Aerial Dispersal of Invertebrates and Mosses Close to a Receding Alpine Glacier in Southern Norway

Authors: Flø, Daniel, and Hågvar, Sigmund

Source: Arctic, Antarctic, and Alpine Research, 45(4) : 481-490

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1938-4246-45.4.481

Arctic, Antarctic, and Alpine Research, Vol. 45, No. 4, 2013, pp. 481–490

Aerial Dispersal of Invertebrates and Mosses Close to a Receding Alpine Glacier in Southern Norway

Daniel Flø and*
Sigmund Hågvar†

*Norwegian Forest and Landscape Institute, Box 115, 1431 Ås, Norway
†Corresponding author: Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Box 5003, 1432 Ås, Norway. sigmund.hagvar@umb.no

Abstract

The 73 km^2 large Hardangerjøkulen glacier in alpine, south Norway is receding. By using sticky and fallout traps, we studied the aerial transport of invertebrates in a foreland with a well-documented succession of mites, springtails, spiders, and beetles. Since mosses are pioneer plants and also food for certain pioneer invertebrates, airborne fragments of mosses were also included in the study. Sampling on 3- to 6-year-old ground revealed aerial transport of several species of mites and springtails. During 4 weeks, the fallout of microarthropods was calculated at around 1000 specimens per m^2. This number may depend strongly on local variations in climate and must be treated with care. Besides typical pioneer species, some species assumed to depend on older soil were also trapped. This indicates that the ability to survive is more limiting than the ability to disperse. A few spiders assumed to have the capability for ''aerial ballooning'' were trapped. Moss fragments, including bulbil diaspores, were common in both trap types. Diptera were sometimes taken numerously, and in sticky traps mainly in those facing away from the glacier. Most aerial transport occurred below 0.5 m height, and the presence of sand grains in sticky traps up to this level illustrated the mechanical force of wind transport. We conclude that aerial transport helps colonization of several non-flying pioneer organisms like mites, springtails, aphids, and mosses.

DOI: http://dx.doi.org/10.1657/1938-4246-45.4.481

Introduction

Due to global warming, glaciers in many parts of the world are receding (Oerlemans, 2005). Several studies have shown that the newly exposed, barren ground around melting glaciers is rapidly colonized by invertebrates, both in the Alps (Kaufmann, 2001; Kaufmann and Raffl, 2002; Kaufmann et al., 2002; Gobbi et al., 2006a, 2006b, 2007, 2010a), on Svalbard (Hodkinson et al., 2001, 2002; Coulson et al., 2003; Hodkinson et al., 2004), and in Norway (Skubala and Gulvik, 2005; Seniczak et al., 2006; Hågvar et al., 2009; Hågvar, 2010; Bråten et al., 2012; Vater, 2012). Typical pioneer animals are microarthropods (Collembola and Acari), which largely belong to the decomposers, and predatory spiders and beetles. Hodkinson et al. (2002) explained the paradox of starting a primary succession with heterotrophic organisms by aerial transport of dead organic matter and living invertebrates, feeding both decomposers and predators. This dependence on wind-blown resources is a parallel to ''eolian biomes,'' which characterize extreme, high-altitude environments that have no or very small primary production (Edwards, 1987; Swan, 1992).

Aerial transport may also be an important dispersal mechanism for the pioneer species themselves. However, there are only a few studies on aerial transport of invertebrates in glacier forelands. On Svalbard, Hodkinson et al. (2001) used water/pitfall traps in the foreland of Midtre Lovénbreen and found a correlation between catches of spiders and chironomids. They assumed that the two groups had been transported by air, as spiders have the capability for ''aerial ballooning'' on silk threads. Using water and sticky traps in an age gradient within the same foreland, Coulson et al. (2003) collected large numbers of Diptera, Hymenoptera, and Araneae by both trap types. These flying groups were taken even in the youngest and unvegetated site. However, evidence of wind dispersal by non-flying groups like Collembola or Acari was lacking. To our knowledge, Hawes (2008), who also worked in the Midtre Lovénbreen foreland, is the only one who has demonstrated eolian fallout of microarthropods in a glacier foreland with a proper method. Using 3- to 4-cm-high, water-filled fallout trays with a sticky tape on the rim to stop surface arthropods attempting to access them, six specimens of Acari (Gamasid spp.) and two specimens of Collembola (*Isotoma anglicana* Lubbock, 1862) were trapped. This small catch during about 2 months gives only weak support for aerial dispersal of pioneer microarthropods. Moreover, no arthropods were found on any of the snow patches examined for any of the sites along the transect.

Outside glacier forelands on Svalbard, Magnussen (2010) documented aerial fallout of several Collembola and Acari species in water traps, although in limited numbers. A convincing case of aerial transport of Collembola has also been reported from the Antarctic Peninsula, based on a few specimens (Hawes et al., 2007).

A fresh study on Iceland showed that springtails and oribatid mites easily colonized recently emerged nunataks, and that isolation of a few kilometers did not affect the colonization (Ingimarsdóttir et al., 2012). These results strongly indicate aerial dispersal, but it remains to be demonstrated.

We studied aerial transport of invertebrates in a Norwegian glacier foreland with a well-documented succession of Acari (Hågvar et al., 2009), Collembola (Hågvar, 2010), as well as spiders and beetles (Bråten et al., 2012). All these groups are able to follow the receding glacier closely. Since mosses are typical pioneer plants, and even feed some pioneer invertebrates (Hågvar, 2012; Bråten et al., 2012), aerial transport of moss fragments and diaspores was included in the study. The glacial melting has been

TABLE 1

Mean catches per sticky trap during 24 hours on 12–13 July 2008, in two different distances from glacier edge. Lower height of traps is indicated.

Distance from glacier (m)	Height above ground (cm)	No. of traps	Acari, Oribatida: *Tectocepheus velatus* (Michael, 1880)	Hemiptera: Aphididae (winged)	Diptera: Brachycera	Diptera: Nematocera	Moss fragments
10–15	2–6	5			2.6	0.8	0.6
	8–12	6			2	0.8	0.2
	18–20	2		0.5	2	1.5	
60–65	6	5	0.2		6.6	2	0.2
	15	3			4.3	1	
	25	1			5	1	

intense during the last few decades, and the ice front receded 154 m between 2001 and 2011. In order to understand the succession pattern in the glacier foreland, a key question is how pioneer organisms disperse.

According to current theories, a successful pioneer species has to pass through two ''filters'': a dispersion filter in order to arrive, and an ecological filter in order to survive and reproduce (Ingimarsdóttir et al., 2012). Already Clements (1916) pointed to these filters in plant succession, and addressed them as ''migration'' for dispersal ability and ''ecesis'' for the ability to establish and grow. Catches of aerially transported invertebrates could illustrate whether typically pioneer species easily pass the dispersion filter, and also whether non-pioneer species are dispersed. For these, the pioneer ground would be a sink.

Our site is significantly more species rich than the cited high-latitude sites, and it is better suited to illustrate possible dispersal of both pioneer and non-pioneer species in the context of a more complex ecosystem.

Methods and Study Area

STUDY AREA

Hardangerjøkulen is a 73 km^2 large glacier in alpine, south Norway. The foreland studied is close to the Midtdalsbreen glacial snout, about 1400 m a.s.l. Aerial photo and further details of the foreland have been given by Bråten et al. (2012). Most samplings were made on or close to a moraine ridge that was pushed up in 2005, following a temporary glacier extension of 7 m during 2004 and 2005. At the end of our sampling seasons in 2008, 2010, and 2011, the glacier had retreated 72, 100, and 111 m, respectively, behind the 2005 position (Atle Nesje, personal communication).

STICKY TRAPS

White sticky traps, 9 cm high and 15 cm long, were used in 2008 and 2011 (type Catchlt produced by Silvandersson AB, Knäred, Sweden). In 2008, the sticky surface faced away from the glacier in order to detect inward transport. During a 24-h period between 12 and 13 July, traps were operated at two different distances from the ice edge. At a distance of 10–15 m, 13 traps with lower rim 2–20 cm above ground level were distributed on 3 wooden sticks. At a distance of 60–65 m, 9 traps with lower rim 6–25 cm above ground level were distributed on 2 wooden sticks (details in Table 1). In addition, 8 traps from the inner site and 7 from the outer site, all below 30 cm height, were left for 2 weeks and sampled 26 July. Due to rainy periods that partly washed away catches, and small sand grains attached to all traps reducing the sticky effect, the 2 week-traps did not have quantitative value. However, they had a qualitative value because they did trap some Collembola, Acari, and Araneida (details in Table 2).

In 2011, double sticky traps were placed on 2 wooden sticks on the 2005 moraine, about 100 m from the glacier edge, and sampled weekly during 4 weeks (Fig. 1, details in Table 3). On one stick, the sticky surfaces faced towards N and S, and on the other stick towards E and W. In this way, aerial transport was detected from all four main directions at each of the following height levels: 5–14 cm, 15–24 cm, 25–34 cm, 35–44 cm, 65–74 cm, and 95–104 cm. Wind-blown sand grains were common in traps up to 44 cm height, but without destroying the sticky ability for invertebrates. Except for the first sampling period, Vaseline grease was smeared on the lower 5 cm of the sticks to prevent invertebrates from climbing up it. Non-flying animals in Tables 1–3 were situated at least 1 cm from the trap edge on all sides, indicating aerial transport.

FALLOUT TRAPS

In 2010, fallout traps with 6.5 cm diameter were made from 2 transparent plastic cups, an outer cup and a smaller inner cup in

TABLE 2

Selected catches from sticky traps operated 12–26 July 2008, in two different distances from glacier edge. Lower height of traps is indicated.

Distance from glacier (m)	Height above ground (cm)	Selected catch of special interest
10–15	15	Collembola: *Bourletiella hortensis* (Fitch, 1863): 1 adult and 1 juvenile
	20	Collembola: *Bourletiella hortensis*: 1 adult
	20	Araneae: *Erigone arctica* (White, 1852): 1 adult, female
	20	Hemiptera: Aphididae: 1 adult, winged
60–65	6	Collembola: *Bourletiella hortensis*: 1 adult
	6	Acari, Oribatida: *Tectocepheus velatus*: 1 adult

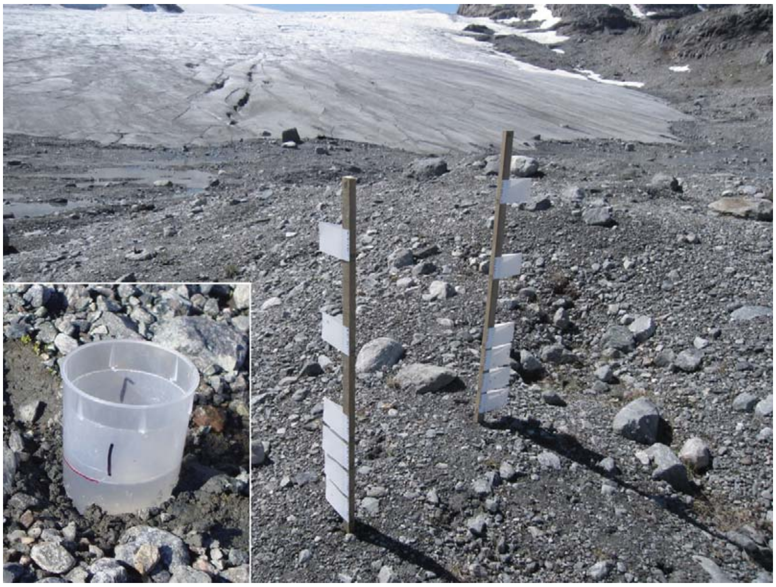

FIGURE 1. Sticky traps in 2011, placed on a moraine from 2005, about 100 m from the retreating glacier edge. They sampled aerial transported material from north, south, east, and west up to about one meter height. Inserted in lower left corner: open fallout trap with 6.5 cm diameter.

TABLE 3

Weekly sticky trap catches on a 6-year-old moraine in 2011. Lower height of traps is given. Data from each height at a given date are the sum of four traps situated towards N, S, E, and W, respectively.

Sampling date	Height (cm)	Acari: Actinedida. Tetranychidae, *Bryobia* sp.	Opiliones: *Mitopus morio* (Fabricius, 1799)	Psocoptera (wingless)	Hemiptera: Aphididae (wingless)	Diptera: Brachycera	Diptera: Nematocera	Diptera: Sciaridae, larvae	Hymenoptera parasitica	Coleoptera: *Nebria nivalis* (Paykull, 1790)	Insecta: indet	Moss fragments	Seeds
3 August	5		2		3	167	35		1			4	
	15					62	24		2			4	
	25	1	1			43	14		1			4	
	35					28	9					4	
	65					20	2		1				
	95					5	2		1				
10 August	5	1		2	3	7	4		1			13	
	15					6	1	1				2	
	25	1				2			1			2	
	35					7						2	
	65		1		1				1				
	95					1							
17 August	5		6			16	3		1	1			1
	15					4							
	25					2							
	35						2						
	65												
	95										1		
24 August	5	1			2	5	3	1				17	1
	15					1	1					11	
	25	1	1										
	35					2						1	
	65					1							
	95												

a lower position, with a fine-meshed bottom (0.25 mm). Saturated saline water and a drop of detergent were used as preservative. Six 1.5-mm holes were drilled 1.5 cm below the rim of the outer cup to allow surplus liquid to escape during heavy rain, so that material was not lost. The traps were dug down so that the rim of each trap was 5 cm above the ground (Fig. 1). This was sufficient to prevent surface active invertebrates from dropping into them. Thirty traps were evenly distributed over the 2005 moraine ridge on an area of 20 × 25 m, with 5 traps along the ridge top, 15 on the slope towards the glacier, and 10 on the other slope. There were 4 weekly sampling periods, from 9 August to 6 September. During sampling, the inner cup was replaced, so that the preservative remained. The salt solution was made from tap water to prevent contamination. A few traps required the addition of a little water or salt during the experimental period. This water was taken from a nearby pond, but under great care to prevent contamination.

In 2011, 25 traps with corresponding surface were placed in a 20 × 20 m grid on the same moraine, but on the inner slope towards the glacier. These traps were made 11 cm high by securing the outer cup to the ground by three 10-cm nails that where pushed through the bottom. Also, a sticky belt of Vaseline grease was applied on the upper outer side to prevent invertebrates from crawling into it. Since salt had a tendency to glue the inner cup to the wall, we chose propylene glycol as the preservative. There were 4 weekly sampling periods, from 27 July to 24 August. The microarthropods in Tables 1–5 were considered to be trapped alive due to intact shape or presence of gut content. Wind-borne exuviae or apparently dead individuals were excluded.

NUMERICAL ANALYSES

Differences in catches between the 15 traps closest to the glacier and the 15 other traps were tested with R, version 2.14.2

TABLE 4

Total catches in 30 fallout traps on a 5-year-old moraine, based on 4 weekly periods in 2010. Trap height is 5 cm. Sampling dates are given.

Taxon	16 Aug	23 Aug	30 Aug	6 Sep
ACARI				
Actinedida	3	5	3	11
Oribatida: *Eupelops plicatus* (C. L. Koch, 1835)		1		
Oribatida: *Oribatula tibialis* (Nicolet, 1855)				1
Oribatida: *Scheloribates initialis* (Berlese, 1908)				2
ARANEAE: Linyphiidae, juv.	1	2	1	
OPILIONES: *Mitopus morio* (Fabricius, 1799)	1			
COLLEMBOLA				
Bourletiella hortensis (Fitch, 1863)	6	2	3	3
Heterosminthurus claviger Gisin, 1958				1
Lepidocyrtys lignorum (Fabricius, 1793)	7	6	10	8
Lepidocyrtus cyaneus Tullberg, 1871	2	1		
Agrenia bidenticulata (Tullberg, 1876)	2	1	9	2
Isotoma viridis Bourlet, 1839	2	1	1	2
Desoria sp.	4	4	2	1
Tetracanthella brachyura Bagnall, 1949				1
Ceratophysella denticulata (Bagnall, 1941)	1			
HEMIPTERA				
Aphididae (wingless)	2	1		
PSOCOPTERA (wingless)	1	2		
DIPTERA				
Nematocera: Chironomidae	57	8	7	9
Brachycera	6	3	3	
Nematocera: Chironomidae: Larvae			2	
COLEOPTERA				
Helophorus glacialis Villa & Villa, 1833				1
Anthophagus alpinus (Paykull, 1790)		1		
Coleoptera: larvae		1		
HYMENOPTERA				
Parasitica	6			1
PLANT MATERIAL				
Moss fragments	110	97	86	13
Seeds	1	6		3

TABLE 5

Total catches in 25 fallout traps on the inner part of a 6-year-old moraine, based on four weekly periods in 2011. Trap height is 11 cm. Sampling dates are given.

Taxon	3 August	10 August	17 August	24 August
ACARI				
Actinedida	2	6	4	1
Oribatula tibialis	1			
COLLEMBOLA				
Bourletiella hortensis		1		
Isotoma viridis	1			
Desoria sp.	1		1	
Indet.	1			
OTHER INVERTEBRATES				
Hemiptera: Aphididae (unwinged)	1			
Diptera: Chironomidae	24	5	2	
Diptera: Brachycera	1	2	1	
Diptera: Chironomidae, larvae		1		1
PLANT MATERIAL				
Moss fragments	57	48	14	57
Seeds		1		1

(R Development Core Team, 2012), with the ''MASS'' package for pairwise *t*-test and Shapiro-Wilk test, and ''stats'' package for Wilcoxon Signed-Rank test. The nearest weather station was Finse research station at 1200 m altitude, 3.7 km NE of the 2005 moraine. Since it did not reflect the local climate at the trap site, and also because each sampling period covered 7 days, we did not find it fruitful to look for relationships between catches and climate data. However, we used the presence of sand grains on sticky traps at different height and direction to indicate the wind's ability to lift and transport small items from the ground. In the first sampling period of 2011, which gave relatively good catches of Brachycera and Nematocera on sticky traps, sand grains of at least 0.5 mm size were counted and related to insect catches. Effects of direction and height were tested by pairwise *t*-test, given normality (Shapiro-Wilk test). Otherwise we used Wilcoxon Signed-Rank test.

Results

STICKY TRAPS

Table 1 shows the 24-h catches in rather low sticky traps on 12–13 July 2008. Nematocera and Brachycera were trapped at all height levels, both close to the glacier (10–15 m) and further apart (60–65 m). A winged aphid was taken at the youngest site, and moss fragments at both sites. Of special interest was an oribatid mite, *Tectocepheus velatus*, at the oldest site. Small sand grains were recorded on all traps. The traps that were left for 14 days, and had partly lost their catches due to rain, gave some interesting qualitative results (Table 2). Four specimens of the large springtail *Bourletiella hortensis* were trapped, 3 of them close to the glacier. Here, also, the spider *Erigone arctica* and a winged aphid were taken. The oribatid mite *Tectocepheus velatus* was again trapped at the oldest site. Various Diptera and Hymenoptera, moss fragments, and seeds are not included in Table 2.

Weekly catches from sticky traps on the 2005 moraine in 2011 are shown in Table 3. The highest catches were generally taken at the lower levels. Several taxa were trapped, with a strong dominance of Diptera early in the season. Of special interest were 5 specimens of relatively large, red Actinedida mites of the genus *Bryobia*, 2 specimens of Sciaridae larvae (Nematocera), and 9 wingless aphids. Moss fragments were often found, below 50 cm height. These included some bulbils, which are small, onion-like distribution units. Also, wind-blown sand grains were abundant below 50 cm, but rare or absent above that. Figure 2 shows some Collembola, Acari, and Araneae taken in sticky traps during 2008 and 2011.

Figure 3 shows that most sand grains had been thrown up by western winds, while Brachycera and Nematocera were trapped predominantly on north-facing traps. Including all heights, significantly more sand grains were found on west-faced compared to north-faced traps ($p = 0.04$) and, nearly as significantly, more towards north than towards south ($p = 0.06$). Both Brachycera and Nematocera were taken significantly more numerously towards north than towards west or south ($p = 0.04$, except Nematocera north-south: $p = 0.07$). Within each column in Figure 3, the lower transverse line indicates the fraction collected at 5- to 14-cm height (the lowest trap), and the upper transverse line the fraction collected together below 34-cm height (the 3 lowest traps). Lumping the 4 directions together, the lowest trap always had significantly higher catches than any other higher trap ($p < 0.05$), both regarding sand grains, Brachycera, and Nematocera. An exception was a non-significant difference of Nematocera among the 3 lowest traps, but numbers were rather low here.

FALLOUT TRAPS

On the same 2005 moraine, fallout traps in 2010 gave a high number of taxa during 4 weeks (Table 4). Nine species of Collembola, 3 species of Oribatida, and a number of Actinedida mites were trapped. Among other non-winged invertebrates were 4 juvenile

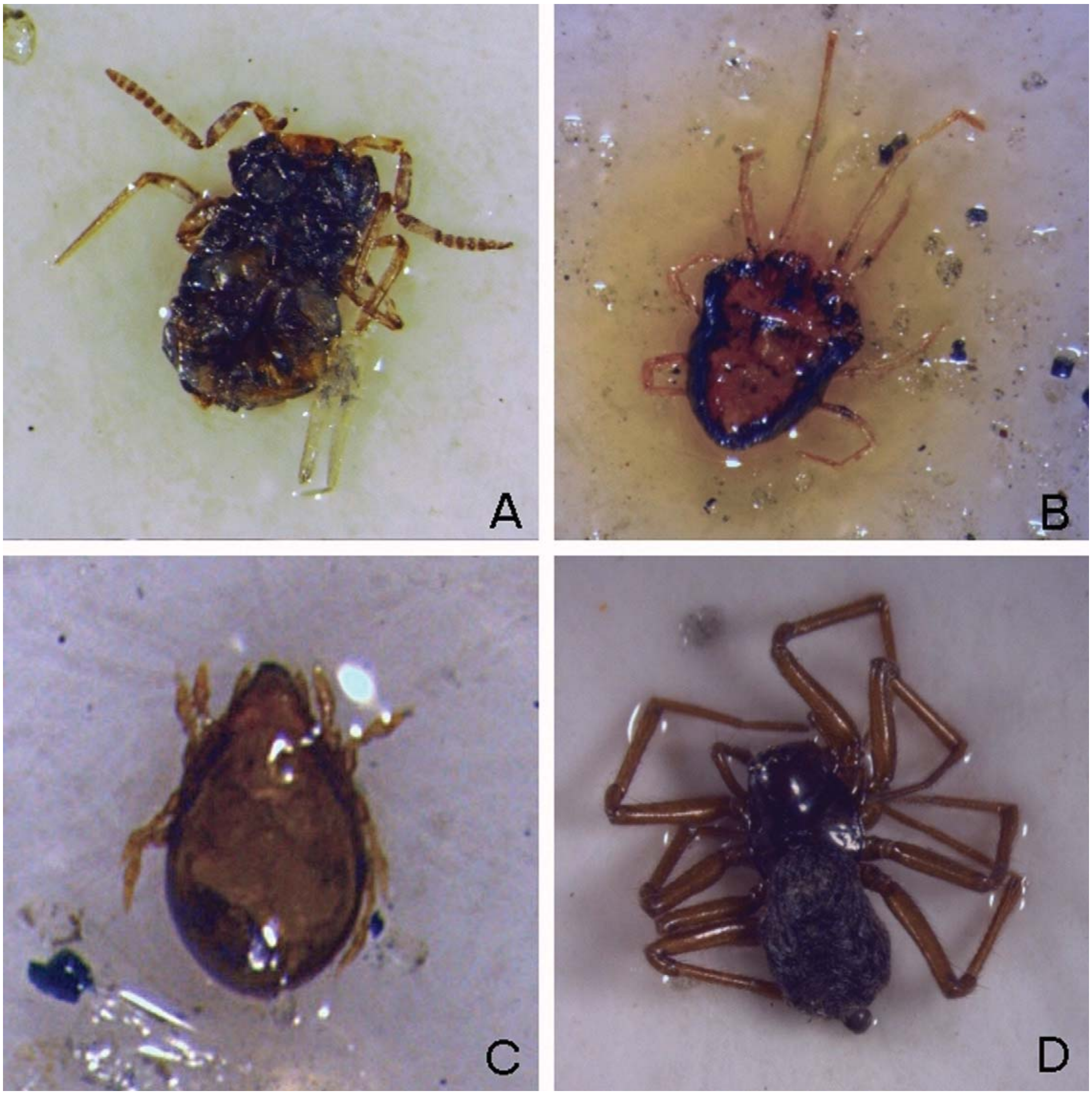

FIGURE 2. Examples of invertebrates taken in sticky traps. (A) *Bourletiella hortensis* (Collembola, Bourletiellidae). (B) *Bryobia* sp. (Acari, Tetranychidae). (C) *Tectocepheus velatus* (Acari, Oribatida). (D) *Erigone arctica* (Araneae, Linyphiidae).

Araneae of family Linyphiidae, 2 larvae of Chironomidae, one of Coleoptera, 3 Aphididae, and 3 Psocoptera. Furthermore, some seeds and a high number of moss fragments were taken. Significantly more moss fragments were present in the 15 traps furthest away from the glacier compared to the other 15 traps (Wilcoxon test, $W = 1205$, P-value $= 0.001$), but the numbers of invertebrates were too low to be tested. Wind-blown sand grains were present in all traps at all samplings. Only very small organic fragments were seen in the traps, so there was no clear transport of dead leaves and other large plant remains. The absence of Carabidae beetles, which were common at the site, shows that the traps were high enough to prevent surface active invertebrates from dropping into them. The 2 non-carabid beetles trapped had probably been flying.

The taller fallout traps placed on the inner side of the 2005 moraine in 2011 gave less material (Table 5). However, several specimens of Actinedida mites were taken, together with one Oribatida species, *Oribatula tibialis*, and at least 3 Collembola species. Among other non-winged invertebrates were 2 Chironomidae larvae and an Aphididae. The traps contained a high number of moss fragments, including bulbils and even protonema (Fig. 4). Again, sand grains in all traps confirmed wind transport in the area.

Discussion

DOCUMENTATION OF AERIAL TRANSPORT

Both sticky and fallout traps illustrated aerial transport of several invertebrate groups close to the receding glacier. This is the first clear documentation of airborne microarthropods in a glacier foreland, except for a few microarthropods recorded in fallout traps in Midtre Lovénbreen foreland at Svalbard (Hawes, 2008). Altogether, 9 species of Collembola and 4 species of Oribatida were identified in our traps. Other wingless groups taken were Actinedida mites, Araneae, Opiliones, Aphididae, Psocoptera, and larvae of Coleoptera, Sciaridae, and Chironomidae. The 2 types of Diptera larvae must be terrestrial, with a certain surface activity.

While even small invertebrates like Actinedida mites could be counted in fallout material, by shifting between a light and a

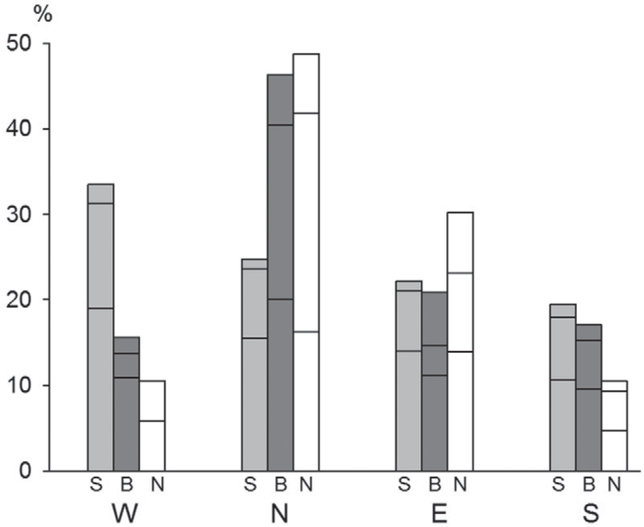

FIGURE 3. Sticky trap catches of sand grains of at least 0.5 mm diameter (S), Brachycera (B), and Nematocera (N) during the first sampling week in 2011. For each category, percent catches arriving from each main wind direction (W, N, E, S) are shown. Within each column, the lower transverse line indicates the fraction collected at 5–14 cm height, and the upper transverse line the fraction collected together below 34 cm height. While significantly more sand grains were taken on west-faced traps compared to north-faced ones, the opposite was the case with Brachycera and Nematocera.

dark background during sorting, small invertebrates were probably underestimated on the white sticky trap surfaces, which could also be heavily contaminated by sand grains.

The 30 fallout traps that covered both the inner and outer sides of the 2005 moraine in 2010 collected 108 microarthropods during 4 weeks: 22 Actinedida, 4 Oribatida, and 82 Collembola (Table 4). Since the total surface of the traps covered 1000 cm^2, the total fallout in this period can be calculated to be 1080 microarthropods per m^2. This is a considerable number and indicates that aerial transport promotes early microarthropod colonization. However, this number should be treated as a guess, since it may depend on episodic input during certain climatic conditions, including small-scale wind turbulences.

Transport of microarthropods by wind has been documented in some studies on aerial plankton. A small number of Collembola were taken in fine-meshed nets in Alaska (Gressitt and Yoshimot, 1974). Several groups of small mites are known to promote their dispersal by wind, for instance ballooning members of the Tetranychidae family (spider mites) (Brandenburg and Kennedy, 1982), some of the plant parasitic members of the Eriophyidae family (gall mites) (Bergh and McCoy, 1997), and some predatory mites of the Phytoseiidae family (Johnson and Croft, 1981; Jung and Croft, 2001). Other studies strongly indicate aerial transport of microarthropods due to their ability to colonize volcanic islands relatively soon after eruptions, like Surtsey (Lindroth et al., 1973), and Krakatau (Thornton et al., 1988). Also, a fresh study from Iceland showed that newly appeared nunataks within a few kilometers distance from the glacier edge were rapidly colonized by certain species of Collembola and Orbatida (Ingimarsdóttir et al., 2012).

Considerable amounts of moss fragments were transported by wind, as shown by both trap types. Some of the moss units were bulbils, which are onion-like, nutrient-rich dispersal units. These readily grow, developing both rhizoids and shoots if placed on a moist surface (Hågvar, 2012). In addition, protonema identified from a fallout trap illustrates the unique ability of mosses to disperse. Also, Bråten et al. (2012) recorded many wind-blown moss fragments in pitfall traps on the same moraine, 3 years after its formation. Pioneer mosses are eaten by 2 pioneer invertebrates: various developmental stages of the Collembola *Bourletiella hor-*

FIGURE 4. Wind-blown protonema of moss, taken in 11-cm-high fallout trap in 2011.

tensis, and both larvae and adults of the Byrrhidae beetle *Simplocaria metallica* (Sturm, 1807) (Hågvar, 2012; Bråten et al., 2012). Only a few seeds of higher plants were trapped.

HOW IS AERIAL TRANSPORT WORKING?

The mechanical force of wind was illustrated by the occurrence of sand grains in all fallout traps, at both 5 and 11 cm height. Also, sticky traps were contaminated by sand grains, most heavily near the ground, and regularly up to 44 cm height. Stony particles up to 25 mg were found at 30 cm height, and small grains could be seen up to one meter height. All windblown moss fragments were trapped below 44 cm height, as were the majority of invertebrates, both unwinged and winged. Taken together, this indicates that aerial transport of life forms into pioneer ground occurs rather close to the ground.

Maybe the main transport of microarthropods occurs at a few centimeters height. This could explain why 5-cm-high fallout traps collected much more microarthropod material than 11-cm-high traps, although the latter were situated somewhat closer to the glacier (Tables 4 and 5). A long dispersal may be the sum of several small transports. Collembola could, for instance, easily be taken by wind when jumping. Transport of microarthropods clinging to wind-blown moss fragments, or even insects, is a possibility. Also, microtopography counts. Hågvar (2012) illustrated how pioneer mosses often established along larger stones, which stopped the aerial transport of moss diaspores towards the glacier. A stony microtopography easily stops aerial transport of organisms, and also allows them to remain in wind-sheltered microsites. Open surfaces, however, leave organisms more susceptible to further wind transport.

While the microarthropod catches did not indicate an effect of sampling period, Tables 3–5 indicate highest catches of Diptera early in the trapping period. In dispersion studies, it is obviously important to cover such phenological changes. Sticky traps sampled on 3 August (Table 3) contained sufficient information about flying Brachycera and Nematocera to discuss height and direction. Both groups were taken mainly below 34 cm height (84% of Brachycera and 85% of Nematocera). Animals were trapped from all wind directions, but mainly on north-facing traps (46% of Brachycera and 49% of Nematocera). As shown in Figure 3, sand grains had been transported mainly by western winds, which means that the 2 insect groups had migrated independent of the sand transport. North-facing traps collected insects on their way towards the glacier, coming from older areas with a richer insect life. A corresponding transport of Diptera to pioneer ground was observed in a glacier foreland on Svalbard (Coulson et al., 2003). They found that nearly all flying insects were trapped below 25 cm height, and assumed that a favorable microclimate close to the ground, including low wind speeds, enabled controlled flight activity largely independent of wind direction. Our catches support near-ground flight of Diptera groups, although sticky trap data do not distinguish between wind-blown insects, active flight, or possibly attraction to a white surface. The data should be treated with care, also because they may depend on episodic wind conditions.

Using water traps outside glacier forelands on Svalbard, Magnussen (2010) tried to correlate aerial transport of invertebrates with climate data. He concluded that Brachycera and Hymenoptera catches were positively related to temperature, but negatively related to wind speed. He assumed that catches were mainly a result of active flight, initiated by a minimum temperature combined with low wind speed. These conditions allow controlled, directional flight close to the ground, without being swept away by wind. Collembola catches were also negatively correlated to wind speed, but positively related to relative humidity. It was assumed that surface activity of Collembola was reduced under dry conditions, and wind is known to reduce humidity. His study indicates that wind speed alone may be a bad indicator of invertebrate transport by air. A common conclusion from Coulson et al. (2003) and Magnussen (2010) is that aerial dispersal of Diptera and Hymenoptera in harsh environments seems to be mainly a result of active flying, and not passive wind transport. Our trappings of Diptera at low heights may fit with this assumption, although our weekly data are not suitable for detailed testing towards weather parameters. Relationships between microclimate and aerial transport of invertebrates should probably be studied hour for hour, but such studies are lacking.

Linyphiidae spiders have the ability of ‘‘aerial ballooning’’ on silk threads, and are efficient colonizers of pioneer ground in glacial forelands on Svalbard (Hodkinson et al., 2001, 2002; Coulson et al., 2003). The few spiders in our material may have used this method. The adult specimen of *Erigone arctica* taken in a sticky trap belongs to a pioneer species (Bråten et al., 2012). Concerning the Opiliones specimens taken in sticky traps (Table 3), they are somewhat problematic because this large invertebrate is a good climber and might even have passed the Vaseline barrier at the base of the pole. However, most of them were trapped at least 5 cm from the sticky edge, so we assume aerial transport of at least some. Since the body is carried upon long legs, it could probably be lifted easily by wind.

DISPERSAL BY FOOT AND FURCA?

Hågvar (2012) and Bråten et al. (2012) noted that springtail *Agrenia bidenticulata* followed the receding ice edge closely and jumped actively on cold-water surfaces when disturbed. At the end of August 2010, after the ice edge had receded about 30 m, the species was sampled by flotation only 4 m from the ice edge. This cold-stenotopic species is a ‘‘super-pioneer,’’ and we assume that it may follow the ice edge by jumping and walking, maybe heading towards the light ice, in contrast to the darker, ice-free ground. The species seems to disappear after 30–50 years (Hågvar, 2010; Bråten et al., 2012). Maybe also other springtail species can disperse a considerable distance by their own movements, and we hypothesize that springtail dispersal occurs by air, by foot, and by using the furca for jumping. Aerial dispersal might be more important for very small Actinedida mites, and for slow-moving oribatids. Among large, red Actinedida mites, the fast-running predator *Podothrombium strandi* Berlese, 1910 was taken numerously in pitfall traps on pioneer ground (Hågvar et al., 2009), but not in aerial traps. Instead, 5 specimens of *Bryobia* sp. were taken in sticky traps, up to the height of 25–34 cm. These mites are usually associated with grasses and low vegetation (Joanna Makol, personal communication), but it is unknown whether they are resident along the glacier.

Opiliones and Carabidae beetles, as well as several spiders, were taken numerously in pitfall traps after 3 years (Bråten et al., 2012). These invertebrates have been observed to move fast on the moraine, so we assume that dispersal by foot may be efficient. On sunny days, the barren pioneer ground may become very warm, and stones help to maintain temperature at night. Like many other alpine Carabidae, the pioneer species *Nebria nivalis* and *Amara alpina* are mainly night active, but behave normally down to 1–2 °C (Ottesen, 1985). We assume that these predators are able to follow the receding glacier by foot. The actual Carabidae species have functional wings, but probably use them rarely. Wingless aphids, on the other hand, would be clearly benefited by passive air transport, in order to colonize pioneer grasses (Bråten et al., 2012). The Psocoptera that appeared in both types of traps (Tables 3–4) have not been identified further, and we assume that they do not belong to the pioneer fauna.

THE ESTABLISHMENT OF PIONEER COMMUNITIES: LIMITATIONS BY DISPERSAL AND ENVIRONMENTAL FACTORS

Several beetles, spiders, and microarthropods, which are typical pioneers in European glacier forelands, have in common the ability to tolerate open ground with little or no vegetation, and some prefer it (Hågvar, 2012; Bråten et al., 2012). If dispersal ability is not a limiting factor, arriving species will be sorted according to this ability. A successful pioneer species thus has to pass through two ''filters'': a dispersion filter in order to arrive, and an ecological filter in order to survive and reproduce.

The problem of disentangling the effects of dispersal and local environment was illuminated by studying colonization success of Collembola and Oribatida species on recently emerged nunataks on Iceland (Ingimarsdóttir et al., 2012). They found that isolation of a few kilometers did not affect the colonization of microarthropods. This indicates strong dispersal abilities, and wind dispersal would be the easiest explanation. At each nunatak, surviving species established according to gradients of soil age and plant richness. Conclusively, there was no strong dispersal filter, but a filter of environmental constraints determined by the temporal evolution of the soil. In fact, the dispersal rate was assumed to be so high that nunataks could be a sink for some of the recorded species.

This way of thinking is relevant for the present material. Earlier soil sampling and pitfall studies indicate that several of the airborne microarthropods are resident on pioneer ground: *Tectocepheus velatus* among Oribatida, and *Bourletiella hortensis, Lepidocyrtus lignorum, Agrenia bidenticulata, Isotoma viridis*, and *Desoria* sp. (probably *olivacea*) among Collembola (Hågvar et al., 2009; Hågvar, 2010; Bråten et al., 2012). Also, various Actinedida mites belong to the pioneer fauna. However, some of the trapped microarthropods have earlier been recorded only from rather old soil in the foreland. The relevant soil samples were limited to *Salix herbacea* vegetation, which occurs both on pioneer ground and on older soil, so we may have overlooked species occurring in other vegetation types. However, *Tetracanthella brachyura* was found only in soil older than 70 years, *Oribatula tibialis* in soil older than 150 years, and *Eupelops plicatus* in soil older than 250 years (Hågvar et al., 2009; Hågvar, 2010). Furthermore, 4 microarthropod species from fallout traps in 2010 have not earlier been recorded in the foreland: the oribatid mite *Scheloribates initialis* and the collembolans *Heterosminthurus claviger, Ceratophysella denticulata,* and *Lepidocyrtos cyaneus.*

The presence of non-resident microarthropods in our fallout material indicates that the dispersion filter allows several species to arrive on pioneer ground, perhaps from a long distance, but that the ecological filter leaves only pioneer specialists to survive and establish. A lack of soil and vegetation is probably the most important constraint, and for some species the pioneer ground would be a sink.

Since the Islandic nunatak study indicates long-distance dispersal of microarthropods (Ingimarsdóttir et al., 2012), it is probable that aerial transport may also occur at much greater heights than documented in the present study. A few extreme windy situations could be sufficient to bring microarthropods from far away. In cases where a rich fallout of winged insects is observed on glaciers or snowfields (Hodkinson et al., 2002), it might be fruitful to sample surface snow and search for wind-transported microarthropods in water after melting. In Italy, Gobbi et al. (2010b) showed that certain cryophil stenotherm invertebrates, including Collembola, could live on debris-covered glaciers. In such cases, colonization of virgin soil could occur from the glacier itself. Another approach could be to study aerial transport in glacier foreland hour for hour, in order to relate transport to changing wind and weather conditions. Finally, the relative importance of aerial transport and active migration remains unclear. In our site, the cold tolerant springtail *Agrenia bidenticulata* easily followed a 30-m glacier retreat during 2010. Having observed it actively jumping on meltwater surfaces, we consider active migration to be possible for this species.

Acknowledgments

We are indebted to the following persons for taxonomic help within certain groups: Kjetil Aakra (Araneae), Joanna Makol (Actinedida), Arne Fjellberg (Collembola), Endre Willassen (Nematocera larvae), and the late Torstein Solhøy (Oribatida). Geir Knudsen kindly provided us with sticky traps, and Ronny Steen helped with statistics. Thanks to Finse research station for hospitality.

References Cited

Bergh, J. C., and McCoy, C. W., 1997: Aerial dispersal of citrus rust mite (Acari: Eriophyidae) from Florida citrus groves. *Environmental Entomology,* 26: 256–264.

Brandenburg, R. L., and Kennedy, G. G., 1982: Intercrop relationships and spider-mite dispersal in a corn peanut agro-ecosystem. *Entomologia Experimentalis et Applicata,* 32: 269–276.

Bråten, A. T., Flø, D., Hågvar, S., Hanssen, O., Mong, C. E., and Aakra, K., 2012: Primary succession of surface active beetles and spiders in an alpine glacier foreland, central south Norway. *Arctic, Antarctic, and Alpine Research,* 44: 2–15.

Clements, F. E., 1916: Plant succession: an analysis of the development of vegetation. Washington, D. C.: Carnegie Institution.

Coulson, S. J., Hodkinson, I. D., and Webb, N. R., 2003: Aerial dispersal of invertebrates over a High-Arctic glacier foreland: Midtre Lovénbreen, Svalbard. *Polar Biology,* 26: 530–537.

Edwards, J. S., 1987: Arthropods of alpine aeolian ecosystems. *Annual Review of Entomology,* 32: 163–179.

Gobbi, M., De Bernardi, F., Pelfini, M., Rossaro, B., and Brandmayr, P., 2006a: Epigean arthropod succession along a 154-year glacier foreland chronosequence in the Forni Valley (Central Italian Alps). *Arctic, Antarctic, and Alpine Research,* 38: 357–362.

Gobbi, M., Fontaneto, D., and De Bernardi, F., 2006b: Influence of climate changes on animal communities in space and time: the case of spider assemblages along an alpine glacier foreland. *Global Change Biology,* 12: 1985–1992.

Gobbi, M., Rossaro, B., Vater, A., De Bernardi, F., Pelfini, M., and Brandmayr, P., 2007: Environmental features influencing carabid beetle (Coleoptera) assemblages along a recently deglaciated area in the alpine region. *Ecological Entomology,* 32: 682–689.

Gobbi, M., Caccianiga, M., Cerabolini, B., Luzzaro, A., De Bernardi, F., and Pierce, S., 2010a: Plant adaptive responses during primary succession are associated with functional adaptations in ground beetles on deglaciated terrain. *Community Ecology,* 11(2): 223–231.

Gobbi, M., Isaia, M., and De Bernardi, F., 2010b: Arthropod colonisation of a debris-covered glacier. *The Holocene,* 21(2): 343–349.

Gressitt, J. L., and Yoshimot, C. M., 1974: Insect dispersal studies in northern Alaska. *Pacific Insects,* 16: 11–30.

Hågvar, S., 2010: Primary succession of springtails (Collembola) in a Norwegian glacier foreland. *Arctic, Antarctic, and Alpine Research,* 42: 422–429.

Hågvar, S., 2012: Primary succession in glacier forelands: how small animals conquer new land around melting glaciers. *In* Young, S. S., and Silvern, S. E. (eds.), *International Perspectives on Global Environmental Change*. INTECH Open Access Publisher, free online <http://www.intechopen.com>, 151–172.

Hågvar, S., Solhøy, T., and Mong, C., 2009: Primary succession of soil mites (Acari) in a Norwegian glacier foreland, with emphasis on oribatid species. *Arctic, Antarctic, and Alpine Research,* 41: 219–227.

Hawes, T. C., 2008: Aeolian fallout on recently deglaciated terrain in the High Arctic. *Polar Biology,* 31: 295–301.

Hawes, T. C., Worland, M. R., Convey, P., and Bale, J. S., 2007: Aerial dispersal of springtails on the Antarctic Peninsula: implications for local distribution and demography. *Antarctic Science,* 19: 3–10.

Hodkinson, I. D., Coulson, S. J., Harrison, J., and Webb, N. R., 2001: What a wonderful web they weave: spiders, nutrient capture and early ecosystem development in the High Arctic—Some counter-intuitive ideas on community assembly. *Oikos,* 95: 349–352.

Hodkinson, I. D., Webb, N. R., and Coulson, S. J., 2002: Primary community assembly on land—The missing stages: why are the heterotrophic organisms always there first? *Journal of Ecology,* 90: 569–577.

Hodkinson, I. D., Coulson, S. J., and Webb, N. R., 2004: Invertebrate community assembly along proglacial chronosequences in the High Arctic. *Journal of Animal Ecology,* 73: 556–568.

Ingimarsdóttir, M., Caruso, T., Ripa, J., Magnúsdóttir, O. B., Migliorini, M., and Hedlund, K., 2012: Primary assembly of soil communities: disentangling the effect of dispersal and local environment. *Oecologia,* 170(3): 745–754, http://dx.doi.org/10.1007/s00442-012-2334-8.

Johnson, D. T., and Croft, B. A., 1981: Dispersal of *Amblyseius fallacis* (Acarina, Phytoseiidae) in an apple ecosystem. *Environmental Entomology,* 10: 313–319.

Jung, C. L., and Croft, B. A., 2001: Aerial dispersal of phytoseiid mites (Acari: Phytoseiidae): estimating falling speed and dispersal distance of adult females. *Oikos*, 94: 182–190.

Kaufmann, R., 2001: Invertebrate succession on an alpine glacier foreland. *Ecology,* 82: 2261–2278.

Kaufmann, R., and Raffl, C., 2002: Diversity in primary succession: the chronosequence of a glacier foreland. *In* Körner, C., and Spehn, E. (eds.), *Global Mountain Biodiversity*: *a Global Assessment.* London: Parthenon, 177–190.

Kaufmann, R., Fuchs, M., and Gosterxeier, N., 2002: The soil fauna of an alpine glacier foreland: colonization and succession. *Arctic, Antarctic, and Alpine Research,* 34: 242–250.

Lindroth, C. H., Andersson, H., Bödvarsson, H., and Richter, S. H., 1973: Surtsey, Iceland: the development of a new fauna, 1963–1970: terrestrial invertebrates. Copenhagen: Munksgaard, *Entomologica Scandinavica, Supplementum 5.*

Magnussen, T., 2010. Aerial dispersal of invertebrates on Svalbard and the influence of weather. Master thesis, University of Oslo, Oslo, Norway, 40 pp.

Oerlemans, J., 2005: Extracting a climate signal from 169 glacier records. *Science*, 308: 675–677.

Ottesen, P. S., 1985: Diel activity patterns of south Scandinavian high mountain ground beetles (Coleoptera, Carabidae). *Holarctic Ecology*, 8: 191–203.

R Development Core Team, 2012: *R: a Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing.

Seniczak, A., Solhøy, T., and Seniczak, S., 2006: Oribatid mites (Acari: Oribatida) in the glacier foreland at Hardangerjøkulen (Norway). *Biological Letters,* 43: 231–235.

Skubala, P., and Gulvik, M., 2005: Pioneer oribatid mite communities (Acari, Oribatida) in newly exposed natural (glacier foreland) and anthropogenic (post-industrial dump) habitats. *Polish Journal of Ecology,* 53: 395–407.

Swan, L. W., 1992: The aeolian biome. *BioScience,* 42: 262–270.

Thornton, I. W. B., New, T. R., McLaren, D. A., Sudarman, H. K., and Vaughan, P. J., 1988**:** Air-borne arthropod fall-out on Anak Krakatau and a possible pre-vegetation pioneer community. *Philosophical Transactions of the Royal Society B, London,* 322: 471–479.

Vater, A. E., 2012: Insect and arachnid colonization on the Storbreen glacier foreland, Jotunheimen, Norway: persistence of taxa suggests an alternative model of succession. *The Holocene,* 22(10): 1123–1133.

MS accepted June 2013