whole biological communities may take part in regulating important ecological processes, such as decomposition (Naeem et al., 2000; Naeem et al., 1994). Community characteristics can affect the decomposition rates of allochthonous material differently, considering the invertebrate diversity, abundance and biomass. It has been shown that shredder diversity, rather than shredder abundance, is positively correlated to leaf litter decomposition rate (Jonsson et al., 2001), which indicates that biodiversity can have a significant effect on the ecosystem processes (Jonsson & Malmqvist, 2000). Some studies have shown that invertebrates play only a minimal role in the litter decomposition process but imply that the process by microorganisms and physical fragmentation are more important (Leff & McArthur, 1989; Stockley et al., 1998). Increased decomposition rate has, in several studies, been associated with fungal biomass (Ferreira et al., 2006; Gessner & Chauvet, 2002). On the other hand, Graça and others (2001) found no relationship between litter decomposition and fungal biomass which means that the decomposition process can be depended on different decomposition processes in various ecosystems.

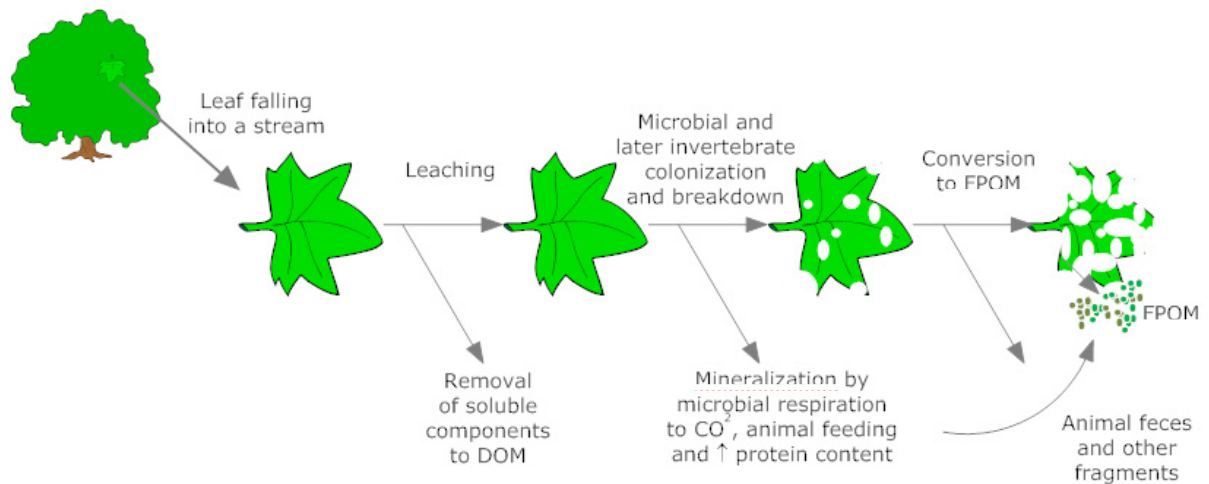


Figure 1: The process of litter decomposition from leaf fall until complete abrasion where the organic matter is converted to nutrients and other inorganic compounds which can be reused in the food chain (based on Figure 7.3 in Allan & Castillo, 2007).

Importance of litter in streams

The importance of allochthonous based energy in streams was first acknowledged in the 1960's (Hynes, 1963; Ross, 1963). Since then much research has been made which point out that the dominant energy source of the low ordered woodland streams is the allochthonous input (e.g. Hynes, 1963). Numerous leaf processing studies have been made with leaves confined in bags made of nylon or other inert material (e.g. Davis & Winterbourn, 1977) or grouped into packs and fastened together with a string (Petersen & Cummins, 1974). Many recent studies of leaf litter decomposition address the changes in land use, e.g. nutrient enrichment of streams (Bergfur et al., 2007b; Ferreira et al., 2006; Royer & Minshall, 2001), to evaluate environmental integrity (Bergfur et al., 2007b; Gessner & Chauvet, 2002; Leff & McArthur, 1989). Most of the studies on land-use change that involve forests are, however, focusing on the loss of forest cover rather than on the establishment of different forests (afforestation) like the present study.

One of the recent research projects studying streams ecosystems is RIVFUNCTION. Their aim was to develop and disseminate a methodology for assessing the functional component of ecological river quality status (RIVFUNCTION, 2001). In this project research has been done with manipulation of various ecosystem factors, i.e. leaf litter quantity (Tiegs et al., 2008), stream acidification (Dangles et al., 2004), stream liming (McKie et al., 2006), forest management like forest clear-cutting and moderate eutrophication (Gulis et al., 2006; McKie & Malmqvist, 2008). Tiegs and co-workers (2007) studied the relationship between

the decomposition rate of natural leaf litter and cotton strip assay to make comparison between streams, between studies and different environment easier. They found that the cotton strip assay could not be used uncritically as a surrogate for natural leaf decay, but could possibly be used to assess stream integrity of stream systems.

Icelandic studies on the effect of vegetation change on streams

In Iceland, the basaltic bedrock has high chemical weathering rates which is partly explained by high runoffs, age of the rocks and mechanical weathering (Gíslason, 2005). The presence of forests in catchments has recently been shown to have up to 4 times higher liberation rates of some chemicals, e.g. calcium and magnesium, than from treeless heathland catchments on basaltic bedrock (Moulton et al., 2000). This may be due to more root secretion of organic acids from forests that dissolve primary minerals from the bedrock and the low pH near the fine roots of the plants or to the increased local rainfall due to higher forest evapo-transpiration (Moulton et al., 2000). Moulton and co-workers also found that birch forest weathers more silicate rock per unit dry mass than the conifer forests, so the chemistry of streams running through different forest types is variable.

A study was made in eastern Iceland on the effects of different forest types on soil water, using downy birch, Siberian larch and lodgepole pine (*Pinus contorta* Douglas.) forest stands (Sigurðardóttir et al., 1999). The results showed significantly higher soil water concentrations of nitrate (NO₃) and total organic carbon (TOC) within the larch stands, than in downy birch and lodgepole pine stands, while within the birch stands there were higher concentrations of inorganic carbon (IC; indicator of chemical weathering). It should however be noted that the soil water concentrations may not reflect the amount of chemicals leached to the streams (Gundersen et al., 2010).

A summary of how Icelandic river types influence the aquatic biota was made by Aðalsteinsson and Gíslason (1998). The geology of the catchment area affects the groundwater and the run-off water chemical concentrations. The chemical weathering is faster on young bedrock in which permeability is high and precipitation is leached down into deeper earth layers. Older bedrock is usually dense so the precipitation remains as soil water and drains relatively quickly to run-off streams and rivers. However, older bedrock normally has higher vegetation cover on the surface and deeper soils on the catchment areas

(Gíslason and Arnórsson 1988, Arnórsson 1997). Aðalsteinsson and Gíslason (1998) described many factors that determine the chemical composition and productivity in rivers, e.g. geology, topography and vegetation cover. Productivity of the rivers also seemed to determine the density of the benthic invertebrates. Rivers originating in lakes and high productivity land cover seem to produce more Atlantic salmon (*Salmo salar* L.) than rivers originating from barren areas in Iceland. There was also an indication where the amount of drifting organic matter (FPOM) seemed to determine species composition of benthic communities.

1.4. Leaf litter decomposition studies in Iceland

Freshwater ecosystems

Studies on decomposition of allochthonous organic matter in streams have only once been made in Iceland before according to available literature. A litter bag study was made in Hengladalir in Iceland in 2004–2009. There the effects of increasing water temperature on the water ecosystem were studied. The study included a litter decomposition study, using litter bags (Friberg et al., 2009). Another study on decomposition of litter in water was made on the freshwater plant genus *Myriophyllum* within lakes on interior highland plateau of NW-Iceland (Aðalsteinsson, 1978). This research was however not a direct decomposition rate study, but an estimation study based on standing crop in different times of collection.

Terrestrial ecosystems

There have been few decomposition studies using litter bags in the terrestrial environment. Sigurðardóttir (2004) studied the effects of earthworms on the decomposition of Nootka lupin (*Lupinus nootkatensis* Donn ex Sims) leaves and stems. The litter bags used in the study were both fine (1 mm mesh size) and coarse (6mm mesh size) and were incubated in a twelve year old lupin patch for 7, 10, 11 and 19 months. The fine mesh bags excluded the earthworms and all larger soil invertebrates but the coarse mesh bags allowed these detritivores access to the litter. The results indicated that the remaining weight of the leaf litter inside the coarse mesh bags was only about 10% of the initial weight after 7 month incubation while about 30% was left in the fine mesh bags. The decomposition of the lupin

stems was much slower, but after 19 month incubation there were still more than 50% left of the initial weight.

Another study on soil microbial activity and its effects on the decomposition using the cotton strip assay (Latter & Walton, 1988) was made by Sigurðardóttir (1998) where some difference in the decomposition activity in differently revegetated areas was observed, i.e. with different main species used for revegetation. The lowest decomposition was found in a non-vegetated area. This method, cotton strip assay, has been used to compare decomposition activity in soils in different ecosystems (e.g. Brown & Howson, 1988) as well as in lotic ecosystems (Tiegs et al., 2007).

The third study on the microbial activity in Icelandic eroded and revegetated soils was made by Oddsdóttir (2002) where decomposition of the cotton strips was found to be higher in soils of revegetated areas than at eroded sites and that the highest decomposition was at a site covered with Nootka lupin. The same study also revealed a significance of invertebrates in the decomposition process, where a significant correlation was found between decomposition of the cotton strip assays and the density of soil mesofauna. Oddsdóttir (2002) also found that microbial activity is low on eroded areas but increases with revegetation.

A study of decomposition in forest soils was made by Arneberg (2005), was a part of the project ICEWOODS (SKÓGVIST). Cotton strips were also used in this study and the same methods as Oddsdóttir (2002) used. Arneberg found that the decomposition rates of the cotton strips was slower in Siberian larch forest stands than in downy birch stands in eastern Iceland and that the decomposition rate decreased with higher age of the forest stands. Arneberg (2005) also found that the slowest decomposition was in soils of non-forested areas (heathlands).

1.5. Main aims of the study

The main aim of this research was to answer questions about the allochthonous litter transport and decomposition in Icelandic stream ecosystems. The main research hypotheses were:

Litter transport

1. *Is there any difference in the amount of litter transported into the streams?*
 - a. Because of the expected difference in the productivity of the different catchment types, it was expected that the amount of litter transported into the streams would be higher in the forested streams than in the heathland streams.
 - b. Considering the composition of the transported litter, it was expected that the dominant vegetation type within each catchment would also have the highest percentage compared to other litter types.

Litter decomposition

2. *Is there any difference in decomposition activity of stream ecosystems in Iceland compared to comparable ecosystems abroad?*
 - c. It has been suggested that decomposition rates vary along a latitudinal gradient, that it is temperature dependent (e.g. Cummins, 1979; Kaushik & Hynes, 1971). It was therefore expected that countries at similar latitudes elsewhere would be comparable considering the litter decomposition rates within streams.
3. *Is there any difference between litter decomposition rates considering different litter types or different catchment types?*
 - d. According to published studies, litter type has an effect on decomposition rate (Dangles et al., 2004; Gessner & Chauvet, 2002; Petersen & Cummins, 1974; Webster & Benfield, 1986). It was therefore expected that decomposition was strongly affected by litter type in the Icelandic streams. Based on the literature it was expected that the decomposition rate of downy birch litter would be fastest, larch needles slower and grass litter would have the slowest decomposition rate (rate of decomposition: Birch > Larch > Grass).
 - e. It was expected that the stream ecosystem would have adapted to the high allochthonous inputs of organic matter where the streams run through forested areas. The River Continuous Concept supports this hypothesis; where headwater streams run in shaded forest areas the amount of shredders should increase as the streams get smaller. Therefore it was expected that the decomposition rate (g per g litter per day) should be higher in forest streams than in the heathland

streams, reflecting the increased importance of invertebrates in the decomposition process.

Invertebrate activity

4. What are the effects of invertebrate activity on litter decomposition in streams?

- f.** Studies have shown that shredders can increase the decomposition rate by 24–40% (Webster & Benfield, 1986). Shredders are reported become more important in lotic ecosystems at higher latitudes (Giller & Malmqvist, 1998). Because of these facts it was expected that the rate of leaf litter decomposition would be faster in coarse mesh bags, where invertebrates could access the litter, than in the fine mesh bags where only microbial organisms could access the litter.

5. Is there any difference in the abundance of invertebrates using litter as their food source, or habitat, in different catchment types?

- g.** It was expected that there would be a higher number of invertebrates that participate in the decomposition in streams that are adapted to the higher allochthonous input of litter in the forests. Similar to the expected difference in decomposition rate between coarse and fine mesh bags and in different catchment types, mentioned earlier.

Eastern Iceland versus southern Iceland

6. Is there any difference in decomposition rate of birch litter between streams in different parts of Iceland with different geology (run-off streams vs. spring-fed streams)?

- h.** It was known that the spring-fed streams in southern Iceland have more stable discharge and temperature, which should result in better environment for the consumers (invertebrates and microorganisms) and therefore lead to a faster decomposition rate in both fine and coarse mesh bags. On the other hand the stream bottoms of the spring-fed streams tend to be sandy due to high erosion activity in southern Iceland, which is not favourable for many invertebrate species. Literature shows that sand bottomed streams have lower productivity than pebble-cobble bottomed streams (Cushing & Allan, 2001), which is the case in most of the run-off strams in eastern Iceland. It was still expected that

the spring-fed streams in southern Iceland would have higher decomposition activity.

- i. It was expected that the amount of dissolved chemicals and pH would be higher in the spring-fed streams in southern Iceland and that it could also possibly increase the decomposition rate, especially of the fine mesh bags (microbial decomposition).

Time of litter transport

7. *Is the time of litter transport into the streams important considering the decomposition rates?*

- j. If much of the decomposition is performed by invertebrates, then the decomposition rate (in the coarse meshed bags) should be faster in the autumn, since most of the allochthonous material goes into the streams as leaf fall in the autumn. It could be expected that the invertebrates should have adapted their life cycle to that extra seasonal input. If, on the other hand, the microbes are the main decomposition agent, the temperature should control the rate of decomposition in both fine and coarse mesh bags. Since air temperature in spring and summer is more often higher than in the autumn the microbial decomposition rate (fine mesh bags) should be higher in the spring and through the summer.

2. Materials and methods

2.1. Study sites

The study was conducted in seventeen first to second order headwater streams and their catchments in eastern and southern Iceland. The geology of these two main areas differs considerably both in age and type of bedrock (Sæmundsson, 1979). The bedrock of eastern Iceland is alkaline with intercalated sediments older than 3.3 million years (Jóhannesson & Sæmundsson, 1998). It is Tertiary flood basalt, which is described as having been formed primarily between 9 and 20 million years B.P. (Ward, 1971). It is characterized by dense and impermeable rock, so the retention time of surface water is low and it ends up in run-off streams. In southern Iceland, on the other hand, the bedrock is relatively young basaltic rock, postglacial and prehistoric (Jóhannesson & Sæmundsson, 1998), which is within the neo-volcanic zone between the Eurasian and North American tectonic plates (Sæmundsson, 1979; Ward, 1971). In contrast to the bedrock of eastern Iceland, the bedrock in southern Iceland is porous, which means that precipitation usually trickles down through the bedrock and emerges as springs in certain places. Therefore, the main source of running water in southern Iceland is spring-fed.

The soils in fully vegetated areas in eastern Iceland are characterized by Brown Andosols in freely drained areas and Gleyic Andosols and Histic Andosols in wetland areas (Arnalds & Óskarsson, 2009). Brown Andosols are often 0.5–2m thick and have allophane and ferrihydrite clay content of about 15–30%. The pH of the soil is generally between 4.5 and 7.5 (Arnalds et al., 2005) which is higher than in other soil types which have high organic matter. The Gleyic Andosols are wetland soils with organic carbon (C) <12% in the surface layers, while Histic Andosols have 12–20% C in surface layers (Arnalds, 2004). At the southern study site, the main soil types were either Brown Andosols or Vitrisols which contains <1% organic C. The surface of Vitrisols usually has limited plant cover and frost heaving is common, especially where there is little vegetation cover. The soils are generally sandy and shallow and volcanic glass is the main mineral constituent (Arnalds, 2004).

Table 1: Mean air temperature and precipitation during 1961–1990 in the study sites in eastern and southern Iceland. The data from eastern Iceland are from Hallormsstaður, which is situated about 0.6–18.3km distance from individual study sites, and in the southern Iceland the data is from the weather station at Hæll, which is situated in about 15.7–18.3km distance from individual study sites. (Data source: (Icelandic Meteorological Office, Retrieved 20. November 2009)

	East	South
Mean annual air temperature (°C)	3.4	3.6
Mean annual air precipitation (mm)	738	1117
Mean 24-h air temp. (°C)		
January	-1.6	-1.8
July	10.2	10.6
Mean max. 24-h air temp. (°C)		
June	12.4	12.6
July	14.1	14.5
August	13.4	13.7

The climate in inland NE and N Iceland is generally more continental (drier, colder winters, warmer summers) than in lowland S or W Iceland (Einarsson, 1976). The study sites in eastern and southern Iceland were, however, outside these main contrasting regions. The southern study area is found quite far inland (ca. 40km) and therefore it is less oceanic than most of the southern and western lowlands. The eastern study site is in Fljótsdalshérað, which is considered having more oceanic climate than the inland NE and N regions (Einarsson, 1976). Therefore, the climatic differences between the study areas are much less than could be expected. The annual precipitation was about 50% higher in southern Iceland, while mean annual temperature and average temperatures of the warmest and coldest months were quite similar (Table 1). It should however be noted that the catchments in eastern Iceland reached to higher altitudes than the catchments in southern Iceland (Figure 2 and 3). Since the average monthly air temperatures in Iceland generally decrease by 0.64°C for each 100m increase in elevation (Wöll, 2008), this difference between southern and eastern Iceland may have influenced how much snow accumulated during winter in the upper parts of the catchments in eastern Iceland with subsequent spring floods.

The growing season in Iceland is mostly dependent on air temperature but is less dependent on the precipitation (Sigurgeirsson & Eggertsson, 2004), which is usually a co-limiting factor for plant growth in countries south of the subarctic and the boreal zones. The hydrological cycle in eastern Iceland is generally quite variable, with massive snowmelt in spring and large spring floods, whereas it is generally much more stable in southern

Iceland, where more of the winter precipitation melts during winter, especially for spring-fed streams (Aðalsteinsson & Gíslason, 1998).

2.1.1. Eastern Iceland

The part of the study which was located in eastern Iceland was conducted in nine headwater streams running through three differently vegetated catchments: Treeless heathlands (AS1, AS2, AS3), native downy birch woodlands (AB1, AB2, AB3) and coniferous plantations (AG1, AG2, AG3). The coniferous plantations consisted mostly of middle-aged stands established in 1940–1960. The dominant coniferous tree species was Siberian larch, but there were also some stands of different pine (*Pinus* sp.) and spruce (*Picea* sp.) trees in between as well as some deciduous tree species, such as birch and willows (*Salix* sp.).

Table 2: Names and locations of the studied catchments in eastern Iceland.

Catchments	Sampling station	Longitude	Latitude
Heathland catchments			
Hrafnsgerðisá	AS1	N 65° 09.247	W 14° 43.891
Fjallá	AS2	N 65° 01.261	W 14° 39.998
Nýlendulækur	AS3	N 65° 01.421	W 14° 39.995
Birch forest catchment			
Klifá	AB1	N 65° 04.582	W 14° 48.126
Kaldá	AB2	N 65° 10.573	W 14° 28.999
Ormsstaðalækur	AB3	N 65° 06.240	W 14° 43.020
Conifer forest catchments			
Buðlungavallaá	AG1	N 65° 04.173	W 14° 49.754
Kerlingará	AG2	N 65° 05.385	W 14° 45.260
Jökullækur	AG3	N 65° 05.126	W 14° 46.323

The catchments were selected following a survey of the whole area and with help from local people working for the Iceland Forest Service. The most difficult task was to find suitable treeless heathland catchments for comparison, since many of prospecting treeless catchments had been drained and fertilized for agricultural purpose, affected by sewage from farms or recent large-scale afforestation that has taken place in such areas since 1990. The area was however well suited for finding extensively forested catchments, since it has among the highest cover of both plantations of native forests and woodlands for Iceland

(Traustason & Snorrason, 2008). The selected catchments were all situated in Fljótsdalshérað and were located between N°65'01 and N°65'10 and W°14'28 and W°14'49 (Table 2). They were located in the forested region of Hallormsstaðaskógur (AB1, AB3, AG1, AG2 and AG3), in Einarssstaðaskógur (AB2), in Geitdalur (AS2 and AS3) and in Fljótsdalur (AS1) (Figure 2). All the streams originate from the same mountain ridge, Hallormsstaðaháls, except for Hrafnsgærðisá (AS1), which originates in Arnheiðarstaðaháls and Kaldá (AB2), which originates in Sandhaugar. Fjallá (AS2) and Nýlendulækur (AS3) run to the eastern hill side of Hallormsstaðaháls while all of the streams running through conifer forested catchments (AG1, AG2, AG3), Klifá (AB1) and Ormsstaðalækur (AB3) run down the west hill side of Hallormsstaðaháls.

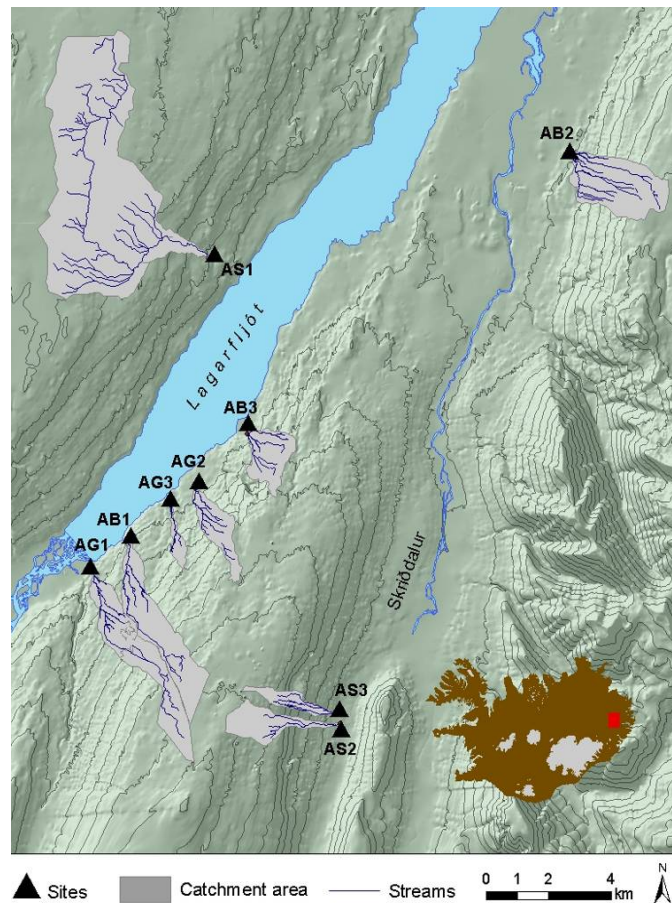


Figure 2: The location of the nine catchments in the eastern Iceland. Heathland catchments are marked with AS1-3, Birch forest catchments are marked AB1-3 and catchments which include conifer forests are marked AG1-3. The numbers from 1-3 refer to catchment replicates. Most of the streams run through Hallormsstaðaskógur which is on the west hillside of Hallormsstaðaháls but two streams are from other areas.

2.1.2. Southern Iceland

In southern Iceland, the study was conducted in eight streams running through two differently vegetated catchments: Downy birch woodlands (SB1, SB2, SB3 and SB4) and barren land that had gone through severe soil erosion (SS1, SS2, SS3, SS4). All the catchments were located south-west of Mt. Hekla, within the boundaries of Svínhagi, Haukadalur, Hólar and Næfurholt farms. All catchments were located between N°63'57 and N°64'00 and W°19'53 and W°19'59 (Table 3).

The catchments were selected following a survey of the whole area and with help from local farmers and people from the Soil Conservation Service of Iceland. It was rather difficult to find undisturbed streams on barren land. The most common disturbance factor was large-scale fertilization of erosion control by the Soil Conservation Service, the local farmers and other landowners. As expected, it was also rather difficult to find whole catchments in forested areas since only few natural woodlands are left in the area due to the historic erosion (Sigurmundsson, 2008). A small part of one catchment (3%), affecting one of the study stream (SS2) was fertilized by synthetic fertilizer during the study period (spring 2008). This could possibly have affected some of our measurements.

All the streams in southern Iceland were first order streams (headwater streams) that originated from underground springs and their catchments, as determined from the surface topography around the stream. It is known that underground springs in southern Iceland may partly origin from distant sources, such as glacial melt water and percolated precipitation in the highlands, tens of kilometers away (Sigurðsson & Einarsson, 1988). Because of their spring-fed origin, the streams in southern Iceland were much shorter than the run-off streams studied in eastern Iceland and their catchments were also smaller.

Table 3: Names and locations of the catchments and streams in southern Iceland.

Catchments	Sampling station	Longitude	Latitude
Unvegetated catchments			
Litlifoss	SS1	N 63° 59.454	W 19° 54.510
Gilið frammi á Sandi	SS2	N 63° 58.297	W 19° 59.368
Uppspretta á Haukadalsöldu	SS3	N 63° 57.678	W 19° 57.833
Litla læna	SS4	N 63° 59.432	W 19° 54.506
Birch forest catchments			
Sporðalækur	SB1	N 63° 59.464	W 19° 58.017
Botnar í Svínhaga	SB2	N 63° 58.167	W 19° 59.496
Botnar í Hellisdal	SB3	N 64° 00.361	W 19° 53.456
Ytri lækur	SB4	N 64° 00.721	W 19° 53.217

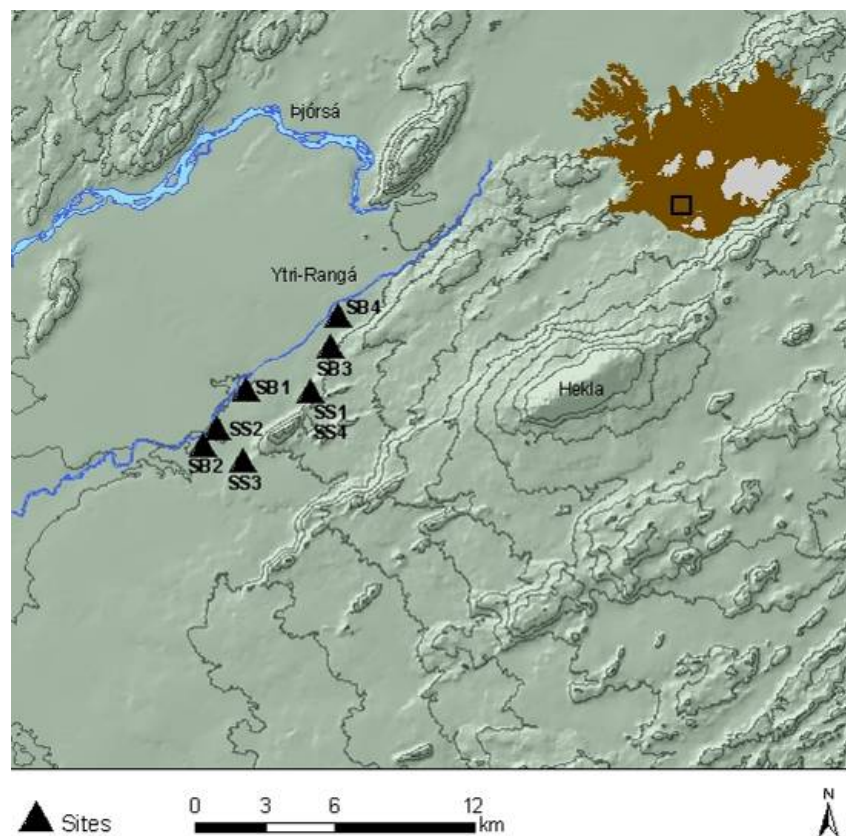


Figure 3: The location of the eight study sites in southern Iceland. Barren sites are marked with SS1-4 and forested catchments with SB1-4. The numbers from 1-4 refer to catchment replicates. All of the streams run into Ytri-Rangá but are situated within the boundaries of the Svínhagi, Haukadalur, Hólar and Næfurholt farms, south west of Mt. Hekla.

2.2. Ecosystem structure

2.2.1. Catchment size and vegetation classes

The size of each catchment, stream length and catchment vegetation cover was mapped by Bjarni D. Sigurdsson and Robert Rosenberg, Agricultural University of Iceland. The data is shown here with their permission.

In southern Iceland the mapping was done by following the topographical ridges from the sampling stations and around the streams and marking their coordinates with a global positioning system (Garmin GPS-96). Similarly the streams were followed and mapped to measure stream lengths accurately (Table 3). As both topographical ridges and streams were followed, the boundaries between vegetation classes (Table 4) were positioned with GPS.

Table 4: Key to the vegetation classes used for mapping of catchments in the ForStreams study.

English name	Icelandic name	Limits
Plantation	Barrskógur	Planted areas.
Woodland	Birkiskógur	Areas dominated by <i>B. pubescens</i> , irrespective of tree stature.
Wetland	Votlendi	All soils with permanently high ground water level.
Grassland	Graslendi	Dominated by grasses
Heathland	Mólendi	Dominated by mosses, sedges, grasses and dwarf bushes. Vegetation cover >
Barren land	Melur	Vegetation cover < 30%
Sand/pebbles	Sandur/möl	
Solid rock	Berg	

The coordinates were transferred into ArcGIS software (version 9, ERSI, Redlands, CA, USA) onto an elevation map of Iceland and SPOT 5 satellite photograph where different vegetation classes within each catchment were identified and mapped manually from their

infrared signature and the coordinates recorded in the field. This resulted in a GIS map of the vegetation classes of all catchments.

In eastern Iceland the catchments were much larger and therefore a modified method was used, which meant that each catchment was manually mapped from its sampling stream reach and well above the forest limit (to ca. 5–600m a.s.l.). After having transferred the data into ArcGIS and to an elevation map merged with a map of all rivers and streams of Iceland (Björnsson et al., 2009), a mixture of automated flow accumulation analysis was made of the topographical surface and a manual mapping by dividing the source area of different streams, and that was used to determine the upper limits of each catchment. Vegetation classes were determined in the same way as for southern Iceland, except that plantation areas were first inserted to the GIS maps from the National Forest Inventory database (Traustason & Snorrason, 2008). For eastern Iceland, two GIS maps and datasets for vegetation covers were created. One describes the vegetation composition in the lowest 400m area of each catchment above the stream sampling reach and the other covering the whole catchment.

2.2.2. Dominant vegetation within each study site

The forest characteristics and biomass of trees, ground vegetation and litter were measured by Brynhildur Bjarnadóttir and Edda S. Oddsdóttir, Icelandic Forest Research. The data is shown here with their permission. The measurements were carried out as point measurements in representative forest stands, and collected in eastern Iceland during 1st–4th of September 2008. Such measurements have not been done in southern Iceland yet.

Trees: The estimate of stand characteristics and living biomass of trees at each forest catchment was based on traditional forest measurements. The trees were measured on 2–3 randomly placed 100m² circular plots within the lowest 400m of each forest catchment. The measured variables were tree species composition, stand density as number of stems and number of individuals, stem diameter at heights of 0.5m and 1.3m for all trees and tree height for trees from three different diameter classes (Figure 4). All trees and bushes >2m were included in the tree layer.

Bush layer: The bush layer was defined as the layer between 50 and 200cm in forested sites. Biomass samples of the bush layer were collected at one or two 25m² plots within each catchment. They were later dried at 80°C for 48 hours and weighed to get information on the biomass.



Figure 4: The method for measuring tree height used in the study. Photo by Edda S. Oddsdóttir

Ground vegetation: The ground vegetation was collected from 4–7 plots within each catchment using a 51×51cm frame (Figure 5). The frames were divided among the most common vegetation classes found in the lowest 400m of each catchment (Table 4). Within

each frame, all living plants <50cm in height, all standing litter and woody debris were collected. The samples were then later separated into different classes: i) woody dicots, ii) herbaceous dicots, iii) grasses and sedges, iv) mosses and lichens, v) litter. Their biomass was determined after drying at 80°C for 48 hours.



Figure 5: The ground vegetation was collected using a 51×51cm frame. In the middle of the figure can be seen a soil corer which was used to collect cores from the soil at the same frames as used for ground vegetation and litter measurements. Photo by Edda S. Oddsdóttir

Litter/humus: the litter layer was collected within each frame after ground vegetation had been removed. The litter samples were dried at 80°C for 48 hours and weighed.

Soil: A soil corer was used to collect cores from the soil at the same frames as used for ground vegetation and litter measurements. They have not been processed yet.

Species-specific biomass functions were used to estimate the total woody biomass in kg dry mass (DM) m⁻² of the tree layer at each site from the diameter and height data (Snorrason *et al.* 2006). The relative distribution of different ground vegetation classes in the lowest 400m of each catchment was used to estimate the average ground vegetation and litter biomass (in kg DM m⁻²) for each catchment from the harvest measurements of different vegetation classes.

2.2.3. Litter transport to streams

The litter traps were installed in late autumn 2007. The traps were made of 10L plastic buckets, 27.7cm in diameter. The lids were cut out so that only the edges of the lids were left. A bag made out of fine meshed filter material was inserted, almost reaching the bottom of the bucket, and the lid ring was put back to hold it in place. The bucket was dug down into the ground in 1m distance from the stream bank, so the edges were even to the ground (Figure 6). In total, ten buckets were installed around each stream, five on each side. Before installing the distance between the buckets was decided and the first buckets were always installed parallel to the sampling station in the stream.

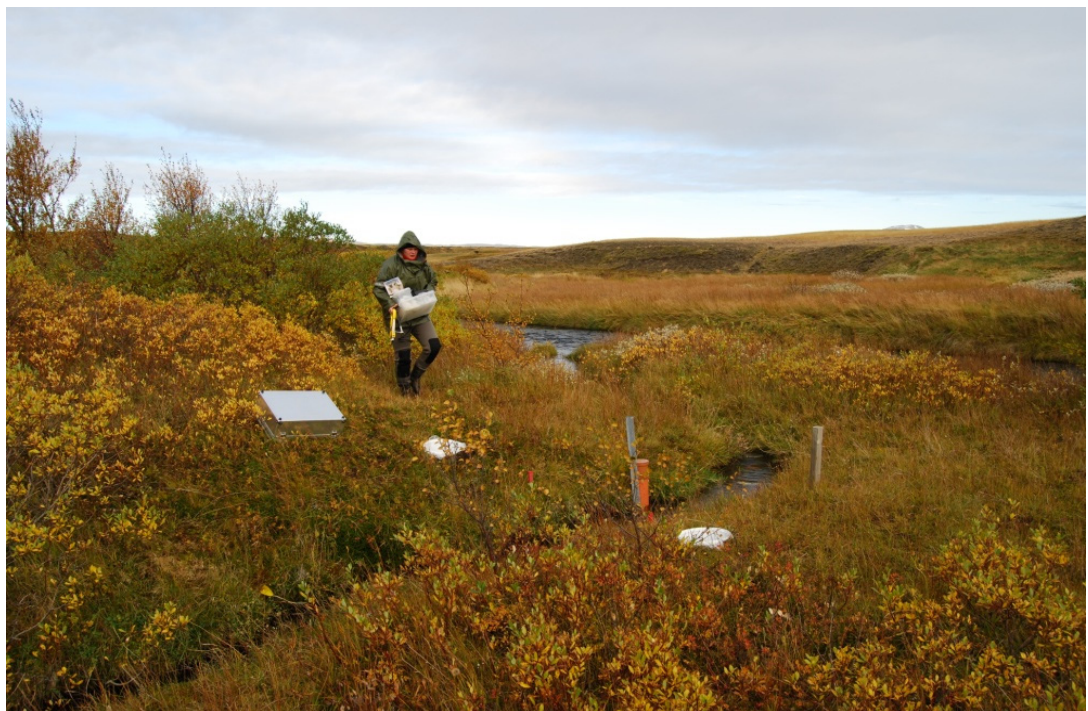


Figure 6: Litter traps were dug into the stream bank (above) about 1m from the water on both sides of the stream (below). Photos by Bjarni D. Sigurðsson (above) and Gintare Medelyte (below).

The litter traps were emptied into paper bags and then air dried and kept by room temperature until analysed a few months later. The litter was separated into five categories which were, birch leaves, needles, grass litter, wood and other material. The bags were then put in an air drying oven for 48–72 hours and then weighed to the nearest 0.01g.

2.2.4. Physical and chemical stream characteristics

Water temperature was logged every 30 minutes in each stream, using Onset TidBit v2 Data Logger (Onset Computer Corporation, Pocasset, MA, USA), from August 2007 to May 2009. The temperature logger was placed in a plastic tube for protection from external disturbance. The tube was then placed in the stream the way that the stream would flow through it (Figure 7). The loggers were emptied in every field trip and data copied on a computer.



Figure 7: Temperature data logger placed in a plastic tube for protection and put parallel to the stream (blue tube) flow in the stream, at the main measuring station of the stream. Photo by Helena Marta Stefánsdóttir.

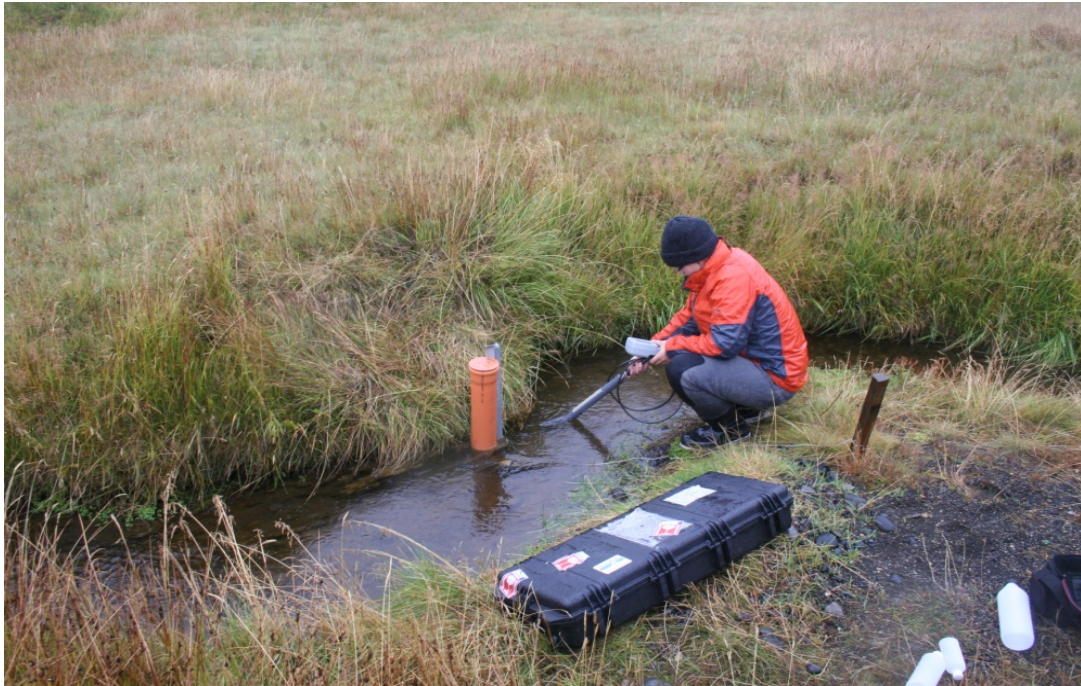


Figure 8: Point measurements of stream temperature, pH and water conductivity were made in every field trip (February, April/May, July and September/October), using YSI 600XLM Multi probe Sonde. Photo by Gísli Már Gíslason

Point measurements of stream temperature, pH and electric conductivity were also made in every field trip (Figure 8), i.e. in February, April/May, July and September/October in 2008, using YSI 600XLM Multi probe Sonde (Yellow Springs Instruments inc., Yellow Springs, OH 45387 USA).

Water velocity was measured in every regular field trip, i.e. in February, April/May, July and September/October in year 2008, using Flowtracker SonTek/YSI ADV Series (Yellow Springs Instruments inc., Yellow Springs, OH 45387 USA). A measuring tape was stretched across each stream and velocity measurements made in ten evenly distributed places across the stream (Gore, 2006; Newbury & Bates, 2006). The stream depth was measured at every measurement point and the water velocity was always measured at 40% of the total depth, as measured from the stream bottom (Figure 9).

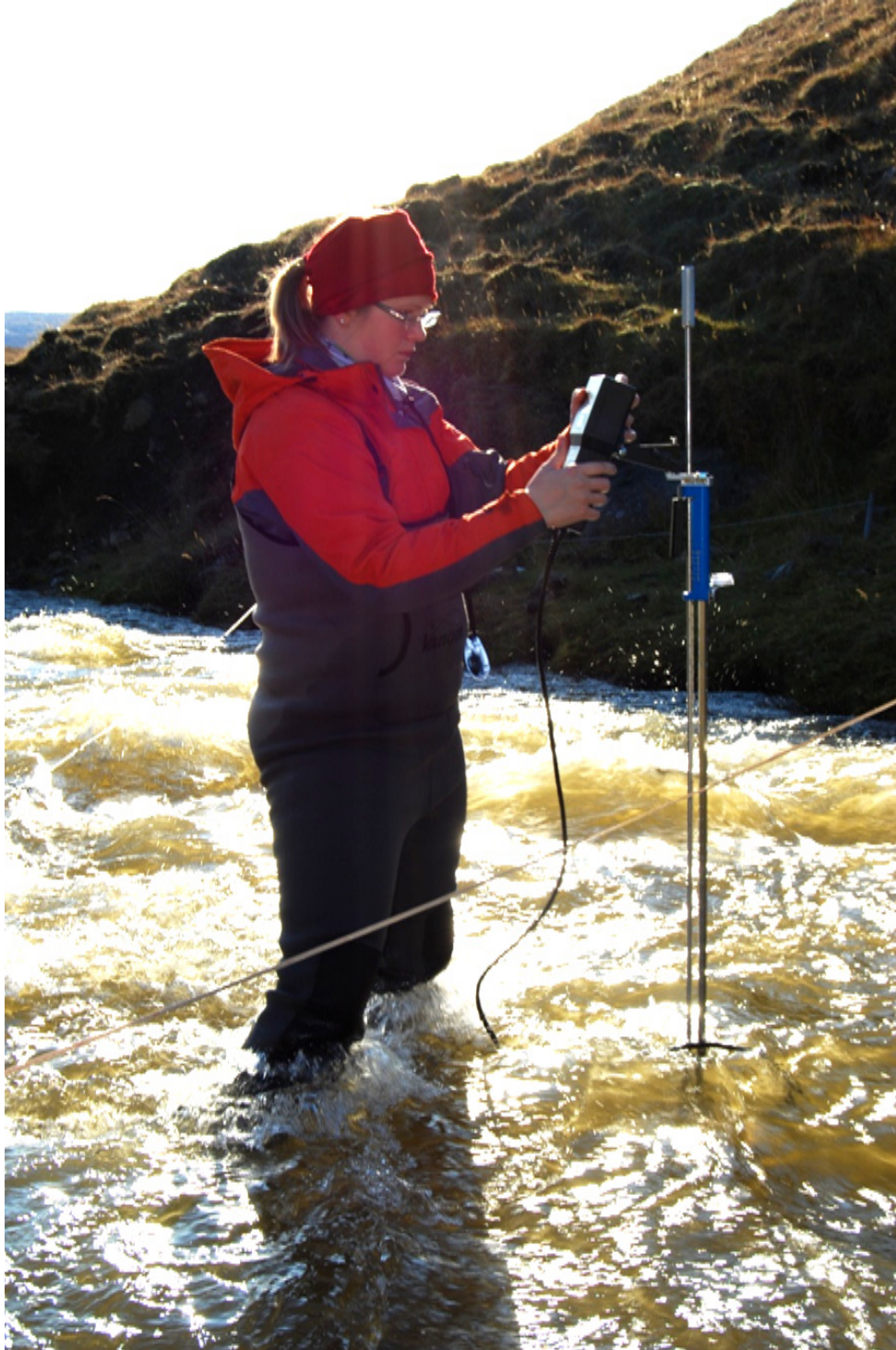


Figure 9: Water velocity was measured in every regular field trip (February, April/May, July and September/October), using Flowtracker SonTek/YSI device. A measuring tape was stretched across each stream and measurements made in ten evenly distributed places across the stream. The stream depth was measured at every measurement point and the water velocity was always measured at 40% of the total depth, as measured from the stream bottom. Photo by Ragnhildur Magnúsdóttir.

Water samples for chemical analyses were collected in every regular field trip. The samples were taken at the sampling station into high-density polyethylene (HDPE) plastic bottles, which had been washed in 1N HCl and rinsed with deionized water, for different kind chemical analyses. The bottles were filled up to about 90% to be able to freeze the water in the bottles, with the spout up to the water current (Figure 10). The water samples were kept in a cool box and put into freezer when arrived to the laboratory in the evenings. Phosphate in the water was measured using stannous chloride method (Tecator, 1983a), nitrate was measured by reducing it to nitrite with copperized cadmium (Tecator, 1983b).

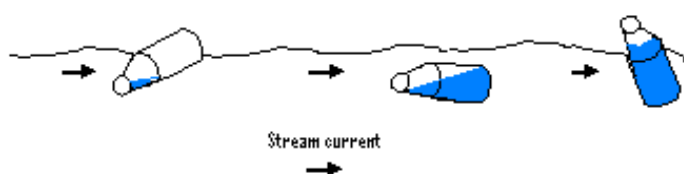


Figure 10: Water samples were collected into bottles with the spout facing up to the water current.

Results from the amount of total nitrogen (N) and total phosphorus (P) in the stream water collected in May 2008 are shown in this thesis but further information about the chemical analyses of the stream water can be found in Medelyte (2010).

2.3. Litter decomposition

Litter types used in this study were chosen from species dominating each of the three catchments. Senescent leaves of downy birch (*B. pubescens*), senescent needles of Siberian larch (*L. sibirica*) and senescent parts of native grasses (*Festuca richardsonii* L., with some *Poa pratensis* L. and *Agrostis capillaries* L.), which is a typical heathland grass mixture in Iceland (Gunnlaugsdóttir, 1985). Birch and larch litter was collected in autumn 2007 from the forest floor following abscission in Heiðmörk and Hallormsstaðaskógur, respectively. The grass litter was collected in autumn 2007 in Hafnarfjörður. The litter was kept in a freezer until spring 2008 when it was oven dried at 50°C (Bärlocher, 2005a) for 48–72 hours. For the litter decomposition experiment, 2.0±0.01g of each litter type was weighed and placed in two types of litter bags, coarse mesh bags and fine mesh bags. The two differently meshed bags were used to include (coarse mesh) or exclude (fine mesh) invertebrates from the litter decomposition.

The coarse mesh bags had 5mm mesh and were made of plastic hen-wire sowed together with a nylon thread (Figure 11a), inside it was placed a 10×15cm 200µm mesh bag with twelve 5mm circular holes in it to allow invertebrates to access the litter. The inner bag was closed with staples to prevent the litter from floating out of the bags. The fine mesh bags were 10×15cm with 200µm mesh size (Figure 11b), closed with a cotton draw-through string (Purchased at Plastok® Associates Ltd, Birkenhead, U.K.). The fine mesh bags were placed in a 80×20cm cover, for protection from external disturbance, made from the same material as the coarse mesh bags, but with 10mm mesh size.

The bags were attached to a 2m long metal chains with plastic straps, 24 bags on each chain (4 bags for each litter type, birch, larch and grass, in fine and coarse mesh bags), randomly distributed along the chain (Figure 12a). In total three chains were put in each stream (72 bags). The chains were then fastened to the stream bed using a metal rod in one end and a stone tile in the other (Figure 12b). The position of the chains was decided considering where it would be least likely the stream would dry out during the summer. Most of the litter bags were put into the streams in May 2008. Three replicates of each litter type and mesh size were collected from each stream at each collection time. Birch litter bags were collected after 48, 89, 140, 175 days of incubation and the needle and grass litter were collected after 89, 140, 175 and 369 days. These different timings of collections of the birch litter compared to the grass and the larch needles were due to the expected difference of decomposition rate of the litter material. It was expected that birch litter would decompose faster than grass and larch litter, as shown in studies by Petersen and Cummins (1974), and therefore it would be better to collect the birch leaves earlier but leave the larch needles and the grass in throughout the winter.

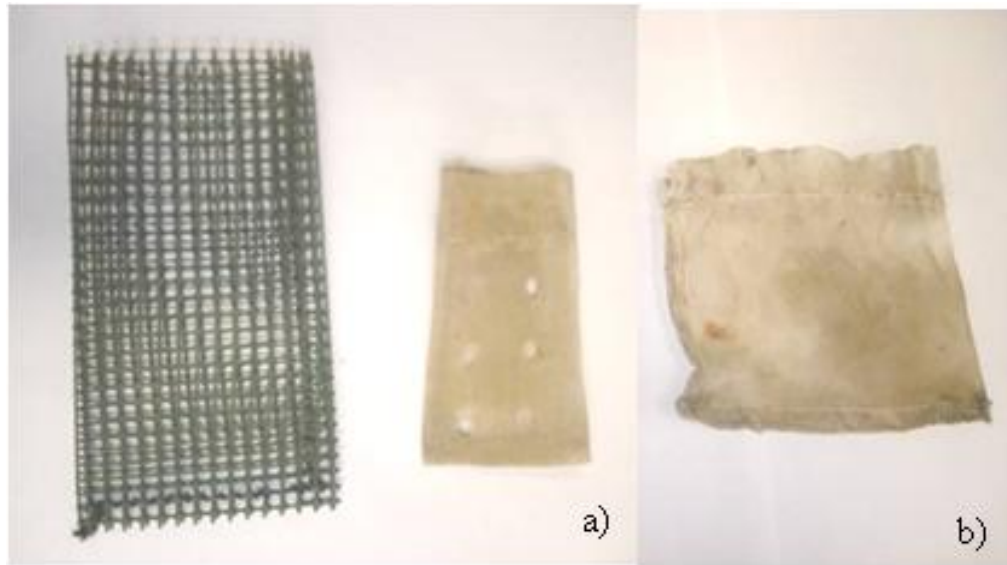


Figure 11: Litter bags used in the study a) coarse mesh bag made of chicken-net sowed together with a nylon thread, inside it to prevent the litter floating away, was placed a fine mesh bag with twelve 0.5mm large holes, closed with staples, and b) fine mesh bags made from 200µm material and closed with a cotton draw through string. Photos by Helena Marta Stefánsdóttir.

Under natural conditions most of the leaf litter, however, enters streams in the autumn, while only a small part enters at other times, e.g. in storms and with spring thaw. To see if this different timing made any difference, birch leaves in fine and coarse mesh bags (8 bags in each stream) was put into each stream in eastern Iceland in September 2008 and incubated for 52 days.

At the same time (September 2008) birch leaves in fine and coarse mesh bags were immersed in the eight streams in southern Iceland (8 bags in each stream, 64 bags in total). Those four replicates of fine and coarse mesh bags were collected 52 days after immersion.

To measure the winter decomposition, one collection of grass and larch needles from the incubation in spring 2008 was collected in the spring of 2009, after 366 days of immersion.



Figure 12: Experimental design of the litter decomposition study in run-off streams in eastern Iceland. a) Fine and coarse mesh bags fastened to an iron chain with plastic straps, different colour for each litter type and b) chain was fastened to the bottom of the stream with a metal rod and a heavy stone tile. Photos by a) Helena Marta Stefánsdóttir and b) Bjarki Sigurðsson.

The collected bags were carefully placed in zip-lock plastic bags, placed in a cooled box and in the evening put in a freezer and then transported to the laboratory. The bags were defrosted and leaves separated and rinsed with tap water (Bärlocher, 2005b) over a 125 μ m sieve, to remove dirt and invertebrates from the leaves. The litter was thereafter oven dried in paper bags by 50°C for 48–72 hours (Bärlocher, 2005b) and weighed to the nearest 0.01g.

2.3.1. Leaching

Leaching of dissolved chemicals during the first days after the litter got submerged in stream water was estimated by exposing fine leaf bags with dried litter in running water in the laboratory (Bärlocher, 2005a). Grass, birch and larch litter was weighed to 2.0 ± 0.01 g and put in fine mesh litter bags that were tied to a string which was fastened to a drain tube (Figure 13). The tube was closed in both ends, but water ran freely from the tabs (two tabs), through the litter bags and then out of the drainage tube pores, so the current was continuous for the whole time. Five (birch litter) or six (larch needles and grass litter) replicates were removed after 18, 42, 66, 90, 114 and 138 hours of incubation, dried and weighed to the nearest 0.01 g.



Figure 13: Leaching experimental design. Fine mesh bags, tied to a string which was fastened to a drain tube which was closed in both ends but water ran freely from the tabs through the litter bags and then out of the drainage pores. Photo by Bjarni D. Sigurðsson

2.4. Invertebrates

The rinsed material from each sample was frozen. Invertebrates were collected from the re-thawed samples and identified to the following groups: Acarina, Chironomidae, Clinocerinae, Coleoptera, *Dicranota*, Gastropoda, Muscidae, Oligochaeta, Plecoptera, Simuliidae, Tipulidae and Trichoptera, using a Leica MZ6 stereomicroscope with $6.3\times$ magnification. The identification of invertebrates within each stream done by Medelyte

(2010) was used to group large taxa groups of invertebrates into functional feeding groups. The ratio of different feeding groups in Medelyte (2010) was used to reclassify the main groups found within the litter bags in the present study. This applies specially for the ratios of Chironomidae.

2.5. Data treatment and statistical analysis

Before the data was analysed some measurements had to be removed from the dataset. All such removals were done based on pre-determined ground rules; e.g. if the litter dry weight was less than 95% of the average weight in the collection before, the value was erased since such a change was biologically improbable. Such removals were mainly done for larch needles and some values for grass litter in the coarse mesh bags at later collections, where the material could have been washed out of the bags. Some replicate fine mesh bags also disappeared in the streams and were missing in the data series, probably because of decomposition of the cotton string which was used to fasten the bags to the protection cover. The fine mesh bags were mainly lost during the winter 2008–2009 and there were too few fine mesh bags remaining in the spring of 2009 to be able to compare them statistically with the coarse mesh bags. Some of the litter bag samples collected in November 2008 got lost during storage. These samples were mainly from streams AS1 (nine fine mesh and nine coarse mesh bags), AB3 (nine fine mesh bags), AB1 (eight coarse mesh bags), AG1 (three fine mesh bags and nine coarse mesh bags) and AG2 (nine fine mesh bags).

2.5.1. Degree days

Temperature data from the Tidbit data loggers was used for determination of accumulated day degree threshold of 0°C diurnal mean temperature (Irons et al., 1994). The number of day degrees was then added up from start of each treatment until the bags were collected from each stream.

2.5.2. K - value

Long-term leaf litter decomposition rate (k-value) was estimated from the weight remaining after summer and autumn decomposition for all litter types, i.e. collection times 1–4 for

birch litter and 2–4 for grass and larch litter. The data was fitted with an exponential decay equation using SigmaPlot (Version 9.0., Systat Software Inc., San Jose, California, USA):

$$W_D = W_0 \times e^{-kD}, \quad (1)$$

where W_D is the amount of leaf material after D number of days in incubation, W_0 is the initial amount of leaf material, k is the rate coefficient and D is the elapsed time in days since the start of the incubation.

2.5.3. Statistical analysis

In the present study the level of significance was always $\alpha = 0.1$. This is in accordance with other published works of e.g., Milton (1992) and Zar (1998).

The comparison of physical stream characteristics was made with one-way analysis of variance (ANOVA) followed by Fisher's least significant difference (LSD), using SAS/STAT® software (SAS system 9.1.3, SAS Institute Inc., Cary, NC, USA).

The comparison of different environmental characteristics was made between the means, where each individual stream was treated as a replicate within each catchment type, i.e. heathland vs. birch forest vs. conifer forest. Here is an example of the model that was used in SAS for this analysis:

```
proc glm data=d1;
class Catchment;
model Width=Catchment/ss3;
lsmeans Catchment /pdiff;
run;
```

The same model of one-way ANOVA followed by Fisher's LSD was used to compare different vegetation types within each catchment area as well as to compare the environmental characteristics of the eastern area and the southern area. It was also used to find if the average decomposition rate (k -values of the dominating vegetation litter types in coarse mesh bags) differed between catchment types.

To test the effects of litter quality on decomposition, k -values from all three litter types in coarse mesh bags in each stream were used in two-way repeated ANOVA (each litter type was repeated within the same stream), followed by Fisher's LSD tests on the interaction

between vegetation type versus litter type. Here is an example of the model that was used in this analysis:

```
proc mixed;  
class Catchment LitterType StrNumb;  
model Kvalue=Catchment LitterType Catchment*LitterType;  
repeated / sub=LitterType*StrNumb type=un;  
lsmeans Catchment*LitterType /pdiff;  
run;
```

To analyse the invertebrate and microbial activity, two-way repeated ANOVA (fine and coarse bags repeated in the same streams) was used on fine and coarse mesh bags in the three different catchment types with their corresponding dominating litter types. Here is an example of the model that was used in this analysis:

```
proc mixed;  
class Catchment StrNumb BagType ;  
model Kvalue=Catchment BagType Catchment*BagType ;  
lsmeans BagType*VegType /pdiff;  
run;
```

For looking at the weight loss of birch litter in fine and coarse mesh bags at different collections, the mean weight (of fine and coarse mesh bags) at each collection time was analysed separately with two-way repeated ANOVA (see the 2nd example), but with catchment and bag types as repeated factor.

The total number of invertebrates was compared between the catchments with corresponding litter type with one-way ANOVA (see 1st the example). The same model was used on the number of taxa of invertebrates in the litter bags.

To test the difference between the number of invertebrates found in the birch litter bags in different collections two-way repeated ANOVA followed by a Fisher's LSD was used (see the 2nd example). The same model was used for analysing this for the number of taxa found in the litter bags. Here is an example of the model that was used in this analysis:

The difference of decomposition between seasons of incubation (spring and autumn) was tested with two-way ANOVA on the average decomposition rate per day (see the 3rd example), followed by Fisher's LSD test on the bag type and season.

The difference between the decomposition in southern and eastern Iceland was found by using two-way ANOVA on litter weight left in the litter bags (see the 3rd example), after six weeks of incubation, followed by Fisher's LSD test on the two bag types and the land region.

To test for the association between different environmental parameters associated with the leaf litter mass loss between the fine and the coarse mesh bags, Pearson r correlation between C/F ratio and different parameters was used. C/F ratio for was calculated by dividing decomposition rate of coarse mesh bags with the decomposition rate of fine mesh bags. Here is an example of the model that was used in this analysis:

```
proc corr;  
var CF Temperature pH Conductivity TotalP TotalN;  
run;
```


3. Results

3.1. Ecosystem structure

3.1.1. Catchment characteristics

The three catchment types in eastern Iceland were not significantly different in size, stream length or average stream width at the sampling station (Table 5). The stream width and depth varied with seasonal changes in discharge, which was indicated with the standard error around the mean. However, heathland streams were significantly deeper than conifer forest streams, but birch forest streams were not significantly different from the others (Table 5). The sampling stations in the heathland streams were in 60–100m higher altitude than the sampling stations for birch and conifer forest streams (Table 5). Furthermore, the sampling stations in the birch forest streams were also at significantly higher altitude than the sampling stations in the conifer forest streams. No significant difference was however between the elevations of the stream sources (upper limits) of the three catchment types in eastern Iceland.

The catchment areas of the four birch and four heathland streams in southern Iceland were not significantly different, nor was there significant difference between their stream lengths, widths, depths, altitudes of the sampling station or the altitude of the stream sources (Table 5).

The run-off catchments in eastern Iceland were larger and the streams were longer than the spring-fed streams in southern Iceland (Table 5). The average catchment size in southern and eastern Iceland was 3.1ha and 504ha, and the average length of the streams was 500m and 13.4km respectively. The spring-fed streams in southern Iceland were slightly narrower and shallower, with average width 70cm and depth 12cm, compared to width of 1.7m and depth of 18cm of the streams in eastern Iceland.

Table 5: Environmental characteristics of the streams in eastern and southern Iceland. Average annual width (\pm standard deviation) and average depth (\pm standard deviation) was based on measurements from February, April, July and September 2008. Also shown (in bold) are the average values (\pm standard error) for each catchment type. Different letters following the average values indicate the significance between different catchment types (one-way ANOVA, followed by Fisher's LSD used to test when significant).

Catchment	Sampling station	Altitude at stream source (m.a.s.l)	Altitude at sampling station (m.a.s.l)	Width (m)	Depth (cm)	Stream length (km)	Catchment size (ha)
Eastern Study Site							
Heathland streams							
Hrafnsgerðisá	AS1	657	161	5.73 \pm 0.03	35.2 \pm 6.0	48	2373
Fjallá	AS2	707	141	2.07 \pm 0.03	17.7 \pm 2.0	5	212
Nýlendulækur	AS3	726	143	1.15 \pm 0.04	18.2 \pm 4.7	8	102
Average		697 \pm 35 a	148 \pm 11 a	2.98 \pm 2.43 a	23.7 \pm 10.0 a	20 \pm 24 a	896 \pm 1281 a
Birch forest streams							
Klifá	AB1	608	91	2.70 \pm 0.00	14.9 \pm 3.2	12	461
Kaldá	AB2	730	97	3.47 \pm 0.08	19.2 \pm 1.0	17	465
Ormsstaðalækur	AB3	445	61	1.25 \pm 0.03	13.1 \pm 2.2	7	210
Average		594 \pm 143 a	83 \pm 19 b	2.47 \pm 1.13 a	15.7 \pm 3.1 ab	12 \pm 5 a	379 \pm 146 a
Conifer forest streams							
Buðlungavallaá	AG1	842	25	3.78 \pm 0.18	16.9 \pm 1.2	14	487
Kerlingará	AG2	563	58	2.00 \pm 0.11	13.6 \pm 1.7	3	51
Jökullækur	AG3	254	60	1.75 \pm 0.15	8.8 \pm 1.5	7	177
Average		553 \pm 294 a	48 \pm 20 c	2.51 \pm 1.10 a	13.1 \pm 4.1 b	8 \pm 6 a	238 \pm 225 a
Southern Study Site							
Unvegetated streams							
Litlifoss Næfurholti	SS1	142	121	1.0 \pm 0.0	14.0 \pm 1.6	0.1	5.3
Lækurinn við gilið á sandinum	SS2	100	90	1.1 \pm 0.1	9.4 \pm 2.7	0.2	9.3
Uppspretta á Haukadalsöldu	SS3	125	114	0.6 \pm 0.0	13.7 \pm 1.5	0.6	0.8
Litla læna Næfurholti	SS4	136	121	0.2 \pm 0.0	7.2 \pm 1.5	0.6	0.3
Average \pm SE		126 \pm 18 a	112 \pm 15 a	0.7 \pm 0.4 a	11.1 \pm 3.3 a	0.4 \pm 0.3 a	4.0 \pm 4.3 a
Birch forest streams							
Sporðalækur Hraunteig	SB1	100	92	0.5 \pm 0.0	15.8 \pm 1.5	0.2	2.0
Lækurinn í botnum Svínhaga	SB2	100	88	0.5 \pm 0.0	15.8 \pm 1.5	1.0	1.3
Lækurinn í botnum Hellisdal	SB3	159	137	0.5 \pm 0.0	16.5 \pm 1.6	0.4	2.9
Ytri lækur Lambatanga	SB4	152	139	1.0 \pm 0.1	6.6 \pm 3.1	1.0	2.9
Average \pm SE		128 \pm 32 a	114 \pm 28 a	0.6 \pm 0.2 a	13.7 \pm 4.7 a	0.6 \pm 0.4 a	2.3 \pm 0.8 a

3.1.2. Catchment vegetation

The average size of catchments in eastern Iceland was 896ha in heathland catchments, 379ha in birch forest catchments and 238ha in conifer forest catchments (Table 5). All the catchments in eastern Iceland extended above the tree line and were therefore not as different as could be expected when compared at whole catchment scale (Figure 14). Nearly 60% of all the three catchment types were covered with continuous vegetation. There was no significant difference (one-way ANOVA, main effect Catchment type: $P = 0.53$) between the catchment types in relative coverage of continuous vegetation (sum of forests, wetlands, grasslands and heathlands). The total forest and woodland cover was ca. 25% for the two forested catchment types. The cover of conifer species in the conifer catchments

was however only 2–10% of their total area and they were mainly located at the downstream parts of those catchments.

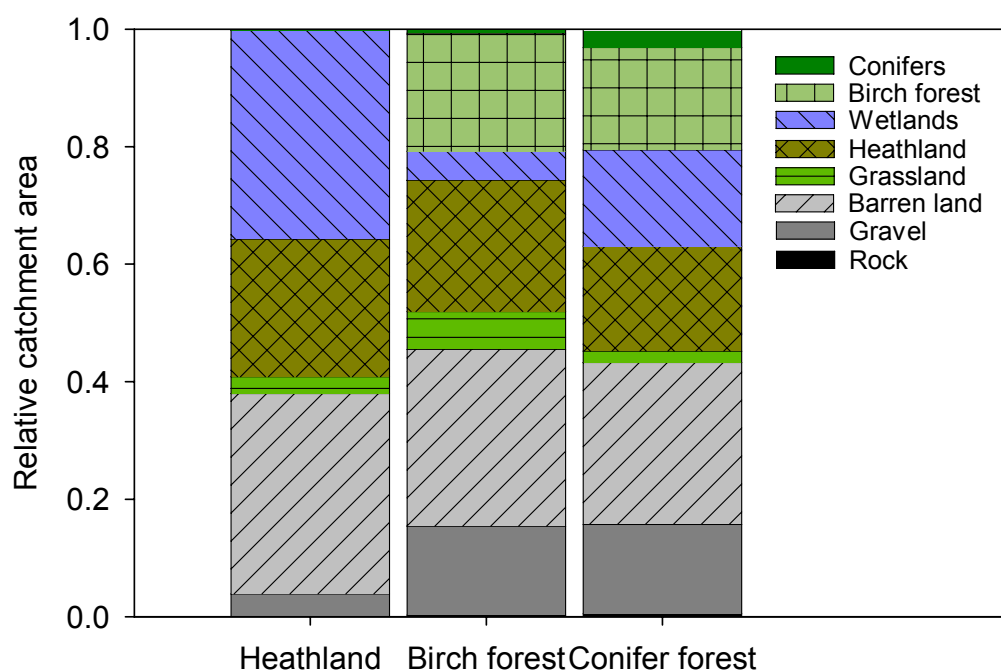


Figure 14: The composition of vegetation within catchments in eastern Iceland, based on averages from three catchments for each catchment type.

When mapping and classifying the catchments, it was revealed that one of the birch catchment (AB3) did extend into a coniferous plantation. There, conifer trees covered 4% of its total catchment area. Similarly, 0.2% of the catchment AS1 was covered by conifer plantation. The plantation extended just over the catchment boundaries at ca. 500m above the sampling station. This is why the birch and heathland catchments are reported to have some coniferous forest (Figure 14). There was about 17–18% of the two forested catchment types covered with heathland vegetation (above tree line), but the heathland catchments did have significantly higher cover of heathland vegetation, or about 32% of the total catchment area (one-way ANOVA, main effect Catchment type, $P = 0.08$). Wetland area was considerable within the catchments; 4%, 13% and 23% for the birch forest, conifer forest and heathland catchment types, respectively, although the difference between catchment types was not significant (one-way ANOVA, main effect Catchment type, $P = 0.10$).

An analysis of vegetation composition 400m above each sampling stations in eastern Iceland proofed to be considerably different from the whole catchment analyses (Figure

15). On average, these defined areas were 7.3ha. The cover of more or less continuous vegetation (sum of forests, grasslands and heathlands) of the two forested catchment types was 91–95%, while the heathland catchments had on average 58%, which was significantly lower (one-way ANOVA, main effect Catchment type, $P = 0.005$). No wetlands existed within the areas, when using this 400m definition. Within heathland catchments a significantly more unvegetated surfaces existed within 400m from the sampling stations (18% compared to 0–2% for the two forested catchment types; $P = 0.04$) and unvegetated surfaces (24% compared to 3–8%, respectively; one-way ANOVA, main effect Catchment type, $P = 0.01$). The cover of forests was 75% and 95% within this 400m area for the birch and conifer catchments respectively and the difference was not significant (one-way ANOVA, main effect Catchment type, $P = 0.45$). The coniferous plantations (mentioned earlier) in the AS1 and AB3 catchments only covered 4% and 8% of the total area within the 400m from the sampling station, respectively.

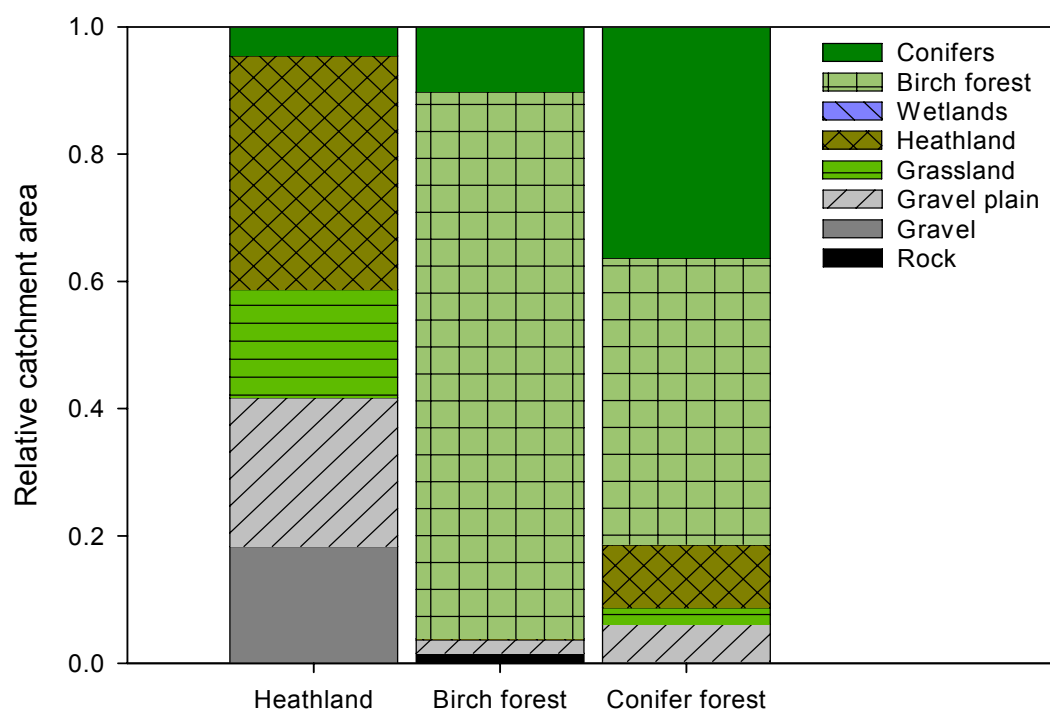


Figure 15: The composition of vegetation within 400m distance from each sampling station in streams in eastern Iceland based on averages from three catchments for each catchment type.

The spring-fed catchments in southern Iceland were much smaller (on average 3ha) than in eastern Iceland (on average 504ha) and therefore the analysis of vegetation composition was only carried out for whole catchments there. The average cover of more or less continuous vegetation (sum of forests, wetlands and grasslands) within the birch forest

catchments in southern Iceland was on average 62%, while the cover of continuous vegetation within the barren catchments was only 6%, which was significantly lower (one-way ANOVA, main effect Catchment type, $P = 0.04$; Figure 16). Gravel and rock dominated the barren catchments, comprising 79% of their total cover compared, to 13% within the birch forest catchments, which was significantly different (one-way ANOVA, main effect Catchment type, $P = 0.003$). The total forest cover was 52% within the birch forest catchments and other prominent vegetation classes were unvegetated (26%), gravel (13%) and grasslands (6%). A patch of wetland vegetation along a stream was within one of the birch forest catchments (SB2), which contributed to 2% of its total area. It should, however, be noted that this area was directly linked to the adjacent stream.

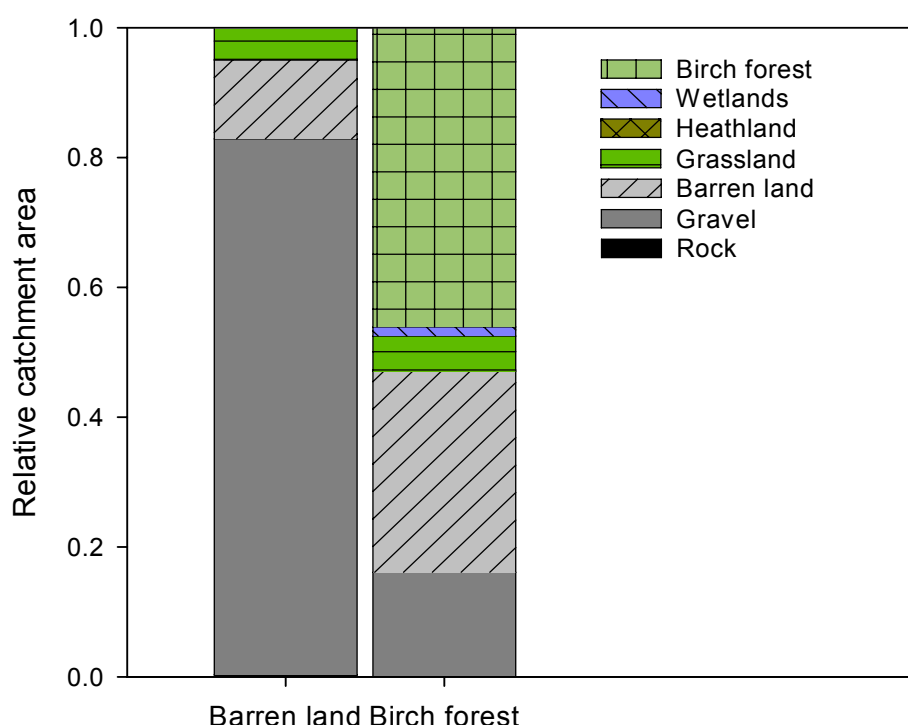


Figure 16: The composition of vegetation composition in southern Iceland based on averages from three catchments for each catchment types. Forest characteristics and vegetation biomass within catchments

Terrestrial vegetation

Only data from eastern Iceland will be reported here, since the measurements of terrestrial vegetation in southern Iceland have not taken place yet. The stand structure of the birch forests and the middle aged coniferous plantations in eastern Iceland was more alike than expected. Both forest types constituted of similar basal areas (ca. $30\text{m}^2\text{ha}^{-1}$) and neither dominant height nor stand density differed significantly between the two forest types (Table

6). The dominant tree height was 33% higher for the conifer forest (12.1m) than the birch forest (9.1m) but this difference was however not statistically significant. The birch forests were 39% denser than the conifer forest, mainly due to the fact that each individual birch tree had on average 1.6 stems compared to 1.3 stems in the conifer plantations (Table 6).

Table 6: Forest characteristics of forested catchments in eastern Iceland. The forest stand density is shown in number of stems and number of individuals per hectare and averages of values within each catchment type \pm standard error, in boldface. Different letters following the averages indicate if there was a significant difference between catchment types (one-way ANOVA, $\alpha = 0.1$).

Catchment	Sampling station	Stand density (# stems ha ⁻¹)	Stand density (# ind ha ⁻¹)	Dominant height (m)	Basal area (m ² ha ⁻¹)
Birch forest catchments					
Klifá	AB1	4500	3050	9.2	31.3
Kaldá	AB2	6992	4135	7.4	15.2
Ormsstaðalækur	AB3	4850	2800	10.6	45.4
Average \pm SE		5447 \pm 779 a	3328 \pm 410 a	9.1 \pm 0.9 a	30.6 \pm 8.7 a
Conifer forest catchments					
Buðlungavallaá	AG1	4350	3750	9.2	21.2
Kerlingará	AG2	3709	3276	14.2	38.7
Jökullækur	AG3	3735	2002	12.9	30.7
Average \pm SE		3931 \pm 210 a	3009 \pm 522 a	12.1 \pm 1.5 a	30.2 \pm 5.1 a

The terrestrial biomass differed less between birch forests and the middle aged coniferous plantations in eastern Iceland than expected. There were no significant differences between any of the biomass components in the two forest types in eastern Iceland (one-way ANOVA, main effect Catchment type, $P > 0.10$; Table 7). Some apparent trends were observed between the two catchment types, even though they were not significantly different, i.e. that the conifer forests had 65% more woody biomass, but similar ground vegetation and litter as in the birch forest. This resulted in 57% higher biomass stored in the conifer forests. The total amount of stored necromass (litter and humus) was similar in the conifer and the birch forests (0.77 and 0.70kgm⁻² respectively; Table 7), these differences were not significant.

There was a clear difference in biomass between the heathland catchments and the two forested catchment types. Within the heathland catchments was 50% higher biomass of ground vegetation in the lowest 400m than within the birch forest catchments and 36% higher than within the conifer forest catchments (Table 7). This difference was not statistically significant ($p = 0.40$). There was neither tree biomass nor bush layer in the

heathland catchments, but there was similar amount of woody litter as within the two forested catchment due to high fraction of dwarf bushes among the ground vegetation (Table 7). However the total litter and humus layer of the heathland catchments was significantly lower than it was within the birch forest (61% lower; $p = 0.01$; Table 7) and the conifer forest catchments (62%; $p = 0.01$; Table 7). The total amount of necromass was also significantly lower in the heathland catchment than within the birch forest catchment (57%; $p = 0.01$; Table 7) and the conifer forest catchments (58%; $p = 0.01$; Table 7). The total biomass within the heathland catchment was 91% and 95% lower than in the birch forest and conifer forest catchments, respectively (Table 7) and this difference was significant ($p = 0.05$ and $p = 0.01$).

Table 7: The biomass of various ecosystem components of the dominant vegetation classes for each catchment in eastern Iceland. The biomass of woody litter is for typical stands of the respective forest type. The ground vegetation and litter masses are spatial averages for the lowest 400m in each catchment type. Also shown, in boldface, are the averages within each catchment type \pm standard error. Different letters following the averages indicate if there was a significant difference between catchment types (one-way ANOVA and Fishers LSD test, $\alpha = 0.1$).

Catchment	Sampling station	Tree layer (kg m ⁻²)	Bush layer (kg m ⁻²)	Ground vegetation (kg m ⁻²)	Woody litter (kg m ⁻²)	Litter and humus layer (kg m ⁻²)	Total necromass (kg m ⁻²)	Total biomass (kg m ⁻²)
Heathland catchments								
Hrafnsgerðisá	AS1	0	0	0.29	0.03	0.21	0.24	0.29
Fjallá	AS2	0	0	0.56	0.06	0.23	0.29	0.56
Nýlendulækur	AS3	0	0	0.86	0.03	0.34	0.36	0.86
Average \pm SE		0	0	0.57 \pm 0.16 a	0.04 \pm 0.01 a	0.26 \pm 0.04 a	0.30 \pm 0.03 a	0.57 \pm 0.16 a
Birch forest catchments								
Klifá	AB1	6.41	0.02	0.36	0.03	0.59	0.63	6.79
Kaldá	AB2	2.45	0.04	0.39	0.04	0.70	0.73	2.87
Ormsstaðalækur	AB3	9.91	0.06	0.40	0.03	0.71	0.74	10.36
Average \pm SE		6.26 \pm 2.16 a	0.04 \pm 0.01 a	0.38 \pm 0.01 a	0.03 \pm 0.00 a	0.67 \pm 0.04 b	0.70 \pm 0.04 b	6.76 \pm 2.16 b
Conifer forest catchments								
Buðlungavallá	AG1	6.01	0	0.46	0.03	0.44	0.46	6.47
Kerlingará	AG2	13.16	0.01	0.40	0.02	0.84	0.86	13.57
Jökulllækur	AG3	11.32	0.04	0.40	0.03	0.80	0.83	11.76
Average \pm SE		10.16 \pm 2.14 a	0.02 \pm 0.01 a	0.42 \pm 0.02 a	0.02 \pm 0.00 a	0.69 \pm 0.13 b	0.72 \pm 0.13 b	10.6 \pm 2.13 b

3.2. Litter transport to streams

The amount of litter that was transported into the lowest 200 m of the streams (i.e. entered the 10 litter traps located at opposite stream sides) was very variable between different catchment types. On average, 1.2g of litter was transported into every metre of the heathland streams in eastern Iceland (Figure 17). This was only a small part of what was transported into the two forested stream types, i.e. 3.2% compared to the birch forest

streams (36.4g) and 2.9% compared to the conifer forest streams (40.2g; Figure 17). This difference was significant ($P = 0.01$; Table 8).

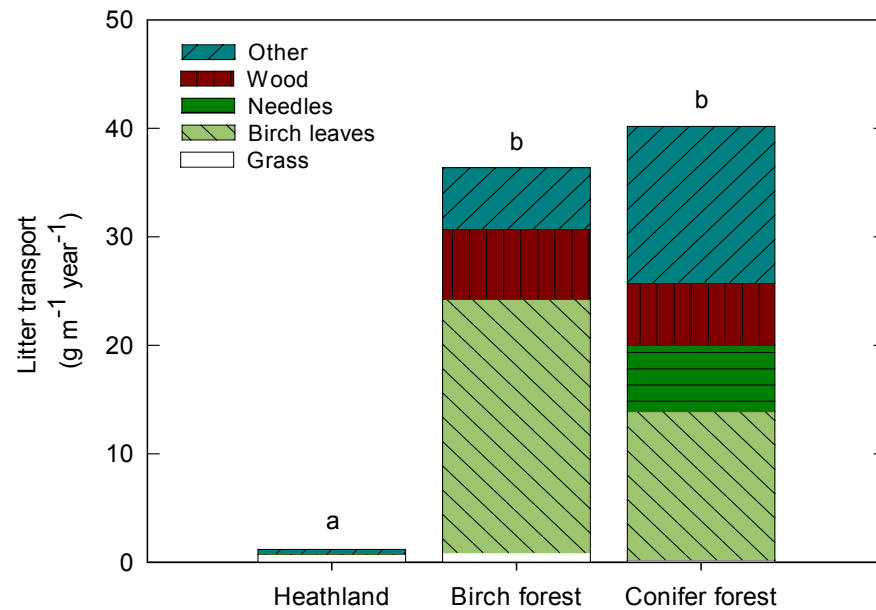


Figure 17: The average amount of litter transported into streams in eastern Iceland. The litter type marked as other litter includes leaves from various woody and non woody plant species and moss. Different letters above the bars indicate the significance level of the total amount of litter between the different catchment types ($\alpha = 0.1$).

There was not a significant difference of the amount of birch leaves or the woody debris between the two forested catchment types (Table 8). There was however significantly more needle litter and other litter (woody and non-woody plant litter other than birch leaves, grass, woody-debris or conifer needles) transported into the conifer forest streams than into the birch forest streams.

Table 8: The P-values from the results of two-way ANOVA followed by Fisher's LSD tests ($\alpha = 0.1$), carried out on different litter types (Figure 17) between the three different catchment types. Significant difference is indicated in boldface.

	Birch	Needles	Grass	Wood	Other	Total
ANOVA	0.04	0.03	0.34	0.02	0.05	0.01
Heathland vs Birch forest	0.01	0.99	0.78	0.01	0.27	0.01
Heathland vs Conifer forest	0.09	0.02	0.27	0.02	0.02	0.01
Birch forest vs Conifer forest	0.21	0.02	0.18	0.70	0.09	0.69

When these results are extrapolated on to the whole catchment area, the total expected amount of litter transport was 4.4kg year⁻¹ for the heathland streams, 61.3kg year⁻¹ for the birch forest streams and 100.3kg year⁻¹ for the conifer forest streams. These calculations took into consideration the composition of the vegetation classes within each catchment and the total length of each stream.

3.3. Temperature and chemical variables

3.3.1. Eastern Iceland

All the streams in eastern Iceland were slightly alkaline, irrespective of catchment type, with the average pH between 7.4 and 7.8 for individual streams (Table 9). There was no apparent difference in the averages of pH between the different catchment types, contrary to what was expected (Table 9). The conductivity of the stream water varied between 51 and 106μS cm⁻¹ (corrected at 25°C) for an individual stream and did not differ significantly between catchment types, which was also contrary to what was expected (Table 9).

The concentration of total phosphorus (P_{tot}) and total nitrogen (N_{tot}), based on measurements from 19th–21st of May 2008, was not significantly different between catchment types (Table 9). Generally, the concentrations were low, or 0.004mg l⁻¹ for P_{tot} and 0.013mg l⁻¹ for N_{tot}. The detection limit for an individual sample was 0.006mg l⁻¹ for P_{tot} and 0.029mg l⁻¹ for N_{tot}, which means that many samples were below or close to a detection limit.

The annual average water temperature in the streams measured by spot measurements (Table 9) was 49% and 28% higher in the heathland streams than in the birch forest streams and the conifer forest streams, respectively. This difference was not significant.

Table 9: Information on temperature, pH, conductivity and concentration of total P and total N in eastern and southern Iceland. All values are annual means (\pm s.d.) based on spot measurements in 2008 (February, May, July and October), except nitrogen and phosphorus concentrations which were only measured in May 2008. Also shown (in bold) are the averages (\pm SE) for each catchment type. Different letters following the standard error values indicate if there was significant difference between catchment types within eastern and southern Iceland (one-way ANOVA, followed by Fisher's LSD test when significant)

Catchment	Sampling station	Water temperature(°C)	pH	Conductivity (mS m ⁻¹)	Total P (mg l ⁻¹)	Total N (mg l ⁻¹)
Eastern Study Site						
Heathland catchments						
Hrafnsgærðisá	AS1	4.0 \pm 4.8	7.7 \pm 0.3	94 \pm 42	0.011*	0.043**
Fjallá	AS2	5.3 \pm 5.4	7.6 \pm 0.2	63 \pm 21	0.007*	0.012**
Nýlendulækur	AS3	8.5 \pm 5.9	7.4 \pm 0.3	74 \pm 19	0.001*	0.012**
Average \pm SE		5.9 \pm 2.3 a	7.6 \pm 0.2 a	77 \pm 16 a	0.006 a	0.022 a
Birch forest catchments						
Klifá	AB1	4.3 \pm 5.6	7.4 \pm 0.4	54 \pm 11	0*	0**
Kaldá	AB2	4.3 \pm 2.8	7.8 \pm 0.5	51 \pm 10	0.005*	0.033**
Ormsstaðalækur	AB3	4.1 \pm 2.3	7.7 \pm 0.3	105 \pm 6	0.012*	0.01**
Average \pm SE		4.2 \pm 0.1 a	7.6 \pm 0.2 a	70 \pm 30 a	0.005 a	0.015 a
Conifer forest catchments						
Buðlungavallá	AG1	4.3 \pm 4.7	7.4 \pm 0.3	53 \pm 17	0*	0**
Kerlingará	AG2	4.8 \pm 2.9	7.7 \pm 0.6	69 \pm 6	0.002*	0**
Jökullækur	AG3	4.6 \pm 3.7	7.4 \pm 0.4	66 \pm 10	0.006*	0.01**
Average \pm SE		4.6 \pm 0.2 a	7.5 \pm 0.2 a	63 \pm 8 a	0.002 a	0.003 a
Southern Study Site						
Unvegetated catchments						
Litlifoss	SS1	2.9 \pm 0.1	8.5 \pm 0.4	212 \pm 20	0.061	0.033
Gilið frammi á Sandi	SS2	6.5 \pm 0.7	8.2 \pm 0.2	143 \pm 17	0.066	0.037
Uppspretta á Haukadalsöldu	SS3	3.4 \pm 0.1	8.7 \pm 0.4	217 \pm 6	0.057	0.101
Litla læna	SS4	2.9 \pm 0.0	8.6 \pm 0.5	216 \pm 10	0.074	0.465
Average \pm SE		3.9 \pm 1.7 a	8.5 \pm 0.2 a	197 \pm 36 a	0.065 a	0.159 a
Birch forest catchments						
Sporðalækur	SB1	5.3 \pm 0.4	7.9 \pm 0.5	159 \pm 4	0.129	0.143
Botnar í Svínhaga	SB2	4.5 \pm 0.6	8.2 \pm 0.5	253 \pm 13	0.061	0.039
Botnar í Hellisdal	SB3	3.2 \pm 0.0	9.1 \pm 0.5	181 \pm 4	0.076	0.071
Ytri lækur	SB4	5.0 \pm 0.4	8.0 \pm 0.5	154 \pm 8	0.081	0.119
Average \pm SE		4.5 \pm 0.9 a	8.3 \pm 0.5 a	187 \pm 46 a	0.087 a	0.093 a

* Limits of detection 0.006 ** Limits of detection 0.029

Continuous temperature measurements

The continuous logging of water temperature showed large fluctuations between seasons in eastern Iceland (Figure 18). The variability of the average day temperature in heathland streams was greater than was found in the two forested stream types. It ranged between -0.8 and 15.0°C compared to -0.2–12.4°C for the birch forest streams and -0.6–13.4°C for the conifer forest streams.

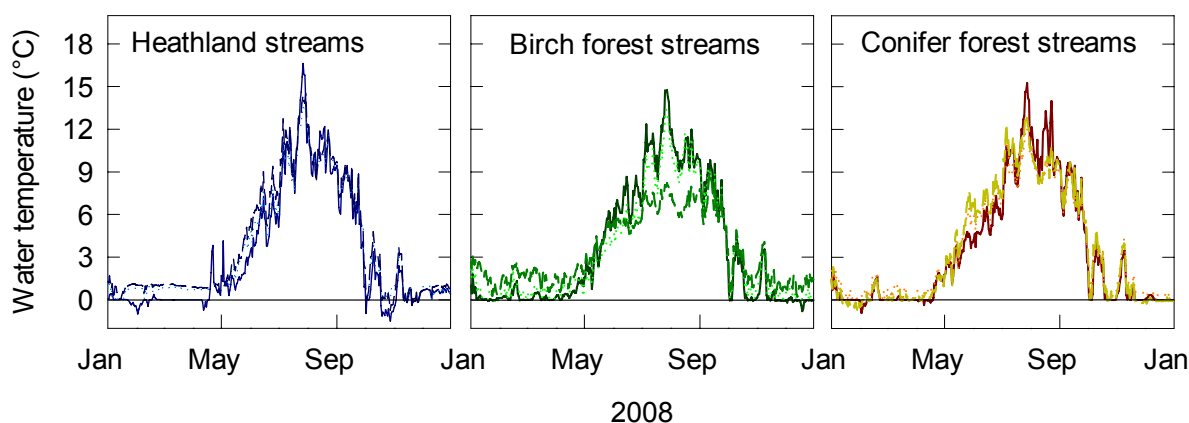


Figure 18: Water temperature recorded by data loggers at 30 minutes intervals in 2008 within the streams in eastern Iceland. Each line represents a single streams temperature within one of the three different catchment types.

3.3.2. Southern Iceland

The pH-values of individual streams in southern Iceland ranged between 7.9 (SB1) and 9.1 (SB3), but no significant differences were found between the two catchment types (Table 9). The average conductivity of the stream water varied between 143 (SS2) and 253 $\mu\text{S cm}^{-1}$ (SB2) (Table 9). There was not a statistically significant difference in conductivity between the two different catchment types, but the trend was that the conductivity of the barren land steams ($197\mu\text{S cm}^{-1}$) was slightly higher than in birch forest streams ($187\mu\text{S cm}^{-1}$), contrary to what was expected.

The spring-fed streams in southern Iceland were more alkaline than the run-off streams in eastern Iceland. The average pH was 8.4 for the spring-fed streams, which was 11% higher than was found in the run-off streams in eastern Iceland (Table 9). The average conductivity of the streams in southern Iceland ($192\mu\text{S cm}^{-1}$) was also 175% higher than in the streams in eastern Iceland ($70\mu\text{S cm}^{-1}$; Table 9).

The average concentration of P_{tot} and N_{tot} in the spring-fed streams, measured 29th–30th of April 2008, was not significantly different between the two catchment types in southern Iceland (Table 9).

The concentration of P_{tot} was 0.076mg l^{-1} , which was almost 20 times higher than it was in eastern Iceland (0.004mg P l^{-1} ; Table 9). The concentration of N_{tot} was four times higher in

the streams in southern Iceland, or 0.126mg l^{-1} compared to 0.029mg l^{-1} in eastern Iceland (Table 9).

It should be noted that a considerable difference was in N_{tot} concentrations in two of the unvegetated catchment streams (SS1 and SS4), which originated from springs that were only few hundred metres apart (Figure 3). These two streams had the lowest and highest N_{tot} concentrations measured in the southern site, 0.033mg l^{-1} (SS1) and 0.465mg l^{-1} (SS4).

The average water temperature in the spring-fed streams, based on spot measurements, was 15% higher in birch forest streams than in the barren land streams in southern Iceland. This was in reverse to what was found in eastern Iceland (Table 9). This difference was, however, not significant. The annual fluctuations in water temperature proved to be much more stable in the spring-fed streams of southern Iceland than was observed in the run-off streams of eastern Iceland (Figures 18 and 19).

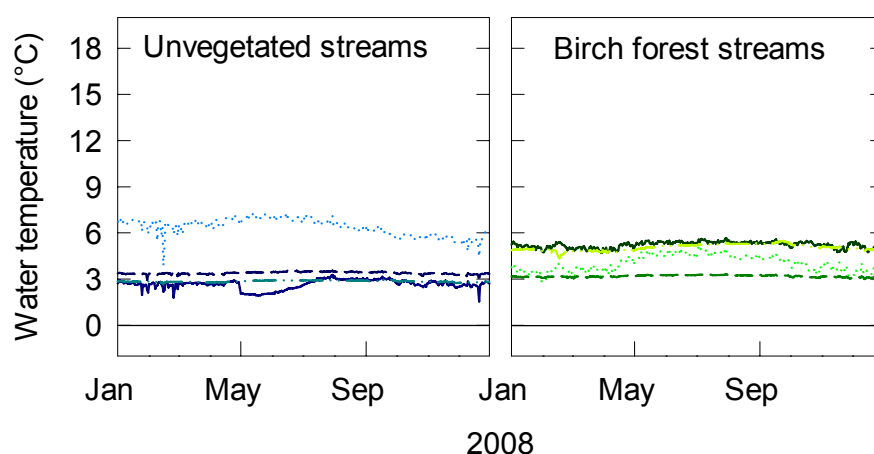


Figure 19: The water temperature recorded by data loggers at 30 minutes intervals measurements in year 2008, in streams in southern Iceland. Each line represents a single streams temperature within one of the two different catchment types.

3.4. Ecosystem activity

3.4.1. The decomposition rate in streams

A comparison of the decomposition rate of the dominant litter types within their corresponding catchments in eastern Iceland (i.e. grass litter in heathland streams, birch

leaves in birch forest streams and conifer needles in conifer forest streams) showed no significant difference (Figure 20; ANOVA main effect catchment type: $P = 0.30$), which was contrary to what was expected. The average decomposition rate (k-value) in all of the streams was $0.0038 \text{ g g}^{-1} \text{ DM day}^{-1}$. It should be noted that the average decomposition rate of grass litter that entered streams with dominating heathland vegetation was somewhat higher than for birch leaf litter and siberian larch needle litter in the corresponding forest streams ($0.0044 \text{ g g}^{-1} \text{ DM day}^{-1}$ in comparison to 0.0033 and the 0.0037 , respectively; Figure 20), although the difference was not statistically significant.

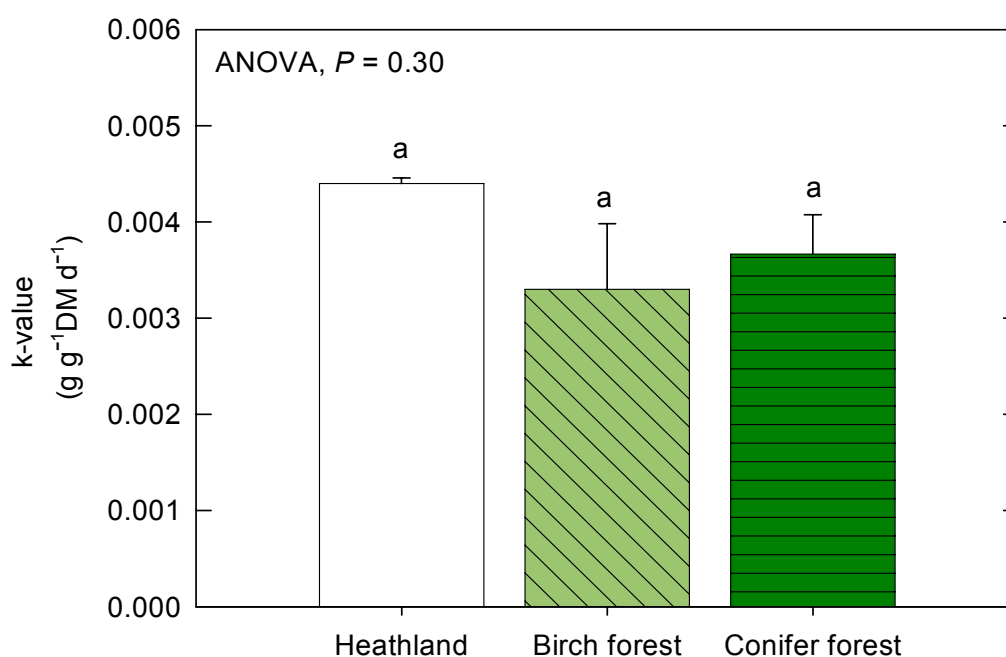


Figure 20: The mean decomposition rate (k-value) for three different litter types which are grass, birch leaves and larch needles in streams with the corresponding dominating catchment vegetation. The bars represent means \pm standard error, $n=3$. The P-value based on One-way ANOVA between catchment types is shown. Different letters above bars indicate post-hoc Fisher's LSD tests for significant differences between catchment types.

3.4.2. The quality of litter entering the streams

To verify if litter quality was equally important for decomposition activity of microbes (bacteria and fungi) and invertebrates in streams, all three litter types (grass, birch leaves and larch needles) were put in coarse mesh bags in all streams in eastern Iceland. There was a significant difference between the decomposition rate of different litter types across all catchment types (Figure 21; ANOVA main effect Litter type, $P = 0.03$). With further analysis it was revealed that the decomposition rate of grass litter was significantly faster

than for the birch leaves (Fishers LSD: $p = 0.07$) and for the larch needles (Fishers LSD: $p = 0.08$) within the conifer forest streams (Figure 21). The decomposition rate for grass litter was also significantly faster than for birch leaves within the birch forest streams (Fishers LSD: $p = 0.03$; Figure 21). The same applied to the larch needles, which also decomposed significantly faster than birch leaves within the birch forest streams (Fishers LSD: $p = 0.03$; Figure 21). However, all litter types decomposed at a similar rate in the heathland streams (Figure 21).

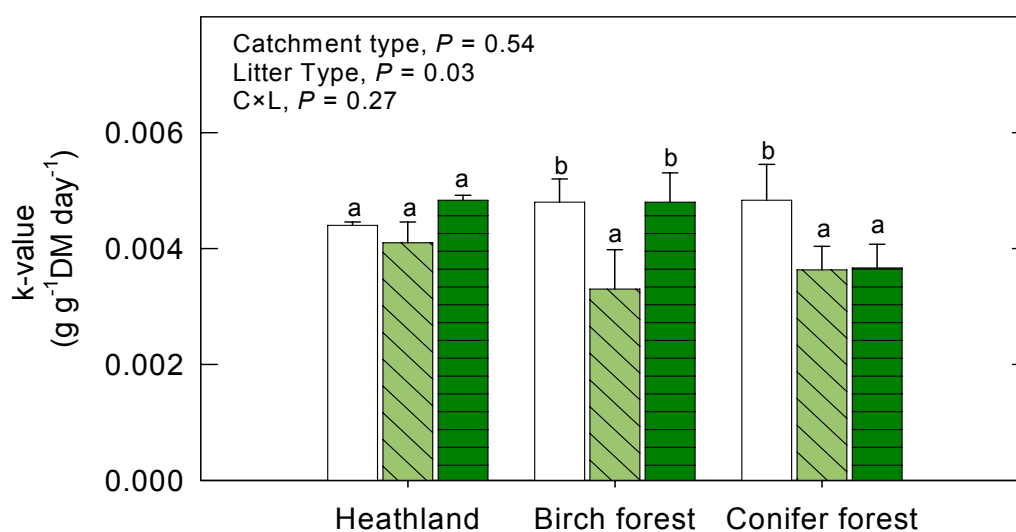


Figure 21: The average decomposition rate (k-value) \pm standard error of all litter types in the three catchment types in eastern Iceland, $n = 3$. White, light green and dark green bars indicate grass, birch leaf and larch needle litter, respectively. Also shown are the main factors and interaction of a two-way repeated ANOVA. Different letters above bars indicate post-hoc Fisher's LSD tests for significant differences between litter types within catchment types. CxL is the interaction between catchment type and litter type.

Even if litter types showed some significant differences within individual catchment types, the average decomposition rate (k-value) of the three litter types was not significantly different when compared across all nine streams in eastern Iceland (Main effect: "Catchment type", $P = 0.54$; Figure 21).

3.4.3. Invertebrates colonizing litter bags

The importance of invertebrates in the decomposition process was studied by using different mesh size litter bags; fine mesh bags excluded invertebrates while coarse mesh bags allowed them to take part in the decomposition. In this analysis, only the dominant

litter types in their corresponding catchment type were analysed (i.e. grass litter in heathland streams, birch leaves in birch forest streams and larch needles in conifer forest streams). The invertebrates did not seem to affect the decomposition process significantly in streams in eastern Iceland (Figure 22, main effect Bag type, $P = 0.36$).

Similar to what was found earlier, there was no significant differences in decomposition rate between catchment types when even fine mesh bags were included in the analysis (Figure 22; ANOVA main effect Catchment type, $P = 0.27$).

Even if invertebrates did not significantly affect the decomposition process (k-values) of dominant litter types in different catchments, there were some noteworthy trends in the data (Figure 22). The decomposition rate of birch leaves in the birch forest streams showed some surprising trends towards faster decomposition when invertebrates were excluded from the decomposition process (Figure 22).

To look further into this negative effect for birch leaf litter, the remaining weight at different collection times were studied. The slower decomposition within the coarse mesh bags was significant in the first collection (48 days of immersion) in streams within all catchment types (Figure 23; ANOVA main effect Bag Type: $P_{\text{birch forest}} = 0.07$, $P_{\text{conifer forest}} = 0.08$ and $P_{\text{heathland}} = 0.06$). The negative effect of the invertebrates on the decomposition rate of birch litter was not significant after the first 48 days in any of the streams (Figure 23).

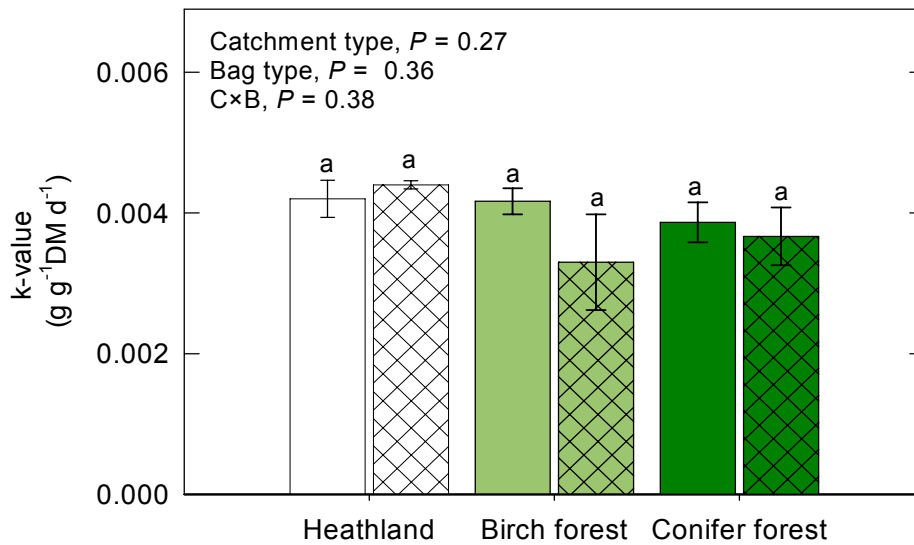


Figure 22: The average decomposition rate (k-value) \pm standard error of dominant litter types in fine and coarse mesh bags in the three catchment types in eastern Iceland, $n = 3$. Litter from fine mesh bags are indicated with empty bars and litter from coarse mesh bags are indicated in coarse meshed bars. Also shown are the main factors and interaction of a two-way repeated ANOVA. Letters above bars indicate results from post-hoc Fisher's LSD tests for significant differences ($\alpha = 0.1$) between bag types within catchment types. C×B is the interaction between Catchment type and Bag type.

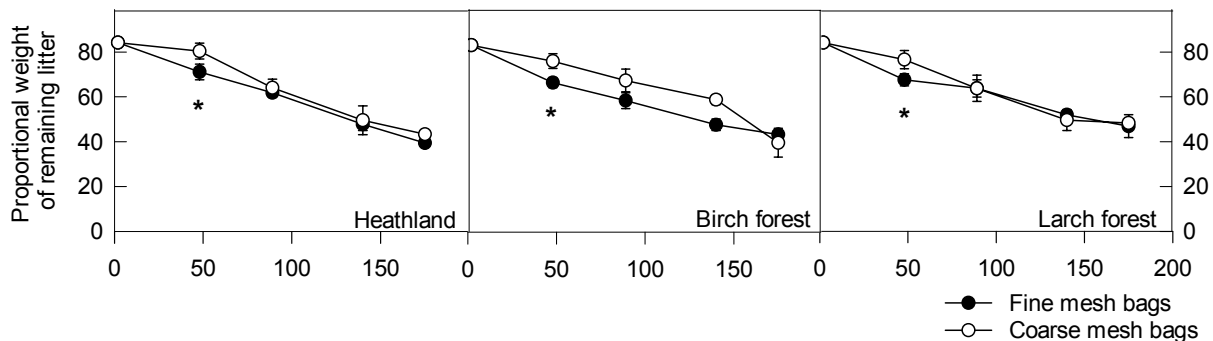


Figure 23: The proportion of weight of remaining litter in fine and coarse mesh litter bags incubated for 48, 89, 140, 175 days in three catchment types in eastern Iceland (%; \pm standard error, $n = 3$). A star indicates a significant difference between fine and coarse mesh bags (two-way repeated ANOVA followed Fishers LSD tests, $\alpha=0.10$).

To look further into this negative effect of allowing invertebrates to access the litter, similar analysis was done by looking at individual incubation times for the three dominant litter types in their corresponding catchment type (Figure 24). When the three litter types were considered in their dominating stream systems, there was no significant difference between the weight of the remaining litter, except for the first collection (48 days) of the birch (as

mentioned earlier) and the fourth collection of the grass litter (175 days) in the heathland streams (Figure 24; Fisher's LSD test: $p_{\text{heathland}} = 0.04$). The presence of invertebrates did therefore generally not seem to consistently affect the rate of decomposition when analysed as remaining weight, which confirmed the earlier finding on the k-values (Figure 22).

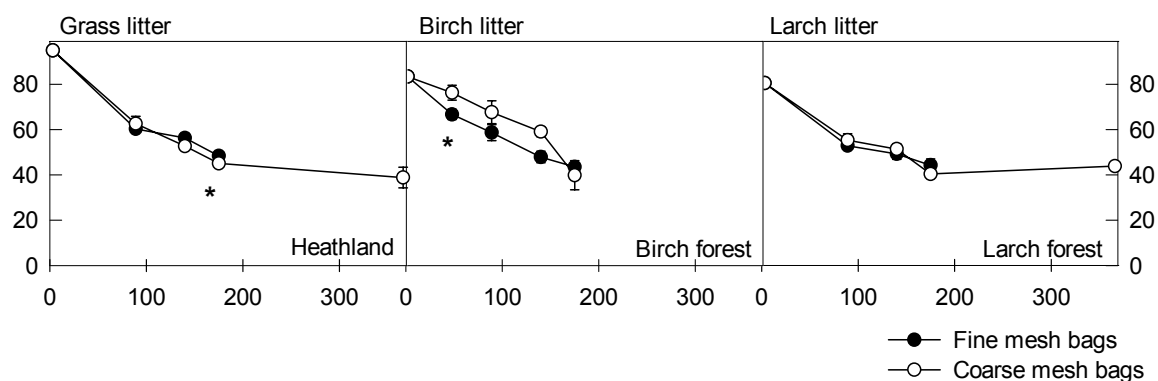


Figure 24: The proportion of weight of remaining litter in fine and coarse mesh litter bags with dominant litter types in their corresponding catchment types in eastern Iceland (%; \pm standard error, $n = 3$). A star indicates a significant difference between fine and coarse mesh bags (two-way repeated ANOVA followed Fishers LSD tests, $\alpha=0.10$).

3.4.4. The invertebrate fauna in coarse mesh litter bags

The analysis of the invertebrate fauna colonizing the litter bags was only performed in the eastern study site. The number of invertebrates found within the bags was 24% higher in streams running through forested catchments than in those running through heathland catchments (Figure 25a). This difference was not statistically significant. On average there were 245 individuals found in each bag for the dominant litter type in the corresponding catchment type. The average number of invertebrates was 218 individuals in the grass litter bags which were incubated in heathland streams, 254 individuals in the birch litter bags in birch forest streams and 269 individuals in larch litter bags which were incubated in conifer forest streams (Figure 25a). The vast majority of invertebrates in all streams belonged to Chironomidae larvae, or 96% of the total number of invertebrates, irrespective of litter and catchment type.

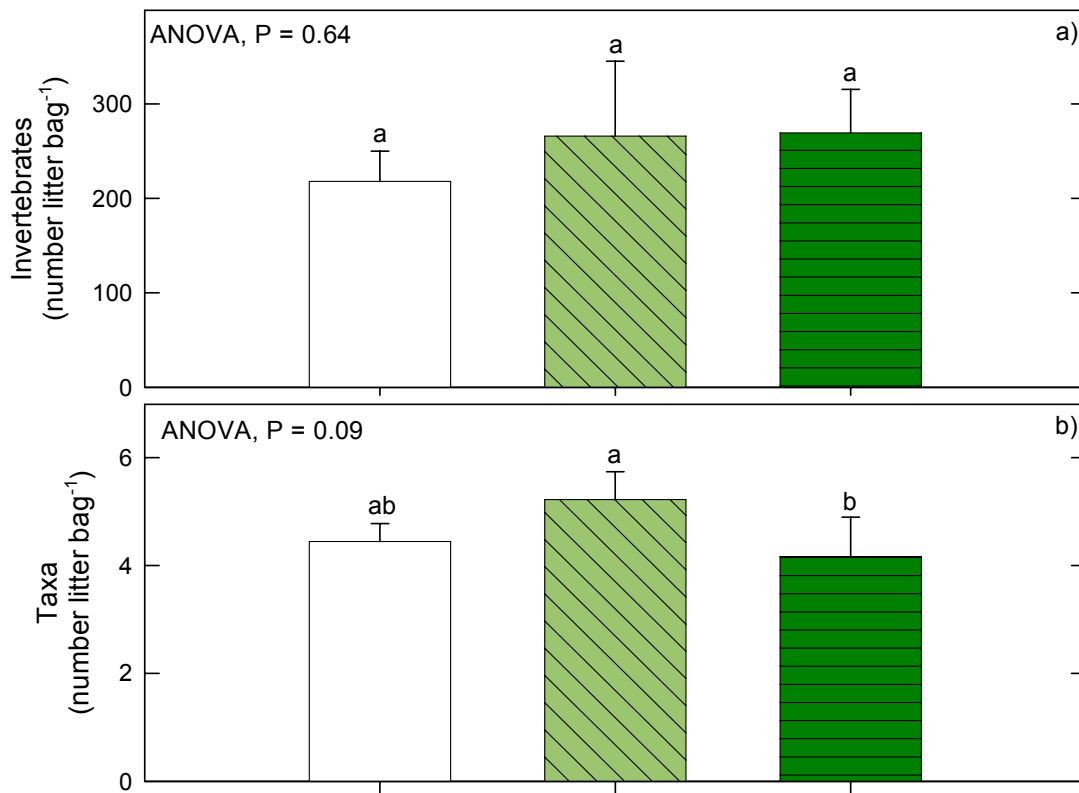


Figure 25: The average number of a) invertebrates in litter bags and b) number of invertebrate taxa in litter bags for three different litter types, grass, birch and larch needles, in streams with corresponding dominating catchment type. Vertical lines on the top of each column show the standard error of the mean. Also are shown the results from one-way ANOVA. Letters above each bar indicate results from post-hoc Fisher's LSD tests for significant difference between catchment types.

Fourteen invertebrate taxa were found in the litter bags, they were: Acarina, Chironomidae, *Clinocera* sp., Coleoptera, *Dicranota* sp., Gastropoda *Limnophora* sp., Oligochaeta, Plecoptera, Simuliidae, Tipulidae and Trichoptera. The average number of taxa within a litter bag was $4.6 (\pm 0.23 \text{ SE})$, when using a dominant litter type in its corresponding catchment type (Figure 25b). The number of invertebrate taxa found in litter bags containing birch litter, incubated in birch forest streams was significantly higher than the number of taxa found in litter bags containing larch needles incubated in conifer forest streams (Figure 25b; ANOVA main effect catchment type: $P = 0.09$). The number of taxa was, however, not significantly different between the conifer forest streams and heathland streams and between heathland and birch forest streams (Figure 25b; Fishers LSD $p = 0.46$ and $p = 0.14$, respectively).

The invertebrates were grouped into the following functional feeding groups:

Filtering collectors: Simuliidae.

Gathering collectors: Chironomidae and Oligochaeta.

Scrapers: Chironomidae.

Predators: Chironomidae, Acarina, *Clinocera* sp., Coleoptera, *Dicranota* sp., Diptera.

Shredders: Chironomidae, Plecoptera, Tipulidae and Trichoptera.

It was apparent that scrapers and gathering collectors were the largest groups within the litter bags of the headwater streams. Surprisingly, there were only about 3–4% of the invertebrates that were identified as shredders, which turned out to be the second smallest functional feeding group found within the litter bags (Table 10). Scrapers were most numerous, with 57% of the individuals, in heathland streams. They were 49% in birch forest streams and 44% in conifer forested streams. Gathering collectors accounted for 36%, 43% and 43% of the total invertebrate number in the heathland, birch forest and the conifer forest streams, respectively.

Table 10: The average number (\pm standard error) of different functional feeding groups among stream invertebrates that were found in litter bags containing grass litter, birch leaves and larch needles incubated in the three catchment types in eastern Iceland.

Catchment	Gathering collectors	Filtering collectors	Scraping collectors	Shredders	Predators	Total number
Heathland	78 \pm 36	3 \pm 4	124 \pm 57	6 \pm 4	7 \pm 4	218 \pm 60
Birch forest	115 \pm 57	3 \pm 2	131 \pm 65	9 \pm 2	8 \pm 2	266 \pm 70
Conifer forest	115 \pm 32	3 \pm 4	119 \pm 34	10 \pm 1	22 \pm 7	269 \pm 55

Analysis on the number of invertebrates at different times of incubation was only carried out on the birch leaves litter bags which had been placed in all three catchment types (Figure 26). There was no significant difference between the average invertebrate numbers in the streams of the three catchment types (Main effect: Catchment $P = 0.49$).

There were, however, highly significant increases in invertebrate density with time (Main effect: Collection $P = <0.001$). When compared separately for each catchment type this effect was only significant for the two forested stream types, but not for the heathland streams (Figure 26). Within the birch forest streams the number of invertebrates increased by 110% between collection 2 and 3 (August and November) and similar change (543%) was seen for conifer forest streams between collections 2 and 3.

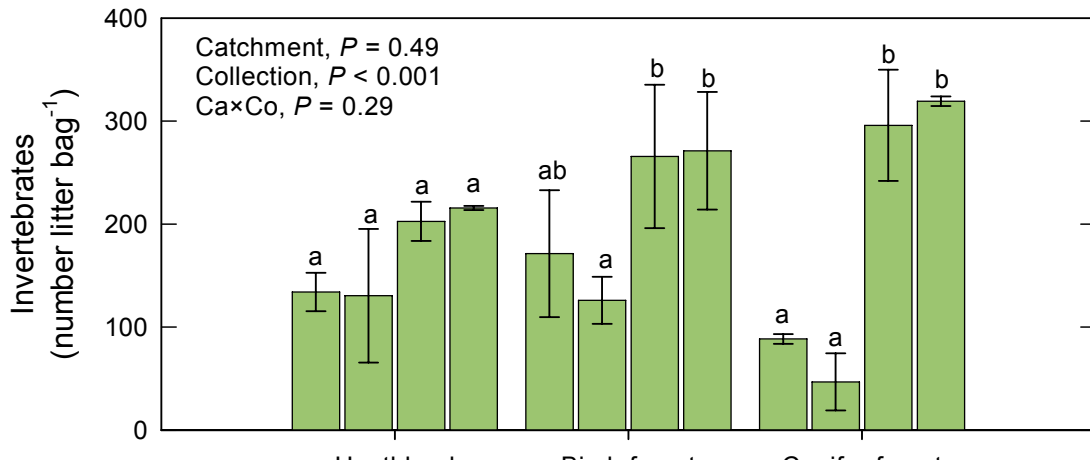


Figure 26: The average number (\pm standard error) of invertebrates within birch litter bags incubated for 48, 89, 140 and 175 days in streams with different catchment types in eastern Iceland. Also shown are the results of a two-way repeated ANOVA. Letters above the bars indicate post-hoc Fisher's LSD tests for significant differences between collection times within each catchment type. Ca \times Co is the interaction between catchment and collection.

The average number of taxa found in birch litter bags was also not significantly different across the three catchment types (Main effect: Catchment $P = 0.54$; Figure 27).

When the number of taxa was analysed at different times there was a significant difference between the collections (Main effect: Coll $P < 0.001$; Figure 27), but there was also significant interaction found between the collection time and the catchment type (Main effect: Ca \times Co, $P = 0.05$; Figure 27). This indicated different responses in taxa numbers with time between catchment types. The interaction was caused by irregular pattern in the taxa number over the season (Figure 27). The highest number of taxa was always found in collection 3 (October) in all catchment types and the average number of taxa significantly decreased by 66%, 77% and 61% in the autumn (collections 3 and 4; October and November) in the heathland, birch forest and conifer forest streams, respectively.

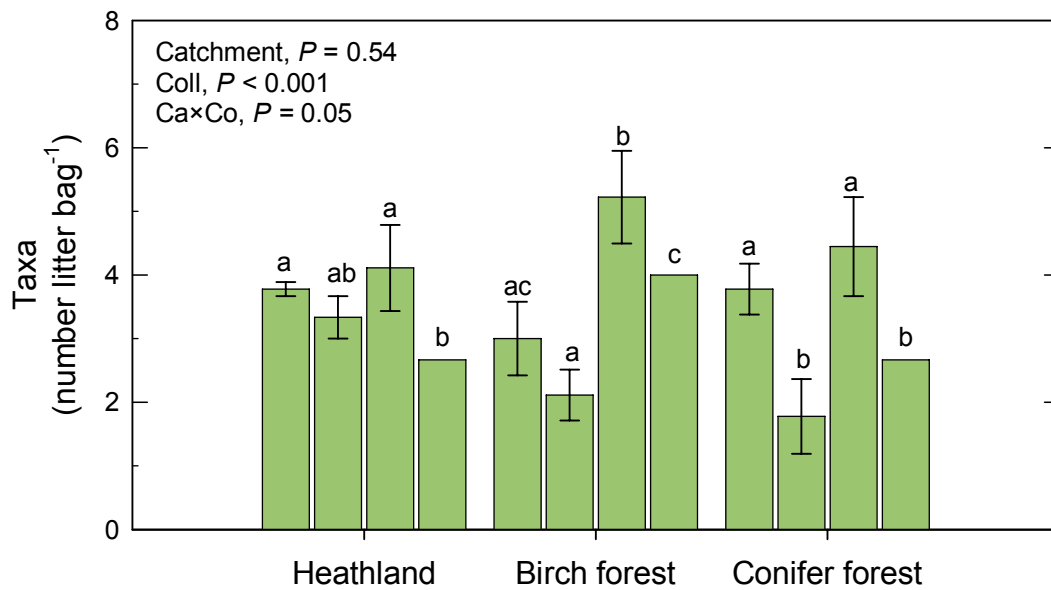


Figure 27: The average number (\pm standard error) of invertebrate taxa within birch litter bags incubated for 48, 89, 140 and 175 days the three catchment types in eastern Iceland. Also shown are the results of a two-way repeated ANOVA. Letters above the bars indicate results from post-hoc Fisher's LSD tests for significant differences between litter types within each catchment type.

3.5. Estimate of total decomposition within streams

To estimate the total decomposition of organic matter within the stream system some predetermined conditions (assumptions) were set: a) all organic matter that is transported into the streams will decompose somewhere within the stream ecosystem (i.e. the amount drifting out of the system is not accounted for), b) temporal fluctuations in litter transport are not considered (irrespective of the fact that the organic matter does not transport evenly in time into the stream ecosystem) and c) annual decomposition rate is a constant (which is not completely true; see winter decomposition, see further in Chapter 3.8). Considering all those assumptions, the total decomposition of allochthonous litter in streams could be estimated.

The total amount of litter decomposed per meter stream within the heathland streams was 20 times less than within the birch forest streams and 25 times less than within the conifer forest streams (Table 11). Since the decomposition rates were similar for different litter types, these results mostly mirror the difference in litter transport to streams. Interestingly the difference between the total amount of litter decomposed in coniferous forest streams was only 20% higher than in the birch forest streams (Table 11).

Table 11: The average total decomposition of litter per metre stream per day ($\text{g m}^{-1} \text{day}^{-1}$), based on numbers from the total amount of litter entering the stream (see Figure 17) and the average decomposition rate for every catchment type (see Figure 20).

Catchment	Birch leaves	Needles	Grass	Wood*	Other**	Total
Heathland	0.000	0.000	0.003	0.0000	0.0016	0.005
Birch forest	0.077	0.000	0.004	0.0004	0.0215	0.103
Conifer forest	0.045	0.023	0.001	0.0004	0.0548	0.124

* decomposition rate based on Krankina and Harmon, 1995

** decomposition rate based on average decomposition of birch leaves, larch needles and grass litter from the present thesis

3.6. Influences of abiotic and biotic parameters on litter decomposition

A correlation analysis was run on the data to see if any of the abiotic factors were affecting the litter decomposition. Abiotic factors were generally not correlated with the decomposition rate in eastern Iceland (Table 12), except the concentration of phosphorus (P_{tot}), which was positively correlated with the k-values across all streams and litter types (Pearson's $r = 0.57$, $P = 0.002$; Figure 28). When individual litter types were analysed, a significant positive correlation was found between P_{tot} and grass litter ($r = 0.71$, $P = 0.03$) and the larch needles ($r = 0.72$, $P = 0.03$), but a similar positive trend was however not significant for the birch leaves, ($r = 0.39$, $P = 0.30$).

The ratio between the k-values of coarse and fine mesh bags (C/F) was used across all three litter types (Table 12), to see if the abiotic factors could explain some of the observed differences in how invertebrates affected the decomposition process. There was no significant correlation between any of the abiotic variables and the $C/F_{k\text{-value}}$ ratio across all litter types. However, there were negative correlations between the $C/F_{k\text{-value}}$ ratios of grass litter across all streams and the concentration of P_{tot} and N_{tot} , $r = -0.72$, $P = 0.03$ and $r = -0.69$, $P = 0.04$, respectively). This negative relationship reveals a faster increase in the decomposition within the fine mesh grass litter than within the coarse mesh bags as P and N concentrations increased in streams. However, the negative response was not significant for grass and larch litter when the k-values or weight remaining were compared for coarse and fine bags in their corresponding catchment types. This negative response mainly occurred for grass and larch decomposition in streams not belonging to their corresponding catchment types (data not shown). The only litter type which had significantly lower k-values in coarse mesh bags, the birch leaf litter, did however not show a significant

correlation to stream P_{tot} nor N_{tot} concentrations ($r = 0.36$, $P = 0.30$ and $r = 0.32$, $P = 0.40$, respectively).

To see if the presence of different groups of invertebrates could explain the effect of allowing the invertebrates to enter the litter bags, the correlation between the invertebrate groups and the C/F_{weight} ratio was calculated. Note that the C/F_{weight} ratio is based on litter mass left in the bags at collection 3 (140 days), when the invertebrates were sampled. Lower C/F_{weight} ratios therefore indicate less litter left in coarse mesh bags, i.e. higher decomposition activity when invertebrates were not excluded. No functional feeding group or invertebrate taxa group was significantly correlated to the C/F_{weight} ratio across the litter types (Table 13), except for Plecoptera (Figure 29). Surprisingly the relationship was positive, which indicated that the increased presence of this group in the litter bags decreased the decomposition rate of the litter.

Table 12: Results from Pearsons correlations (r) between annual mean values of abiotic factors measured in the stream water and the average decomposition rates (k -values) and the ratio between the coarse and fine mesh litter bag decomposition rates (C/Fk -value) as well as their P -values. N denotes the number of values used in the analysis. Significant correlations are indicated in boldface.

Parameter vs	k-value			C/F (k-values)		
	r	P	N	r	P	N
Temperature (°C)	0.205	0.306	27	0.117	0.560	27
pH	-0.074	0.713	27	0.063	0.755	27
Conductivity ($\mu\text{S cm}^{-1}$)	0.223	0.264	27	-0.002	0.993	27
N_{tot} (mg l^{-1})	0.173	0.388	27	0.012	0.953	27
P_{tot} (mg l^{-1})	0.570	0.002	27	0.145	0.472	27

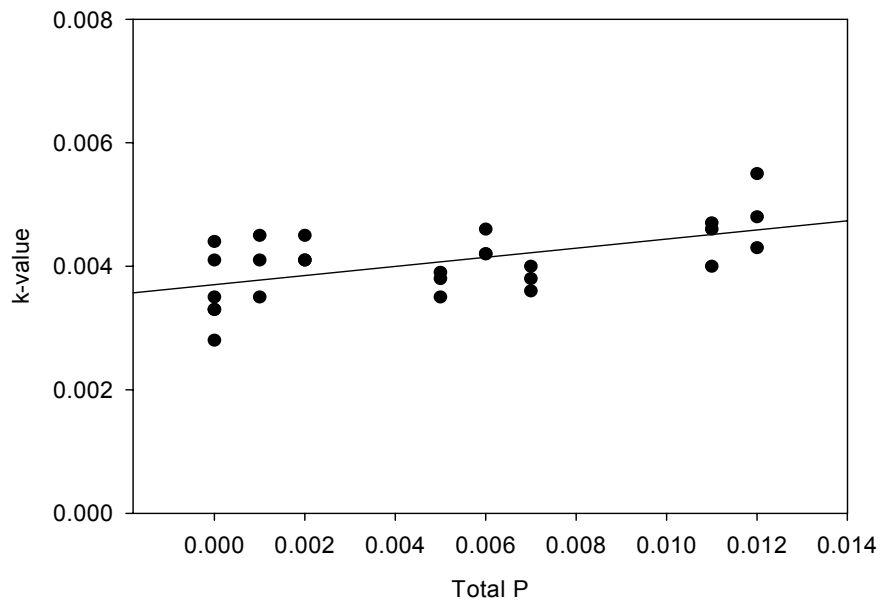


Figure 28: Correlation (Pearsons r) between the average decomposition rates (k-value) of fine mesh litter bags of all litter types in all catchment types, and the concentration of phosphorus (P_{tot}) measured in streams in eastern Iceland in end of May 2008.

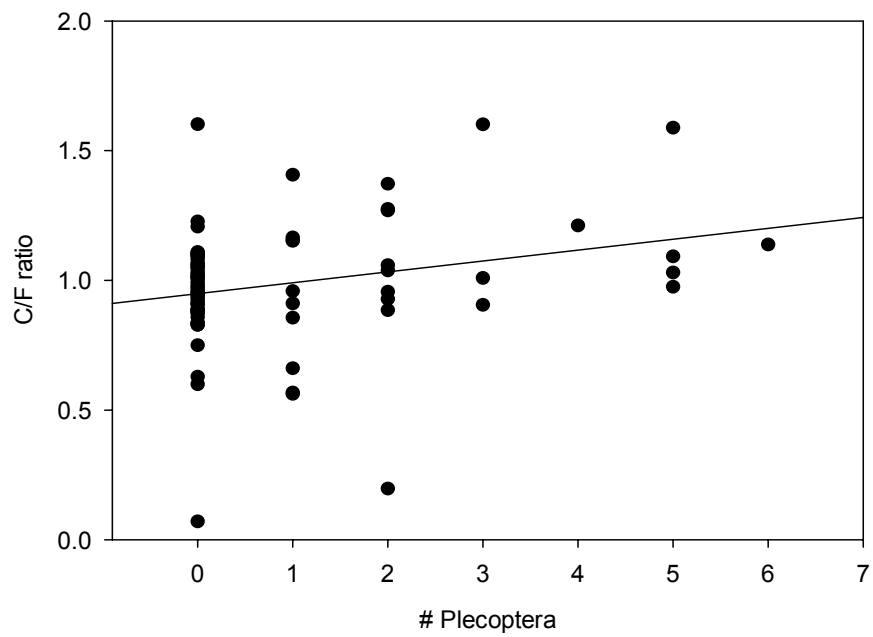


Figure 29: Correlation (Pearsons r) between the C/F_{weight} ratio (litter mass remaining in coarse mesh bags divided by litter mass remaining in the fine mesh bags) across all catchment types and all litter types and the number of Plecoptera found in the coarse mesh litter bags.

Statistically significant correlations were found between some of the invertebrate groups and C/F_{weight} ratios (Table 14). As stated earlier, birch litter was the only litter type which had significantly lower k-values in coarse mesh bags (Fig. 22 and 24). A negative correlation was found between the C/F_{weight} ratio of birch litter and number of *Clinocera* sp. and a positive correlation between the C/F_{weight} ratio of birch litter and number of Oligocheta.

A significant positive correlation was found between larch litter C/F_{weight} ratio and invertebrate abundance, Chironomidae (Total number), Chironomidae scrapers, Chironomidae gathering collectors and Tipulidae (Table 14). Increased densities of all these groups were correlated with more negative effect of allowing invertebrates access to the litter bags (higher C/F_{weight} ratios). There was a negative correlation between grass litter and number of predatory Chironomidae larvae. In this case, a negative relationship indicated that there was a faster decomposition within the coarse mesh litter bags (less weight left in the bags). Most of the correlations were found between the invertebrates and the larch litter, or nine in total (Table 14).

Table 13: Results from Pearson's correlations (r) between number of invertebrates found in coarse mesh litter bags after 140 days of incubation and the ratio between the litter weight left of coarse mesh litter bags and fine mesh litter bag decomposition rates (C/F_{weight}), across all litter types and all catchment vegetation types. Significant correlations are indicated by boldface. P stands for P-values and N stands for number of measurements included in the analysis.

Parameter vs C/F	r	p -value	N
Invertebrate abundance	0.14	0.22	77
Invertebrate taxa richness	0.10	0.40	77
Functional groups			
Gathering collectors	0.16	0.16	78
Filtering collectors	-0.09	0.45	78
Scrapers	0.16	0.16	78
Shredders	0.10	0.39	78
Predators	-0.14	0.22	78
Taxa			
Acarina	0.08	0.50	77
Chironomidae (Total)	0.15	0.19	75
Predators	-0.14	0.21	77
Scrapers	0.16	0.16	77
Gathering collectors	0.16	0.16	77
Shredders	-0.06	0.62	77
<i>Clinocera</i> sp.	-0.14	0.24	77
Coleoptera	-0.07	0.55	77
<i>Dicranota</i> sp.	-0.01	0.94	77
Gastropoda	0.03	0.78	77
<i>Limnophora</i> sp.	-0.08	0.48	77
Oligocheta	0.18	0.11	77
Plecoptera	0.25	0.03	77
Simuliidae	-0.09	0.44	77
Tipulidae	0.15	0.19	77
Tricoptera	0.00	0.99	77

Table 14: Results for Pearson's correlations (r) between number of invertebrates found in coarse mesh litter bags after 140 days of incubation and the ratio between the litter weight left in coarse mesh litter bags and fine mesh litter bag decomposition rates (C/F_{weight}), for three different litter types, across all catchment types. Significant correlations are indicated by boldface. Blanks indicate that no invertebrates were found of the particular taxa group in the particular litter bags

Parameter vs C/F	Grass litter			Birch litter			Larch litter		
	r	P	N	r	P	N	r	P	N
Invertebrate abundance	0.00	0.98	77	0.11	0.58	77	0.39	0.06	77
Invertebrate taxa richness	0.07	0.72	77	-0.01	0.95	77	0.27	0.20	77
Functional groups									
Gathering collectors	0.00	1.00	27	0.14	0.47	27	0.42	0.04	24
Filtering collectors	-0.05	0.80	27	-0.28	0.16	27	0.64	0.00	24
Scrapers	0.05	0.82	27	0.13	0.51	27	0.35	0.09	24
Shredders	-0.10	0.61	27	0.06	0.78	27	0.38	0.07	24
Predators	-0.30	0.12	27	-0.25	0.20	27	0.24	0.25	24
Taxa									
Acarina	0.06	0.76	27	0.08	0.70	26	0.02	0.94	24
Chironomidae (Total)	0.00	0.99	27	0.12	0.58	24	0.39	0.06	24
Predators	-0.34	0.08	27	-0.20	0.33	26	0.19	0.37	24
Scrapers	0.05	0.82	27	0.13	0.52	26	0.35	0.09	24
Gathering collectors	0.00	1.00	27	0.14	0.47	26	0.42	0.04	24
Shredders	-0.21	0.30	27	-0.14	0.50	26	0.30	0.16	24
<i>Clinocera</i> sp.	-	-	-	-0.35	0.08	26	0.08	0.70	24
Coleoptera	0.06	0.78	27	-0.13	0.53	26	-	-	-
<i>Dicranota</i> sp.	0.06	0.76	27	-0.15	0.47	26	0.17	0.43	24
Gastropoda	-	-	-	0.02	0.92	26	-	-	-
<i>Limnophora</i> sp.	-0.08	0.70	27	-	-	-	-	-	-
Oligocheta	0.06	0.76	27	0.39	0.05	26	0.03	0.89	24
Plecoptera	0.21	0.30	27	0.24	0.24	26	0.28	0.18	24
Simuliidae	-0.05	0.80	27	-0.28	0.16	26	0.10	0.64	24
Tipulidae	0.04	0.84	27	-0.07	0.73	26	0.44	0.03	24
Tricoptera	-0.08	0.70	27	0.10	0.64	26	0.00	0.99	24

3.7. The influence of seasonality on the timing of litter input

Decomposition was 213% and 94%, faster for fine and coarse mesh bags, respectively, when leaves entered the streams in the spring than when they entered the streams in the autumn (Figure 30; ANOVA, main effect Season $P < 0.001$).

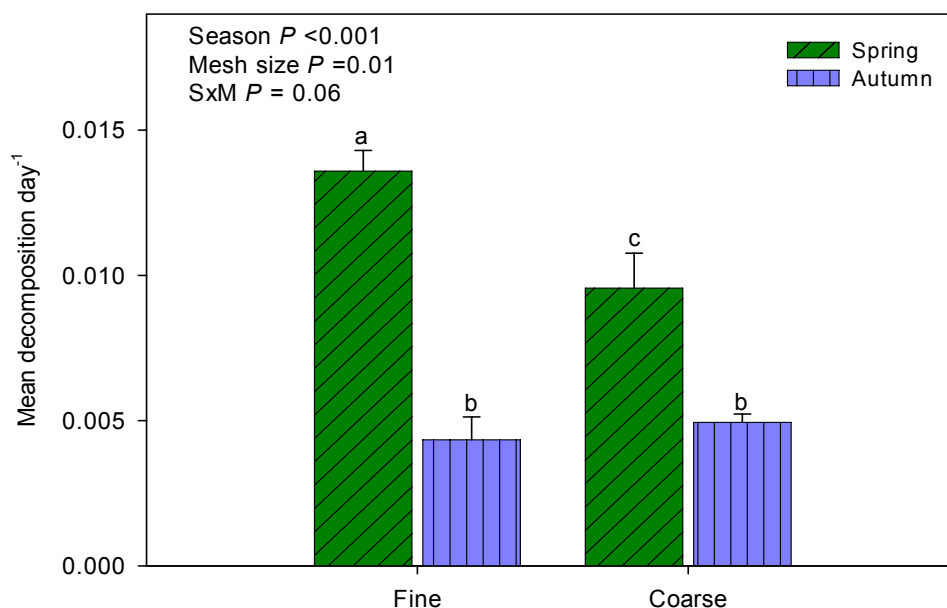


Figure 30: The average decomposition rate of birch litter (*B. pubescens*) per day, in fine and coarse mesh litter bags, in birch forest streams, after 48 days of incubation in the spring (green bars) and 52 days of incubation in autumn (blue bars), \pm SE, $n = 3$ for spring and $n = 4$ for autumn. Also shown are the results from a two-way repeated ANOVA followed by a Fisher's LSD test. Letters above the bars indicate if the difference between the decomposition in the different bag types or in the different places is significant at $\alpha < 0.10$. (S = Season, M = Mesh size)

The effect of including different meshed bags and the interaction between mesh size and season were significant (main effect Bag size, $P = 0.01$; Interaction, $P = 0.06$; Figure 30) when both datasets were analysed together. There was no difference in decomposition rate between fine and coarse mesh bags in the autumn (Fisher's LSD test, $p = 0.64$; Figure 30) opposite to what it was in the spring (Fisher's LSD test, $p = 0.002$). The invertebrates did not significantly increase the litter decomposition in eastern Iceland when the leaves were immersed into the streams in the autumn, and the apparent negative effect of allowing the invertebrates to enter the litter bags during the first 48 days of incubation in the spring (see Chapter 3.5.3) did not appear in the autumn.

To answer what explains the difference between the two seasons and to evaluate if temperature influenced the difference in decomposition rate, day degrees were used (Table 15). The difference between the decomposition in the spring and in the autumn was reduced by 16% and 8%, respectively, and then it was not significantly different between seasons (Figure 31; ANOVA: main effect Season $P = 0.65$). This indicated that the water

temperature explained almost all of the difference between the various decomposition rates between the seasons.

Table 15: Average total number of day degrees (0°C threshold) in streams running through heathland, birch forests and conifer forests in eastern Iceland, at different collection times \pm standard error of the means. Immersions were in spring and autumn 2008.

	Number of days	Heathland/ Unvegetated	Birch forest	Conifer forest
Eastern Iceland				
Spring immersion				
Collection 1	48	277 \pm 24	282 \pm 23	310 \pm 23
Collection 2	89	747 \pm 23	684 \pm 73	751 \pm 17
Collection 3	140	1096 \pm 32	1020 \pm 88	1103 \pm 20
Collection 4	175	1134 \pm 41	1084 \pm 77	1161 \pm 20
Collection 5	366	1292 \pm 64	1312 \pm 14	1340 \pm 26
Autumn immersion				
Collection 1E	52	92 \pm 18	126 \pm 13	121 \pm 10
Southern Iceland				
Collection 1S	52	192 \pm 37	227 \pm 27	-

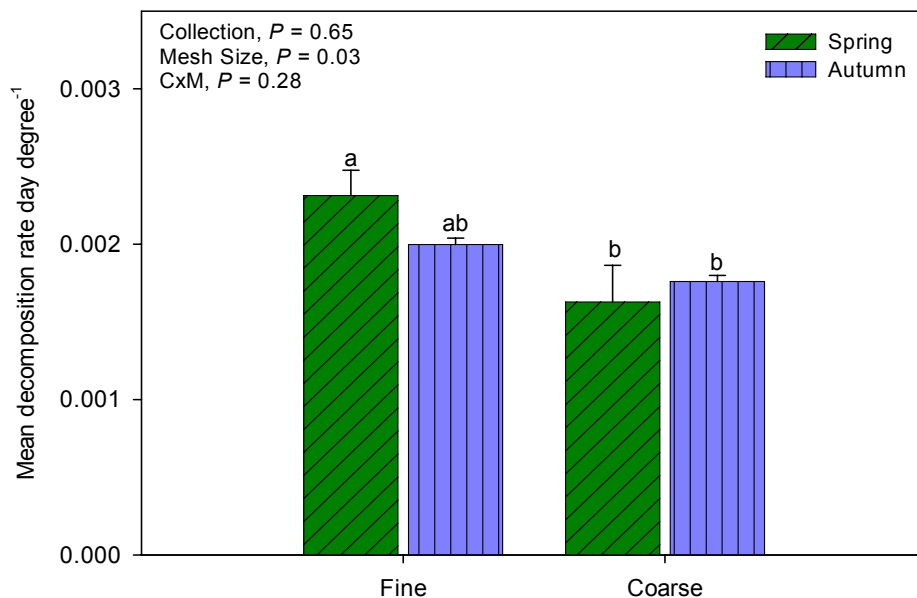


Figure 31: The average decomposition rate per day degree of birch litter (*B. pubescens*), in fine and coarse mesh litter bags, in streams with birch vegetation, \pm SE, $n = 3$ for spring and $n = 4$ for autumn. Also shown are the results from a two-way repeated ANOVA followed by a Fisher's LSD test. Letters above the bars indicate if the difference between the decomposition in the different bag types or in the different places is significant at $\alpha < 0.10$.

3.8. Decomposition rates during winter

The decomposition rate during the winter months was only carried out on grass litter and larch litter in coarse mesh litter bags. The average rate of decomposition during the winter months was slow compared to the average decomposition rate of the grass and the larch litter in spring to late autumn (Figure 32). The winter decomposition rate of grass litter in the heathland streams was only 25% of the average decomposition rate calculated from the k-value for the first four collections. The winter decomposition rate of the larch litter in conifer forest streams was also only 41% of the average decomposition rate calculated from the spring-autumn k-value. The winter decomposition rates of these two litter types were even lower when incubated outside their dominant catchment types (Data not shown).

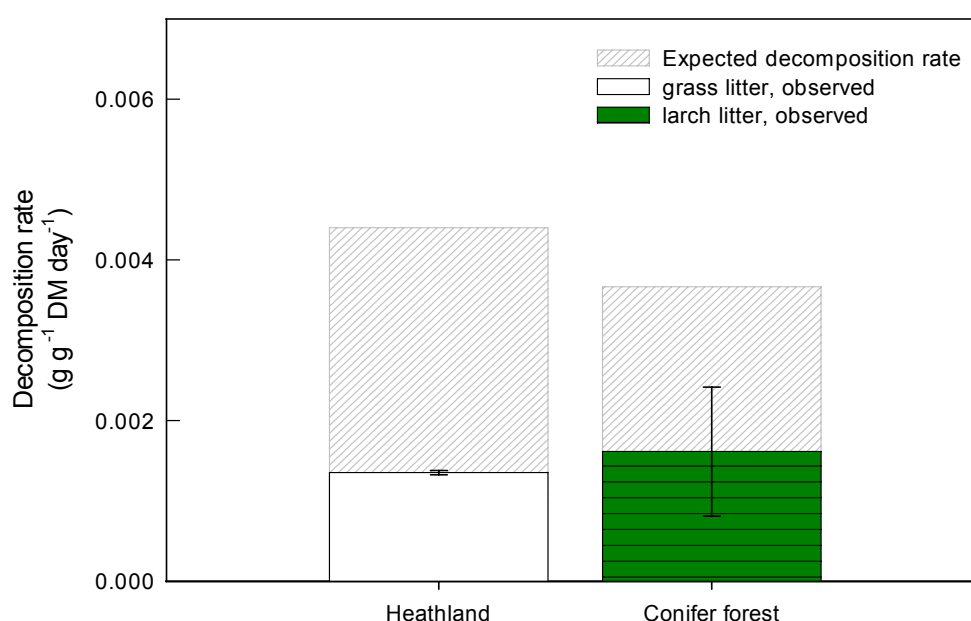


Figure 32: A comparison of the expected (gray bars) and observed decomposition rate of grass litter (white bar) in heathland streams and larch litter (green bar) in conifer forest streams during winter 2008–2009 (194 days of incubation) \pm SE. Expected values are the k – values shown in Figure 20.

The number of day degrees during the winter period, between collection 4 and 5; were 158, 228 and 179 in the heathland, birch forest and conifer forest, respectively, during those 191 days of immersion (Table 15). The decomposition rate during the winter months was compared to the average decomposition rate in late autumn, which is regarded as the end of the growing season and used to calculate the k-value. The main result showed that different temperature did not explain the observed difference in decomposition rates between the two seasons, since the average decomposition was significantly different between winter and

autumn decomposition when expressed in day degree units instead of time units (ANOVA; Main factors: Coll $P = 0.05$; Figure 33). The difference between the decomposition rates in the two different seasons cannot be explained only by the difference in day degrees during winter.

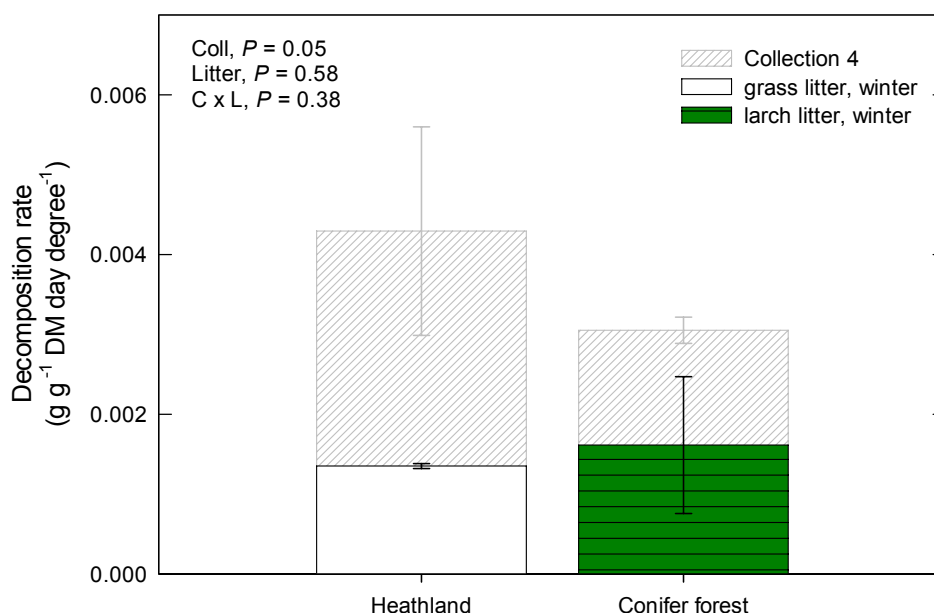


Figure 33: A comparison of the decomposition per day degree from collection four (November; gray bars) and winter decomposition rate of grass litter (white bar) and larch needles (green bar), per day degree, during winter 2008–2009 (194 days of incubation since collection 4) \pm SE.

3.9. Effects of stream type on decomposition rate considering the stream type (south vs. east)

Like mentioned earlier, there are different types of headwater streams in Iceland, most of them are either run-off fed or spring-fed. In the present study only the decomposition of birch litter was studied in spring-fed streams in southern Iceland. The decomposition rates in southern Iceland showed that the decomposition rate was significantly higher in birch forest streams than in barren land streams (ANOVA, main factor catchment type: $P = 0.07$; data not shown).

A comparison of the decomposition rate between streams in southern and eastern Iceland showed that the litter decomposition rate was significantly higher in the spring-fed streams in southern Iceland than in the run-off streams in eastern Iceland (ANOVA, main effect: Place, $P = 0.02$; Figure 34). The decomposition rates in fine and coarse mesh bags in the

birch forest streams in southern Iceland were 50% and 234% higher than in eastern Iceland, respectively. The difference between the decomposition rate within the fine mesh bags between the two places was not significant (Fishers LSD, $p = 0.38$), but the difference was highly significant when measured in coarse mesh bags (Fishers LSD: $p = 0.01$), indicating that allowing the invertebrates access to the litter bags significantly increased the decomposition rates in southern Iceland compared to eastern Iceland. The two stream types may therefore differ in this respect.

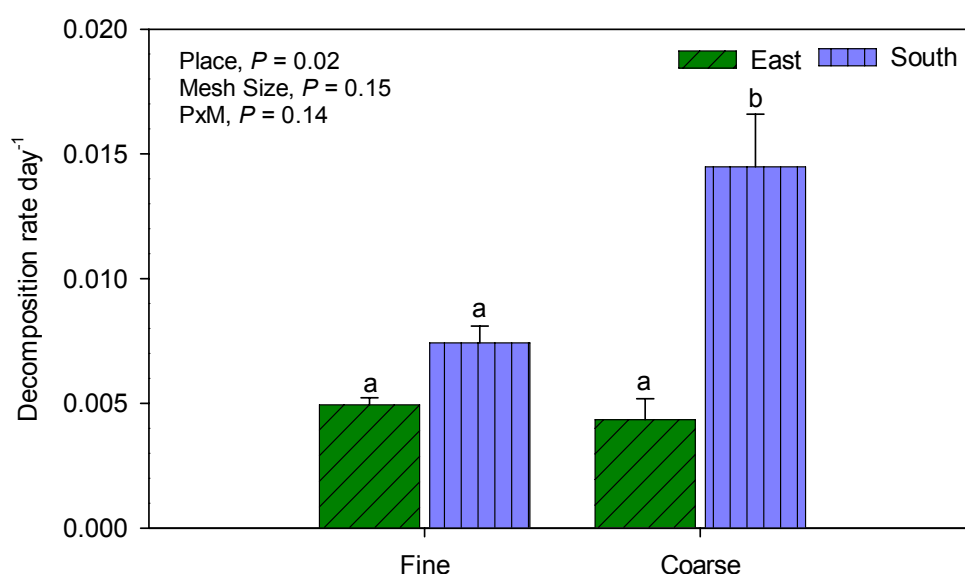


Figure 34: Average decomposition rate of birch leaves per day, in fine and coarse mesh litter bags, in streams with birch vegetation, after 51 days of incubation in eastern (green) and southern (blue) Iceland, \pm SE, $n = 4$. Also shown are the results from a two-way repeated ANOVA followed by a Fisher's LSD test. Letters above the bars indicate if the difference between the decomposition in the different bag types or in the different places was significant at $\alpha < 0.10$. P×M refers to the interaction between Place and Mesh Size.

Additional analysis to test if temperature difference between southern and eastern Iceland could explain the different decomposition rates revealed that different temperature did partly explain the observed difference in decomposition rate between the study sites. The average decomposition was not significantly different between southern and eastern Iceland when expressed in day degree units instead of time units (Fig. 35; Main factors: Place: $P = 0.25$). All differences in microbial decomposition in the fine mesh bags between southern and eastern Iceland could be explained by temperature differences.

When expressed in day degree units the difference in decomposition rate in fine mesh bags between southern and eastern Iceland was only 16% (Fig. 35; not significant difference).

The decomposition rate was, however, still 85% higher in the coarse mesh bags in southern site compared to the eastern site, when expressed per day degree unit (Fig. 35). It was therefore clear that invertebrates contributed more to the decomposition process in the spring-fed streams in southern Iceland than in the run-off streams in eastern Iceland. Unfortunately no data is available on the invertebrate fauna in the litter bags in southern Iceland.

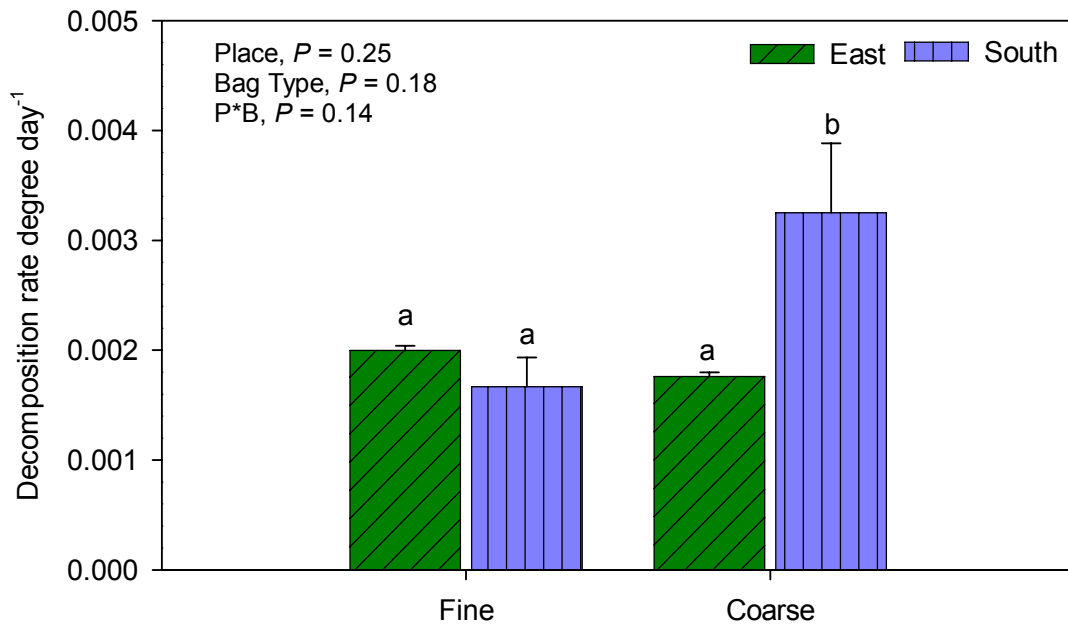


Figure 35: Average decomposition of birch leaves (*B. pubescens*) per day degree, in fine and coarse mesh litter bags immersed in birch forest streams, after 51 days of incubation in eastern (green, diagonal lined) and southern (blue, striped) Iceland, \pm SE, $n = 4$. Also shown are the results from a two-way repeated ANOVA followed by a Fisher's LSD test. Letters above the bars indicate if the difference between the decomposition in the different bag types or in the different places is significant at $\alpha < 0.10$. $P \times B$ = interaction between place and bag type.

4. Discussion

The importance of allochthonous material to forested stream communities has been emphasized by many ecologists (e.g. Cummins, 1974) and therefore the catchment vegetation cover is shown to be closely linked to the stream ecosystem (e.g. Vannote et al., 1980).

4.1. A variation in litter transport into streams

Quantity of transported litter

The total amount of litter which was transported into the heathland streams was very low compared to the forested streams, where it was 30–33 times higher (Figure 17). Similar differences in litter transport between forested and treeless catchments have also been observed elsewhere, such as in Kansas, USA (Gurtz et al., 1988). It has been shown that most streams at latitude higher than 50° (N and S) have often low or no litterfall input, although catchment vegetation type (forested vs. non-forested) is also important in the determination for the litterfall (Benfield, 1997). This difference between the forested and non-forested catchments was confirmed in the present study.

A large relative difference can be seen when the total terrestrial biomass measured in the birch and the conifer forest catchments is compared to the amount of litter transported into the streams. The total terrestrial biomass was 11–19 times higher in the forested catchments than in the heathland catchments (Table 7), while the litter transport was 30–33 times higher in the two forested catchments. The forested catchments therefore had more material falling vertically into the streams due to higher terrestrial biomass, but also because of relatively higher lateral transport of litter into the streams. The importance of lateral litter transport has been noted in other studies (Abelho, 2001; Benfield, 1997). Broadleaved litter (e.g. birch, willows) is more easily transported laterally by wind than conifer needles and grass litter due to its large surface area. Grass litter and litter from many dwarf-bushes are not easily detached and therefore mostly decomposed *in situ*, which means that it is not easily moved laterally by wind.

The observed terrestrial biomass was 1.5 times higher in the conifer forest than in the birch forest. Surprisingly, the amount of litter transported into streams running through conifer forest was not significantly higher than for those streams running through birch forests. This might be explained by a higher lateral transport of birch leaf litter than of coniferous needles which mostly accumulate at the forest floor and are not as easily transported laterally by wind.

The mean total amount of litter transported into streams running through birch and conifer forests was ca. $40\text{g m}^{-1}\text{ year}^{-1}$. The litter transport into streams has more often been expressed per square metre of litter traps than to each metre of stream (Benfield, 1997). Expressing litter transport in that way, the total amount of transported litter in the present study was ca. 5g m^{-2} into streams running through heathland catchments, 162g m^{-2} into those running through birch forest catchments and 179g m^{-2} into streams running through conifer forest catchments. These values were within the range found in other studies in different vegetation classes in Boreal, Arctic or Antarctic conditions (Table 16), where on average 380g m^{-2} of litter was transported into the streams. It should be taken into consideration that the range was high, or between 0 and $2,789\text{g m}^{-2}$ (Table 16).

A study from treeless area in Antarctica showed less litter transport than in the present study at the heathland streams, or 0g m^{-2} (McKnight & Tate, 1997). Other studies on treeless areas have mainly been focused on agricultural land or pastures, rather than heathlands. Studies on pasture land in Australia showed that litterfall was between 6 and 9g m^{-2} (Campbell et al., 1992a) but it was much higher in New Zealand, where it was 187g m^{-2} (Scarsbrook et al., 2001).

The values of litter transport to birch forest streams in the present study were found to be lower than comparable values from deciduous forests or shrub-lands in New Zealand, Alaska and Canada which were $216\text{--}761\text{g m}^{-2}$ (Harvey et al., 1997; Irons & Oswood, 1997; Naiman & Link, 1997; Quinn et al., 1997; Scarsbrook et al., 2001), but higher than values from deciduous forests or shrub-lands from other studies such as Alaska and Canada where the litter transport was $3\text{--}81\text{g m}^{-2}$ (Irons & Oswood, 1997; Naiman & Link, 1997; Table 16). The observed litter transport for streams within birch catchments was therefore

comparable to other studies within deciduous forests or shrub-lands in the Arctic or the Boreal zones.

There was less litter transported into conifer forest streams in eastern Iceland than generally found in other studies in coniferous forests (Table 16). There the average litter transport was 1090 g m^{-2} . Webster and Meyer (1997) found that the litter inputs into conifer forest streams in Oregon, USA, were between 218 and $2789 \text{ g m}^{-2} \text{ y}^{-1}$, which is considerably higher than the values found in the present study. This can possibly be explained by the relatively young age of the conifer forests plantations (40–60 years) used for the present study. It is not unlikely that needle litter transport into streams will increase as tree height increases and branches grow further into the riparian areas. Another possible explanation is species differences, but the dominant coniferous tree in the eastern study area was the Siberian larch. It is a deciduous conifer which has lower density needles compared to other conifer species (Eckenwalder, 2009).

Table 16: Litterfall inputs into streams in different vegetation types within the Boreal, Arctic or Antarctic regions. Based on information from Abelho (2001) and Benfield (1997b).

Vegetation	Location	Litterfall ($\text{g m}^{-2} \text{ year}^{-1}$)	Reference
Treeless catchments			
Open	Canada St, Antarctica	0	McKnight and Tate (1997)
Pasture	Waikato, New Zealand	187	Scarsbrook et al (2001)
Pasture	Southeast Australia	6–9	Campbell et al (1992)
Deciduous forested catchments			
Deciduous	New Zealand	216	Quinn et al. (2000)
Deciduous	Waikato, New Zealand	415	Scarsbrook et al (2001)
Deciduous/Tundra	Kuparuk R, Alaska, US	384	Harvey et al (1997)
Mixed deciduous	Beaver Cr, Quebec, Canada	273	Naiman and Link (1997)
Mixed deciduous	First Choice Cr, Quebec, Canada	761	Naiman and Link (1997)
Mixed deciduous	Moisie R, Quebec, Canada	3	Naiman and Link (1997)
Mixed deciduous	Caribou Cr 3, Alaska, US	37	Irons and Oswood (1997)
Mixed deciduous	Matamek R, Quebec, Canada	19	Naiman and Link (1997)
Mixed deciduous	Monument Cr, Alaska, US	81	Irons and Oswood (1997)
Mixed deciduous	Caribou Cr 2, Alaska, US	37	Irons and Oswood (1997)
Mixed deciduous	Alaska, US	37	Irons and Oswood (1997)
Mixed deciduous	Muskrat R, Quebec, Canada	41	Naiman and Link (1997)
Coniferous forested catchments			
Coniferous	Oregon, US	1204–2789	Webster and Meyer (1997)
Coniferous	Oregon, US	218–736	Webster and Meyer (1997)
Coniferous	Waikato, New Zealand	485	Scarsbrook et al (2001)

Litter composition

The litter composition transported into streams was quite unexpected within the conifer forest, since the main part of the litter was not produced by the conifer trees, only by other species of woody and non-woody plants, like birch, willow and vascular plants. This may be due to that the conifer forest catchments have an abundant riparian vegetation along the streams and are also mixed with other tree species. In the conifer forests in eastern Iceland there is a shrub-layer of birch and willows and there is also a fair amount of herbaceous ground vegetation after their ticket stage (Sigurdsson et al., 2005). The larches are the only coniferous trees that are deciduous, shedding their needles during autumn (Eckenwalder, 2009). This opens up the coniferous forest and may increase the lateral transport of broadleaved litter from the shrub-layer and from ground vegetation species that detach their leaves in the autumn.

4.2. Decomposition rates in streams

One of the initial hypothesis for this study was that decomposition rate in Icelandic streams would be similar to what has been found in streams in climatically comparable countries. In the present study the litter decomposition rates were between 0.0033 and 0.0044g g⁻¹ DM day⁻¹ for the three different litter types (Figure 20), but in streams in comparable places, like Alaska, the decomposition rates of various species were between 0.0013–0.0259 g g⁻¹ DM day⁻¹ (Irons et al., 1994; Table 17). Studies in Switzerland showed a range of decomposition rates between 0.0029 and 0.0305g g⁻¹ DM day⁻¹ (Robinson & Gessner, 2000) and in New Zealand it ranged between 0.0036 and 0.0510g g⁻¹ DM day⁻¹ (Hicks & Laboyrie, 1999). The results from the present study are within the lower range of the values from all of those studies, so the Icelandic streams do not clearly separate themselves from decomposition rates experienced elsewhere.

Birch litter

Internationally, there are few studies that have been done on litter decomposition using the same litter species as in this study. One of few studies where the downy birch (*B. pubescens*) has been used in a decomposition study revealed that the decomposition rate was 0.0033g g⁻¹ DM day⁻¹ (Escudero et al., 1991). This value is similar to what was observed in the present study although the study area was located in Spain. However, the

Table 17: Litter decomposition rates in different areas within the Boreal and Arctic regions. Table based on information from Abelho (2001) and Petersen et al. (1995).

Leaf species	Location	Mesh size (mm)	Decomposition rate (g g ⁻¹ day ⁻¹)	Reference
Grass species				
<i>Agrostis stolonifera</i>	Ontario, Canada	LP	0.0020	Bärlocher et al 1978
<i>Deschampsia cespitosa</i>	Alberta, Canada	3.5	0.0018	Hodkinson 1975*
<i>Chionocloa ridiga</i>	South Island, New Zealand	LP	0.0017-0.0026	Niyogi et al 2003
<i>Juncus tracyi</i>	Alberta, Canada	3.5	0.0011	Hodkinson 1975 *
Desiduous species				
<i>Acer saccharum</i>	Alaska, U.S.	20	0.0117	Irons et al. 1994
<i>Alnus crispa</i>	Alaska, U.S.	20	0.0259	Irons et al. 1994
<i>Alnus glutinosa</i>	Sweden	LP	0.0056-0.0879	Petersen et al 1995
<i>Alnus glutinosa</i>	Sweden	LP	0.0175-0.0912	Petersen et al 1995
<i>Alnus incana</i>	Sweden	LP	0.0091	Petersen et al 1995
<i>Alnus incana</i>	Sweden	LP	0.0088	Petersen et al 1995
<i>Alnus rugosa</i>	Alaska, U.S.	20	0.0231	Irons et al. 1994
<i>Beilschmiedia tawa</i>	New Zealand	2×3	0.0036	Hicks and Laboyrie 1999
<i>Betula lenta</i>	North Carolina, U.S.	5	0.0036–0.0100	Meyer and Johnson 1983
<i>Betula pubescens</i>	Cairngorm, Scotland, UK	LP	0.0085-0.0331	Collen et al. 2004
<i>Betula pubescens</i>	Norway	-	0.0014-0.0026	Traaen 1977
<i>Carya glabra</i>	Sweden	LP	0.0079	Petersen et al 1995
<i>Carya glabra</i>	Sweden	LP	0.0092	Petersen et al 1995
<i>Fagus grandifolia</i>	Alaska, U.S.	20	0.0037	Irons et al. 1994
<i>Melicytus ramiflorus</i>	New Zealand	2×3	0.0507	Hicks and Laboyrie 1999
<i>Pithecellobium longifolium</i>	Alaska, U.S.	20	0.0013	Irons et al. 1994
<i>Populus tremula</i>	Sweden	LP	0.0095	Karlström 1976
<i>Populus tremula</i>	Sweden	LP	0.0049	Petersen et al 1995
<i>Populus tremula</i>	Sweden	LP	0.0083	Petersen et al 1995
<i>Quercus alba</i>	Sweden	LP	0.0041	Petersen et al 1995
<i>Quercus alba</i>	Sweden	LP	0.0093	Petersen et al 1995
<i>Quercus falcata</i>	Alaska, U.S.	20	0.0020	Irons et al. 1994
<i>Quercus rubra</i>	Alaska, U.S.	20	0.0050	Irons et al. 1994
<i>Salix alaxensis</i>	Alaska, U.S.	20	0.0160	Irons et al. 1994
<i>Salix sp.</i>	Alberta, Canada	3.5	0.0027	Hodkinson 1975*
<i>Trema micrantha</i>	Alaska, U.S.	20	0.0263	Irons et al. 1994
Conifer species				
<i>Pinus sylvestris</i>	Cairngorm, Scotland, UK	LP	0.0015-0.0034	Collen et al. 2004
<i>Pinus contorta</i>	Alberta, Canada	3.5	0.0006	Hodkinson 1975*

LP = Leaf Pack study; * Pond study

differences in decomposition along a latitudinal gradient must be considered when comparing the litter decomposition rates between countries (Irons et al., 1994). Another study using birch leaves in Iceland in cold and warm spring-fed streams found a decomposition rate between 0.0189 and 0.0450g g⁻¹ DM day⁻¹ in coarse mesh litter bags (Friberg et al., 2009). These values are much higher than what was found in the present study in the run-off streams in eastern Iceland, but the difference might be explained by the difference in stream type. The average decomposition rates after 52 days in coarse mesh

bags in the spring-fed streams in southern Iceland were also much higher, or $0.015 \text{ g g}^{-1} \text{ day}^{-1}$), which were comparable to lower range found by the Friberg et al. (2009) for cold streams. In a study made in Scotland, the decomposition rate of downy birch leaves was between 0.0085 and $0.0331 \text{ g g}^{-1} \text{ DM day}^{-1}$ (Collen et al., 2004), another study, in North Carolina, sweet birch (*B. lenta*) leaves had the decomposition rate between 0.0036 and $0.0100 \text{ g g}^{-1} \text{ DM day}^{-1}$ (Robinson et al., 2000). In all these studies, the decomposition rate was either equal or considerably higher than found in the present study ($0.0033 \text{ g g}^{-1} \text{ DM day}^{-1}$), which seems to be one of the lowest values of decomposition found for birch litter.

Larch needle litter

Conifer needles are generally considered to be a poorer quality food resource for invertebrates processing it than the deciduous leaves (Petersen & Cummins, 1974) and are therefore generally considered to have slower decomposition rates. The decomposition rate of conifer needles in Spain and Portugal was found to be between 0.0010 and $0.0039 \text{ g g}^{-1} \text{ DM day}^{-1}$ (Escudero et al., 1991; Graça & Pereira, 1995). The decomposition rate of European larch needles (*Larix decidua*) in streams in the Swiss Alps ranged between 0.0017 and $0.0055 \text{ g g}^{-1} \text{ DM day}^{-1}$ (Robinson et al., 2000). European larch needles were found to have decomposition rate ranging between 0.0019 and $0.070 \text{ g g}^{-1} \text{ DM day}^{-1}$ in South Germany and Switzerland (Rosset et al., 1982). All of the values for decomposition rates seem to be comparable to the decomposition rates reported in the present study for Siberian larch needles.

Grass litter

Only few decomposition studies have been made where grass litter has been used as a litter source. In the present study some common native heathland grass species such as *Festuca richardsonii*, *Poa pratensis* and *Agrostis capillaries* were used but there are no records where these species have been used for measuring decomposition rates. However, studies using similar grass species like *Agrostis stolonifera* in a lake ecosystem gave a decomposition rate of $0.0020 \text{ g day}^{-1}$ (Webster & Benfield, 1986) which was considerably slower than the decomposition rate in the present study. It is known that decomposition rates are generally slower within lakes or ponds than within streams (Irons et al., 1994). The decomposition rate of grass litter has been studied in New Zealand streams and was reported to vary between 0.0017 and $0.0026 \text{ g g}^{-1} \text{ DM day}^{-1}$ (Niyogi et al., 2003; Table 17)

and another study made in Alberta, Canada showed the decomposition rate of the grass *Deschampsia caspitosa* to be $0.0018 \text{ g g}^{-1} \text{ DM day}^{-1}$ (Hodkinson, 1975). The observed decomposition rates for the Icelandic grasses were somewhat higher than these published rates.

The most comparable environmental conditions to Iceland, apart from Scotland and New Zealand, are undoubtedly the northern part of the Scandinavian countries. Therefore, it is relevant to compare the present results to studies made there. The only Scandinavian study using downy birch litter decomposition rate found the rate to range between 0.0014 and $0.0026 \text{ g g}^{-1} \text{ ash free dry weight day}^{-1}$ (Table 17), that study was made in Norwegian streams (Traaen 1977). These rates are considerably lower than found in the present study. It must however be considered that in Traaen's study was used ash free weight but not dry weight as used in the present study, which makes comparison difficult. It must also be considered that the study streams in Norway were more acid (pH ranging between 4.3 and 6.3) than the Icelandic streams (pH ranging between 7.4 and 7.8) which might slow down the decomposition processes since it is well known that decomposition rate is negatively related to pH (Dangles et al., 2004; Mackay & Kersey, 1985).

The decomposition rates found in the present study were generally lower than has been found in comparable Scandinavian studies (Table 17). The decomposition rates of various species are 0.0041 – $0.0095 \text{ g g}^{-1} \text{ DM day}^{-1}$ and as high as 0.088 – $0.091 \text{ g g}^{-1} \text{ DM day}^{-1}$ for common alder (*Alnus glutinosa*; leaf packs) in Sweden (Petersen & Cummins, 1974). It must, however, be taken into consideration that these values are based on different litter types, which may accelerate decomposition if they are of higher quality (Irons et al., 1994; Leroy & Marks, 2006). Examples of this are the rates for the common alder, which is a nitrogen-fixing species with leaf litter which contains unusually high nitrogen concentrations (Molles, 1999). The Swedish studies may also have been conducted at latitudes below the 63° N , which is then at lower latitude than Iceland. It is known that decomposition rates can be affected by latitude (Irons et al., 1994), which is why they suggested that a comparison of decomposition per day degree might be more appropriate when rates are compared across areas at different latitudes.

4.3. Effect of litter quality or catchment type on decomposition rate?

Litter quality

Based on earlier findings the litter used in the present study was expected to decompose in the order that grass litter would have the lowest decomposition rate, then larch and the birch litter would decompose fastest (Leroy & Marks, 2006). However, there did not seem to be any difference between the decomposition rates of the dominant litter types within their corresponding catchment types (Figure 21). These results were unexpected since literature generally shows different rates for different litter types (Leroy & Marks, 2006; Petersen & Cummins, 1974; Webster & Benfield, 1986). The decomposition rate of various leaf litter has been divided into groups; i.e. slow ($<0.005 \text{ g g}^{-1} \text{ DM day}^{-1}$), medium ($0.005\text{--}0.010 \text{ g g}^{-1} \text{ DM day}^{-1}$) and fast ($>0.010 \text{ g g}^{-1} \text{ DM day}^{-1}$; Petersen & Cummins, 1974; Suberkropp & Chauvet, 1995). It has been suggested that the decomposition rates would be transferable between streams in different catchment types, in different biomes and on different continents. Based on these criteria it could be expected that at least birch leaves should fall into the group of medium decomposition rate, but in fact all the litter types in the present study fell into the group of slow decomposition rates. It has however also been found that decomposition rates of single species can fall into all of the groups (Irons et al., 1994), which clearly indicates that not only the litter quality can be used to explain differences in decomposition rates as has been suggested in other studies (Petersen & Cummins, 1974). A study made along a latitudinal gradient clearly showed that decomposition rate is greatly affected by ecosystem structure and temperature regimes of the study areas (Irons et al., 1994). Therefore, it was maybe not surprising that all the Icelandic litter types fell into the group of slow decomposition rate.

There was an interesting trend in every catchment type where the decomposition rate of the dominant litter type in the corresponding catchment type was slowest. The differences between the decomposition rates of the three litter types were not significant in the present study but it is difficult to explain, possibly it was related to the general lack of shredders in the streams in eastern Iceland and the dominance of microbial decomposition (see further discussion later).

Catchment types

There was no difference in average decomposition rate between catchment types (Figure 21), there were however differences of the decomposition rates of different litter types when compared across all catchment types (Figure 21). The difference was in an unexpected direction. The decomposition rate of birch litter was significantly slower than of the grass and the larch litter in streams running through birch forest catchments. This was opposite to one of the research hypothesis, where the litter was expected to decompose faster in their dominant catchment type streams. The same trend occurred in the conifer forest streams, where the decomposition of larch needles was significantly slower than the decomposition rate of the grass litter. This might be because of a feeding specialisation of the invertebrates within the streams, i.e. the invertebrates don't feed directly on the litter but are used to feed on the bacteria and fungi colonising the litter that naturally falls into the streams. Therefore, the invertebrates might scrape the bio-film off the litter instead of eating the litter itself.

Energy transport from the terrestrial ecosystem into the streams

The average decomposition rate was, as stated earlier, $0.0038 \text{ g g}^{-1} \text{ DM day}^{-1}$ across all litter types and catchment types. The decomposition rate does, however, not indicate how much energy is available from the terrestrial litter in the streams of the different catchment types. For those calculations, both the amount of litter transported into the streams and the rate of litter decomposition have to be known. Those two factors combined indicate the total amount of energy transposed from the terrestrial ecosystem into the stream ecosystem. This part of the thesis has already been published in Icelandic in Stefánsdóttir et al. (2010). There was no difference between decomposition rates of dominant litter types in their corresponding catchment types, which indicated that the average k -value of all litter types in their corresponding catchment type could be used for all litter types of the run-off streams in eastern Iceland. To estimate how much organic matter was decomposed within different catchment types we assumed that: a) all of the organic matter that was transported into the streams decomposed somewhere within the catchment area, b) temporal variability in litter transport to streams was not considered, and c) temporal variability in decomposition rate in the streams was not considered (low decomposition rates during winters). The total decomposition within the birch forest streams and the heathland streams was 83% and 4% of the total decomposition within the conifer forest streams, respectively.

This indicated that there was much higher amount of energy available within the forested streams than within the heathland streams. This estimation is however depended on the assumptions used and might therefore be overestimated. To be able to calculate a more reliable estimation of the total energy input from allochthonous material, factors like litter drift and transport within a stream, more thorough study of the decomposition rates of other litter types and more thorough time plan of the litter transport into the streams would be necessary. It would also be interesting to include the autochthonous energy production in the streams and do a total instream energy budget for the whole stream ecosystem (Cummins, 1974; Minshall, 1978).

4.4. The effects of invertebrate activity on litter decomposition in streams

Effect of excluding invertebrates

The decomposition rate can be divided into two different rates considering the activity of different organisms, either microbes or invertebrates (Bergfur et al., 2007b; Hanlon, 1982; Irons et al., 1994; Rounick & Winterbourn, 1983; Stockley et al., 1998; Winterbourn, 1978). By using different mesh size litter bags allows us to include or exclude invertebrates from the litter. One of the present research hypotheses was that decomposition would be faster in the coarse mesh bags because of the effect of invertebrates. Irons and co-workers (1994) suggested that the importance of invertebrates changed along a latitudinal gradient, i.e. invertebrates became more important in colder water of high latitudes and high altitudes. The results from eastern Iceland show, however, that the decomposition rate was not significantly affected when invertebrates were excluded (Figure 22). This was inconsistent with results from many studies, showing that the presence of invertebrates positively affects the litter decomposition rates (Kaushik & Hynes, 1971; Stockley et al., 1998). There are, however, few other studies that have also shown no difference between the decomposition rates within the fine and the coarse mesh bags (Graça, 2001).

Shredders are generally considered important in the litter processing in most stream water ecosystems (Cummins et al., 1989; Graça, 2001; Vannote et al., 1980). The lack of response of excluding invertebrates in the present study can most probably primarily be explained by a lack of this important functional group. What could explain this lack of shredders in the Icelandic streams? Can it be explained with the isolation of the country and that shredders

are sparsely colonizing Icelandic streams? Have shredders become extinct since most of the forests and woodlands were cleared in Iceland following the human settlement in the late 9th century? (Hallsdóttir, 1995). The catchment vegetation affects the population of shredders since: a) vegetation is the source of leaves, b) stream invertebrates are selective on leaf types as food source and c) invertebrates can be limited by the food source (Cummins et al., 1989; Graça, 2001). But why aren't there more shredders found in streams that have catchments covered by forests and woodlands in Iceland if it is mainly the food availability that controls the population of shredders? Eggertsson (2009) has shown that birch forest cover rapidly decreased in the study area in eastern Iceland following the human settlement in the 9th century, but increased again following the plague in the 14th century. Another decline, but not as great, was experienced in the 19th century, but birch cover has increased much in the past century (Eggertsson, 2009). Therefore, the lack of shredders in the forest and woodland streams today in eastern study area could possibly be explained by that shredders became extinct during earlier deforestation phases and have not re-colonized the woodland streams despite that the forest cover has increased. Iceland is a country with steep mountains and most of the headwater streams have high water current velocities that rapidly transport leaf litter downstream, to lakes or larger rivers. A lack of shredders in the headwater streams could therefore also partly be explained by that most of the leaf litter is not retained there but transported further downstream. This was used as an explanation by Rosset and co-workers (Rosset et al., 1982) for a lack of shredders in headwater streams in New Zealand. It has also been noted that shredders are not strongly associated with CPOM in New-Zealand streams (Rounick & Winterbourn, 1983; Winterbourn et al., 1981). In Iceland the shredders are, however, not only lacking in headwater streams, but also in larger rivers and lakes (Friberg et al., 2009; Gíslason et al., 2001; Petersen JR et al., 1995), which seems to support the isolation or extinction speculations considered earlier.

Invertebrate impact

The presence of invertebrates did not increase the rate of decomposition when looking at k-values, but when the individual dry weights of litter bags were analysed some interesting trends were apparent. An unexpected trend towards a faster decomposition rate within the fine mesh bags containing birch litter was observed (Figure 23). The presence of invertebrates did result in less weight loss during the first 48 days of immersion (Collection 1) for birch litter in all the catchment types in eastern Iceland. This trend for faster initial

weight loss in fine mesh bags has also been observed in few other studies (Bergfur et al., 2007a; Rosset et al., 1982), but in most studies the weight loss is always faster within the coarse mesh bags where the invertebrates have access to the litter (Rosset et al., 1982). This might be effects from the invertebrate activities, e.g. that they slow down the decomposition of the litter caused by microbes by scraping it off the litter, but no explanation of this negative trend was found in the literature.

4.5. Abundance of invertebrates using litter as their food source or habitat

Number of invertebrates

Regarding the number of invertebrates in the litter bags, it was hypothesised that the abundance would increase within the streams running through forested catchments due to a generally higher supply of organic matter. There was however no statistically significant difference in invertebrate density in incubated litter bags in different catchment types (Figure 25a). However, there was a trend towards a lower invertebrate density within the heathland streams, but it should be considered that the standard error was high and the number of invertebrates ranged between 1–686 individuals in each litter bag. The high variability could reflect a clumped distribution which is common for benthic invertebrates (Allan & Castillo, 2007) and since there were only used three replicates in each stream the variance was bound to be great. Many studies have measured both decomposition rates and densities of invertebrates using litter (bags) as their habitat (Abelho & Graça, 1996; Bergfur et al., 2007b; Cummins et al., 1989; Stockley et al., 1998). Some studies have reported a clear positive relationship between invertebrate density and catchment vegetation (Meyer, 1980), while others found no clear relationship between the two factors (Kaushik & Hynes, 1971; Minshall & Minshall, 1978).

Functional feeding groups

In the present study, shredders were only about 3–4 % of the invertebrates found in the litter bags and were the second smallest functional feeding group (Table 10). Many studies have shown that shredder abundance is closely linked to the timing of the litter input (e.g. Cummins, 1974; Cummins et al., 1989), and they convert coarse organic matter into smaller particles. Therefore they are very important to other stream organisms which utilize the

smaller particles as food source and thereby decompose the litter further. The importance of CPOM as a major energy source in small forest streams has been emphasised by stream ecologists (Cummins, 1974) and how important the role of shredders are within these systems (Cummins et al., 1989; Hynes, 1975; Vannote et al., 1980). In New Zealand shredders are poorly represented in the headwater streams (Parkyn & Winterbourn, 1997; Winterbourn et al., 1981), which is in contrast to what has been published for other countries (Vannote et al., 1980). The streams of New Zealand might in this way be comparable to streams in Iceland and therefore to the present findings, where shredders are very poorly presented. However, scrapers in Icelandic spring-fed streams have been found to be quite efficient in scraping off the leaf tissue only leaving the leaf veins in spring-fed streams in Hengladalir (Friberg et al., 2009), but that is similar to the act of shredders. This might indicate an adaptation of the invertebrates to different energy inputs, i.e. that new food sources lead to adaptation of the organisms present in the streams.

Other functional feeding groups than shredders composed 96–97% of the invertebrate abundance in the litter bags (Table 10). The majority belonged to Chironomidae, which contributed between 93 and 97% of the total number of invertebrates found in the litter bags. Chironomids are known to be the most common algae-feeders in Icelandic rivers and in run-off fed rivers the chironomids are usually dominating in the invertebrate community (Aðalsteinsson & Gíslason, 1998). The high abundance and proportion of Chironomidae in the present study was similar to what was found in New Zealand headwater streams (Parkyn & Winterbourn, 1997). No Icelandic data are presently available on the functional feeding groups of Icelandic run-off streams or rivers, apart from Medelyte (2010) that did her studies in the same streams in eastern Iceland.

4.6. Environmental abiotic and biotic control of decomposition across all streams in eastern Iceland

Abiotic factors

Many environmental factors are known to affect the rate of decomposition. Leaf decomposition rate has been associated with pH in streams (e.g. Friberg et al., 1980; Webster & Benfield, 1986), stream water temperature (Bärlocher, 1992; Campbell et al., 1992b; Cummins, 1979; Gulis & Suberkropp, 2003; Irons et al., 1994; Kaushik & Hynes,

1971; Linklater, 1995; Webster & Benfield, 1986) and concentration of nutrients like nitrogen and phosphorous (Buttimore et al., 1984; Webster et al., 1999). In the present study the only significant correlation was found between the total concentration of phosphor in the stream water and decomposition rate (Table 12). Only a few studies have found such relationship (Elwood et al., 1981; Kaushik & Hynes, 1971), while others have failed to show any acceleration of the leaf decomposition at higher phosphor concentration (Brock et al., 1985; Egglshaw, 1972). There are two possible explanations for this relationship: a) microbes are dependent on dissolved phosphorus from the stream water to be able to decompose the phosphorus low and carbon rich litter. The decomposition in the present study seems to be primarily driven by microbes in eastern Iceland and this positive relationship may indicate that the microbial activity was strongly controlled by phosphor concentration. b) Icelandic Andosols (volcanic soils) have high capacity to immobilise phosphor (Arnalds, 2004) and therefore run-off water usually has very low concentration of phosphor, even from cultivated agricultural soils (Þorsteinsson et al., 2004). It is therefore also possible that the litter decomposition was the main contributor of dissolved phosphorous in the stream water, i.e. the higher phosphor concentrations were the result of the accelerated decomposition, but not the reason for it.

Biotic factors

Abundance and assemblages of invertebrates and microbes have commonly been shown to affect the decomposition rate of allocthonous material in streams. Only one species of invertebrates was significantly correlated to the decomposition rate of leaf litter, which was Plecoptera, which is categorised as a shredder. The abundance of Plecoptera did, however, seem to decrease the decomposition rate of the litter within the coarse mesh litter bags. This negative relationship was unexpected and contrary to most published results for shredders and no studies were found in the literature that reported such negative effects of shredders on litter decomposition. What could explain this surprising result? Is the group of Plecoptera not really acting as shredders in Iceland? This would be an interesting topic for further studies.

4.7. Decomposition rate of birch litter in southern and eastern Iceland (run-off streams vs. spring-fed streams)

The hypothesis was that decomposition rate would be higher in the spring-fed streams in southern Iceland than in the run-off streams in eastern Iceland because of more stable environment. The findings of the present study partly supported this hypothesis. The decomposition rate within the coarse mesh bags was significantly higher in the southern site than in the eastern site, but when the invertebrates were excluded the difference was not significant (Figure 34). The difference between the fine and coarse mesh bags in southern Iceland are comparable to what was found in Hengladalir, where the leaf mass loss was almost twice as high in coarse mesh bags as in fine mesh bags (Friberg et al., 2009).

When decomposition rate was expressed per day degree instead of time (Figure 35), the decomposition was still higher in coarse mesh bags in southern compared to eastern Iceland, but all difference disappeared for fine mesh bags (microbial decomposition). The trend for higher microbial decomposition rate in S-Iceland was therefore probably solely explained by the effect of different temperature regime between the two localities/stream types.

In the spring-fed streams in southern Iceland the invertebrates clearly stimulated the decomposition rate, and there it was not primarily driven by microbial activity and environmental factors as in the run-off streams in eastern Iceland. There the invertebrate activity was important. Unfortunately no data is available in the present study on the invertebrate density or composition in the litter bags in southern Iceland. Medelyte (2010) found, however, 30–36 times higher number of invertebrates in the stream bottoms of the southern sites than in the eastern sites. This may support the findings in the present study, that mainly invertebrate activity explained the faster decomposition rate in southern Iceland/spring-fed streams. There have not been any other studies made to compare the decomposition rate of leaf litter between these two different stream types.

4.8. Methodological issues

The choice of method to measure litter decomposition

The use of litter bags in decomposition studies has been discussed in many papers during the past 40 years (Bärlocher, 2005b; Webster & Benfield, 1986; Winterbourn, 1978). In the present study both fine and coarse mesh bags were used, to exclude and include invertebrates in the decomposition process. The fine mesh nylon bags used in this study had a density of 200 μm and had a draw through string used to seal them. Such a fine mesh size should effectively exclude the invertebrates. Unfortunately the draw through string that was made from cotton decomposed after several months in the streams. This resulted in a loss of some fine mesh litter bags during the immersion period, especially the ones that were left over winter.

The coarse mesh bags were made of the 0.5 cm coarse plastic material, but since the larch needles and the grass litter was very fine and easily lost from the coarse bags, we put an inner bag of 200 μm nylon with twelve 0.5 cm wide holes into it to hold the litter. Originally, when the lack of response was seen in decomposition rate in the coarse bags in eastern Iceland, it was questioned if invertebrates were able to get into them. Later, when it had been verified that the coarse mesh bags indeed contained high densities of invertebrates and their exclusion also led to lower decomposition rates in southern Iceland, this concern was deemed unjustified.

It has been pointed out that litter bags may create artificial conditions around and inside the group of leaves within them which is an unnatural stage in the decomposition, and this may create artificial differences between fine and coarse meshed bags (Petersen & Cummins, 1974). The effect of bag mesh size has shown very different results, but some studies showed no effect of mesh size while other indicated a faster decomposition rate within the coarse mesh bags (Abelho, 2001; Benfield et al., 1979; Webster & Benfield, 1986). It may be argued that using an inner bag, as was done in the present study, should have made the two types of litter bags more comparable, creating similar conditions in both fine and coarse mesh bags.

Another method often used to measure litter decomposition rates is the leaf pack method, where leaves are packed together with a string before the immersion to the stream-water.

This method has been used in many decomposition studies with broadleaved litter (Abelho, 2001; Benfield et al., 1979; Petersen & Cummins, 1974; Webster & Benfield, 1986). It is considered a more natural way to assess the breakdown rates of leaves in the streams, but there is always a risk of losing large fragments of material which might result in a wrong estimation of weight loss (Boulton & Boon, 1991). This method is not usable for fine litter, such as larch needles and grass, which was included in the present study.

The third possible method to study the decomposition activity is the cotton strip method, or cotton strip assay, which might be a good way to estimate the relative microbial activities in the decomposition process in different catchment types, but does not give absolute rates of leaf litter decomposition (Tiegs et al., 2007). This method has been used in soil biology, but has not been used in many studies that focus on the activity within stream water (Brown & Howson, 1988; Latter & Walton, 1988; Tiegs et al., 2007).

The choose of litter types

Another methodological issue was the decision to use three litter types, birch leaves, larch needles and grass litter, and to incubate them all in all streams in eastern Iceland. This was a decision made to address the importance of litter quality groups and also to study the adaptation of the biota in different catchments towards a specialization to the dominant litter type. This approach has been used in various other studies (e.g. Abelho & Graça, 1996; Webster & Benfield, 1986). It must be noted here that although we picked those specific litter types, there were many other species that could be used since the diversity of litter that actually falls into the streams is much higher.

Time of immersion

In the present study the treatments started in the spring and followed the decomposition until the late autumn. In nature most of the leaf transport occurs however in the late autumn. To study if the time of immersion was very important, an extra batch of birch leaves was immersed in the spring and compared to leaves incubated for the same amount of time in the autumn. There was significant difference between the decomposition rates of birch litter considering the time of immersion to the water (Figure 30). To look further into the results the decomposition was analysed per day degrees instead of days. This was made to see how

large the impact of temperature was on the decomposition. The difference between the two seasons almost disappeared when analysed per day degree (Figure 31). This showed that the difference in decomposition rate if the litter was immersed in spring or autumn was probably only due to temperature differences, but not primarily because of different seasonal composition of invertebrates or microbes. This finding was important. It shows that the timing of immersion was not radically affecting the direction of the response (only simple temperature effect).

Estimates of the decomposition constant (the k-value)

An exponential decay model is normally applied to estimate the decomposition constant of the leaf litter decomposition (Abelho, 2001; Bärlocher, 2005b; Petersen & Cummins, 1974). Initially the spring weights of the following year were included in the calculations of the k-value for larch needle and grass litter. This did not work, because during winters the weight loss was very low in eastern Iceland and therefore it was impossible to include winter decomposition when the k-values were estimated.

The decomposition during winter was only about 25–41% of the decomposition rate that was observed during the other seasons (Figure 32). To see if the low decomposition rate during the winter was only caused by the low winter temperatures, the decomposition rate was transferred to day degrees instead of days. This transformation did not seem to decrease the differences between the decomposition of the seasons (Figure 33), which might indicate that the decomposing organisms become dormant or have low populations during the winter time. The lack of decomposition activity during winters in Icelandic streams is different from what was observed in various other studies e.g. in Scandinavia and Australia (Campbell et al., 1992a; Petersen et al., 1995), where it could be included in an exponential model when expressed per day degree.

Catchment classification

When the studied streams were chosen, they were divided into three main classes based on their dominant catchment vegetation. Unfortunately, when the catchments were later carefully mapped there were some unfortunate complications within some of them. There was a small patch of conifer forest found within one of the heathland catchments and also in one of the birch forest catchments. These patches were only 0.2% of the heathland

catchment and 4% of the total birch forest area (Figure 14), and should therefore not have had any major effect on the results of the present study. The natural environment is, however, mosaic and therefore the lack of response to catchment type in eastern Iceland could possibly be attributed to the fact that all catchments also had other vegetation classes within them than the dominant vegetation class. It can be asked what is most important, the vegetation composition in the whole catchment or the vegetation composition within the catchment closest to the study area? This thesis was most focused on the vegetation composition within a 400 m distance from the sampling stations, i.e. the area nearest the riparian zone of the sampling stations.

Origins of the spring-fed streams

In the south site the streams were much shorter and therefore their mapped catchments were smaller and with more homogeneous vegetation. The catchments were mapped based on the water boundaries between catchments based on topography and altitude. However, we cannot know for sure where the water in the spring-fed streams originated from, and surely part of the spring-fed water originated from far away sources. Mapping of spring-fed streams at Þingvellir in S-Iceland has shown that they partly originate from glacial melt water that filters into the bedrock tens of kilometres away from where the streams surface (Sigurðsson & Einarsson, 1988). Therefore it should be borne in mind that only part of the water in the spring-fed streams came from draining of the mapped catchments.

Conclusions

- The present research was the first ecosystem study made in Iceland that connected forests and streams running through them. It revealed many factors that did not mirror the results found in comparable ecosystems abroad. This difference shows how important it is to do more research in Icelandic ecosystems to fully understand their function and how they are affected by land-use change, such as afforestation.
- These results indicated a strong relation between the terrestrial vegetation and the amount of litter entering the streams. This litter transport increased the amount of energy that was available in the streams which might increase the abundance of organisms living further down the streams. Catchment vegetation is important when considering the amount of organic matter transported into the streams and is available for the stream biota.
- Different organic matter seemed to decompose at similar rates in all run-off streams in eastern Iceland, which is different from what has been observed in other countries and the average rate of decomposition might then possibly be used for all litter types in all streams in run-off fed streams in eastern Iceland.
- Microbial activity seems to be much more important than invertebrate activity in the decomposition processes in the run-off streams in eastern Iceland. There were very few shredders found in the litter bags which reflects the findings in other streams in Iceland and that they are not important in the decomposition processing of litter in Icelandic streams. It is also possible that invertebrates have adapted to the low supply of transported organic matter and may have become opportunists.
- The decomposition rate was negatively correlated with the number of shredder Plecoptera found in the litter bags in the run-off streams in eastern Iceland. This could indicate a different feeding activity of the group and needs to be studied further.
- The microbial activity was not different between southern and eastern Iceland which indicates that the invertebrate activity explains the faster decomposition rate in southern Iceland/spring-fed streams.

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Appendix 1: The proportion of weight of remaining grass litter, birch litter and larch litter in fine and coarse mesh litter bags incubated for 48, 89, 140, 175 and 366 days in three catchment types in eastern Iceland (%; \pm standard error, $n = 3$). A star indicates a significant difference between fine and coarse mesh bags (two-way repeated ANOVA followed Fishers LSD tests, $\alpha=0.10$).

