

# Effects of experimental snowmelt and rain on dispersal of six plant species

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## ABSTRACT

Water flows affect dispersal of propagules of many plant species, and rivers and streams are therefore very important dispersal vectors. However, small water flows such as trough rain and snowmelt are much more common, but their effects on dispersal are barely studied. The importance of this form of dispersal deserves attention, especially when considering that climate change is predicted to change the amounts of rain and snow worldwide. Dispersal through melting snow and rain was addressed experimentally, using artificial soils mounted on slopes with different angles and subjected to a melting snow pack or an equivalent amount of dripping water. Seeds on the soil moved on average 3.02 cm ( $\pm 1.81$  SE) in rain treatments and 0.23 cm ( $\pm 0.3$  SE) in snowmelt treatments. Tracking plastic granules in field conditions further showed that snowmelt exhibited minimal dispersal capacity. Dispersal distances by rain were enhanced by increasing slope angles and with decreasing seed volume. Given that many species in cold environments have small seeds, dispersal by rain could provide an important (secondary) dispersal mechanism in these habitats. © 2016 The Authors. *Ecohydrology* published by John Wiley & Sons Ltd.

KEY WORDS boreal ecosystems; bythisochory; climate change; dispersal vector; erosion; hydrochory; rain; snow

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## INTRODUCTION

Water is probably the most efficient dispersal vector for plant propagules, as both seeds and vegetative propagules exert long floating times (Kleyer *et al.*, 2008; Sarneel, 2013). The quantity of water available (rain vs waterbodies) and the flow dynamics (lentic vs lotic water bodies) in combination with seed traits will determine the dispersal distances (Nilsson *et al.*, 2010; Sarneel *et al.*, 2014, van Leeuwen *et al.* 2014). Therefore, many different forms of water dispersal are distinguished, which sometimes leads to ambiguous nomenclature in the literature (Nilsson *et al.*, 2010). Long-distance dispersal of floating propagules by flowing water (hydrochory) is very efficient and therefore best studied (Andersson *et al.*, 2000; Nilsson *et al.*, 2010). Buoyancy of the seed is considered a key trait (Ozinga *et al.*, 2009) together with seed shape, which interacts with wind shear on the water (Soomers *et al.*, 2011; Sarneel *et al.*, 2014). However, next to these large-scale water movements, smaller flows are thought to be able to disperse seeds locally or secondary to other dispersal vectors. Rain falling on plant

seed heads (ombrohydrochory) and propelling away the seeds typically results in dispersal distances of less than 30 cm (Parolin, 2006). This is thought to be a strategy to survive in small favourable habitat patches in a hostile environment such as deserts or high elevations (Pufal *et al.*, 2010; Walck & Hidayati, 2007). All other water-related dispersal via small water flows close to the soil surface is called bythisochory (Gurnell *et al.*, 2008; Nilsson *et al.* 2010). It is hypothesized that bythisochory does not depend on seed traits such as buoyancy but that soil characteristics like roughness and slope are determining dispersal distances. Such smaller water flows can occur frequently during rain events, but in colder climates also during snowmelt. Little is known on the factors driving these types of dispersal events, and snowmelt is barely recognized as dispersal agent (Nilsson *et al.*, 2010; Tekiela and Barney, 2013). Yet it is important to address these types of dispersal events and their capacity to disperse seeds as they could provide an important (secondary) dispersal pathway. Moreover, as magnitude and multitude of rain and snow events are expected to change because of global warming, understanding their relative effects on dispersal has increased importance.

Many species from cold habitats, like alpine and boreal zones, have impermeable seed coats and corky tissues, which typically indicate a high potential of dispersal via water (Andersson *et al.*, 2000; Ozinga *et al.*, 2009). Yet dispersal

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via hydrochory may be less efficient compared with temporal zones as many large waterbodies will be frozen for large parts of the year. Besides, snow will have less impact on seed heads compared with rain and thereby is unlikely to result in ombrohydrochorous dispersal. Snowmelt, on the other hand, is known to cause substantial erosion, especially if the top layer is not frozen (Singh *et al.*, 2009; Sukhanovskii, 2008). That is, snowmelt can induce small, continuous water flows, especially on sloping terrain. It can be hypothesized that seeds are governed by the same physical laws as soil particles and therefore can be moved considerable distances by snowmelt. Dispersal during snowmelt will further bring seeds to locations (located downhill) with relatively high soil moisture, which may stimulate germination after dispersal. This may thereby increase the importance of dispersal during snowmelt for establishment and vegetation composition. This is supported by the observation of Cortes *et al.* (2014) who observed that ridges acted as a source for the genetic diversity of lower lying snow bed locations that formed gene sinks.

To address what factors govern dispersal by rain and snowmelt, this research will experimentally test the effect of precipitation type on dispersal. Because of the similarity to erosion, it can first be hypothesized that rain and snow are able to disperse seeds and second that increasing soil slope will increase dispersal distances through rain and snowmelt, as erosion of soil particles and snow accumulation are related to slope (Williams and Tarboton, 1999). Last, I hypothesized that bigger seeds are more resistant to transport compared with small round seeds.

## METHOD

### *Seed mats as artificial soils*

Six species with contrasting seed properties were obtained from seed companies (Table I) and were sown in artificial

soils that were created from AstroTurf mats (30 × 30 cm; AstroTurf Classic Mat & Classic Roll, Dalton, GA, USA; van Leeuwen *et al.*, 2014). The hereafter called seed mats were filled with potting soil (10% sand, 90% organic soil; Rölunda produkt, Bålsta, free of seeds) so that the artificial grass was completely covered. Afterwards, a seed mixture with 0.1 g of each of the six species was sown on top of the soil in a horizontal line, 6.5 cm from the top of the seed mat.

### *Snowmelt simulation*

To investigate the effect of snowmelt, nine ramps (1.5 m long and 45 cm wide) were built outdoors with wood and chicken wire covered with plastic (Figure 1). The ramps had a 15-cm-high border on each of the long edges and were mounted in angles ranging from 60° to flat. At the bottom of each ramp, one seed mat was placed. On 3 March, a layer of 15 cm of snow was placed on top of the ramp and the seed mats. The snowpack contained 20.8 (±0.44 SE  $n=3$ ) l of water. The snow gradually melted completely during the following 7 days under outdoor conditions (4.4 °C ± 0.5 SE mean air temperature). The seed mats were taken from the ramps into the greenhouse, at 17.5 °C light for 16 h a day with a mean light intensity of 115 (±14 SE)  $\mu\text{mol}^{-1}$ . Seed mats were randomized weekly through the greenhouse space. After 1 month of germination, the distance from the sowing line and the species identity was determined for every seedling on the seed mat.

### *Rain simulation*

The snow simulation experiment was placed outside, and the cold temperatures there potentially could have influenced viability. Therefore, simulate the cold experienced in the snow simulation; the seed mats used in the rain

Table I. Species characteristics.

Species	Buoyancy <sup>a</sup> (t50)	Seed volume <sup>b</sup> (mm <sup>-3</sup> )	Seed shape	Seed weight <sup>c</sup> (g 1000 <sup>-1</sup> )	Seed number <sup>d</sup> (0.1 g <sup>-1</sup> )	Germination (%)
<i>Betula pubescens</i> <sup>e</sup>	47	1.25	Flat, wings	0.28 ± 0.01	174 ± 17.2	4.41
<i>Festuca ovina</i> <sup>f</sup>	n.a.	3.35	Cylinder	0.60	167	48.23
<i>Filipendula ulmaria</i> <sup>g</sup>	17	7.81	Twisted cylinder	0.63 ± 0.01	154 ± 3.8	1.37
<i>Lepidium sativum</i> <sup>h</sup>	n.a.	4.36	Cylinder	2.10	48	52.15
<i>Prunella vulgaris</i> <sup>g</sup>	0	2.17	Cylinder	0.96 ± 0.01	108 ± 1.3	6.17
<i>Solidago virgaurea</i> <sup>g</sup>	0.3	1.52	Cylinder	0.42 ± 0.004	237 ± 2.4	8.49

<sup>a</sup> t50 indicates the time (days) needed for 50% of the seeds to sink. Measured in glass pots filled with tap water ( $n=5$ , 30 seeds per pot), with stirring before each measurement (following Kleyer *et al.* 2008).

<sup>b</sup> Obtained from the digital seed atlas. <http://seeds.eldoc.ub.rug.nl/> (last visited March 2016).

<sup>c</sup> Average of 300 seeds ± SE *Lepidium sativum* and *Festuca ovina* are based on the Kew database (<http://data.kew.org/sid/>, March 2016) and therefore have no SE.

<sup>d</sup> Average of five batches of 0.1 g ± SE *Lepidium sativum* and *Festuca ovina* are based on the Kew database.

<sup>e</sup> Seed origin: Svenska Skogsplantor, Hallsberg, Sweden.

<sup>f</sup> Seed origin: Econova Garden AB, Åby, Sweden.

<sup>g</sup> Seed origin: Jelitto staudensamen GmbH, Schwarmstedt, Germany.

<sup>h</sup> Seed origin: Nelson Garden AB, Tingsryd, Sweden.

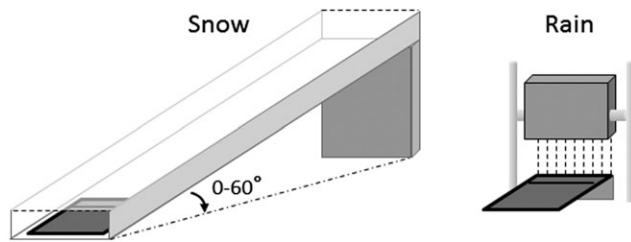


Figure 1. Schematic overview of the ramps with snow (left) and rain (right) dispersal experimental setup. Dark grey squares are the seed mats filled with soil, and the black line on the seed mat indicates the place where seeds were sown. The arrow indicates the slope angle.

simulation were placed in a refrigerator (5 °C) in the dark for 7 days prior to the rain simulations. To test the effect of rain, a watertight box (30 × 10 × 20 cm) was perforated with a line of 20 holes, using a 3.5-mm-thick nail. As the water made the edges of the holes swollen, the water dripped from the holes. The box was filled with 20.8 l of water, in batches of ~3–5 l. The water took 45 min to 1 h to drip through the holes in the box. Underneath the line with dripping water, a seed mat was mounted at an angle ranging from 0° to 65°, in approximately identical steps as in the snow experiment. The water dripped at the top of the seed mat, and not directly on the sowed line, to prevent dispersal by the impact of the falling drops. After the simulated rainfall event, seed mats were placed flat in boxes in the greenhouse and treated as in the snow experiment.

#### Outdoor snow dispersal

As a crude test of the potential for seed dispersal by snow under outdoor conditions, two tests were performed that simulated the way seeds could be dispersed by snow. First, to test the dispersal of seeds that got trapped under the snow, five small, brightly coloured plastic granules (Ø 5 mm, 4 mm height) were placed under the snow, by inserting them in a small hole (<1 cm) in the snow. This was carried out on 4 March 2014 on ten locations that differed in angle, aspect and snow depth (13–24 cm). However, seeds that disperse during winter or early spring are deposited on top of the snow. Second, therefore, five granules were placed on top of the snow at five locations. Deposition places were marked with a stick. After the snow had completely melted (~10–14 days), and before rain events had occurred, the distances of the granules from the sticks were measured.

#### Statistics

To check potential differences in germination between the rain and snow treatments, an independent *t*-test on total number of seedlings per seed mat was performed, considering the different seed mats as replicates.

To test the effect of slope per seed mat, the mean distance the seedlings moved away from the sowing line was calculated for total seedling numbers and for each of the six species separately. Separate general linear model (GLM) analyses (seven) were performed with rain and snow treatment and seed mat angle, and their interaction as independent variables. To test the effect of species traits, a GLM was fitted for the snow and rain simulations separately, using seed mass and seed volume as independent variables and average dispersal distance per seed mat as dependent variable. Residuals were checked for normality. All statistics were performed in IBM statistics for windows 22 (Armonk, NY: IBM Corp).

## RESULTS

### Snowmelt and rain simulations

All species germinated in the experiment. The total number of germinated seeds did not differ between the snow and rain treatments. Seeds were spread out over the seed mat in the rain treatment and barely moved in the snow treatment (Figure 2). Movement was mostly downward but summed over all seed mats, 4.7% of the seedlings moved uphill in the rain seed mats and 1% in the snow seed mats. Mean dispersal distance of a seedling in the rain treatment was 3.02 cm (±1.81 SE) and 0.23 cm (±0.3 SE) in the snow treatments. In the GLM analyses, however, no significant overall effect of precipitation type was observed.

Mean dispersal distances increased with seed mat angle, but only in the rain treatment (Figure 3a), as there was a significant interaction between precipitation type and seed mat angle. Already at an angle of 30° (which is a 1:2 slope), a few seeds reached the end of the seed mat in the rain treatments, and at the steepest angle measured (2:1 slope), a considerable fraction (9%) of seeds was observed in the lowest third of the seed mat (Figure 2). At the steepest slope, 16% was found on the lowest third of the seed mat. This pattern was also observed within the individual species as significant interaction terms between precipitation type and seed mat angle were found for *Betula*, *Festuca*, *Filipendula* and *Solidago* (Table II).

In the snow treatment, all species dispersed over equal distances, while in the rain treatment, *Betula* and *Solidago* moved further compared with *Filipendula* and *Lepidium*, which did not disperse (Figure 3b). GLM analyses showed that for the snow simulation, neither seed volume nor seed weight could explain the differences between species. In the rain simulation, seed volume and seed weight both significantly determined dispersal distances. Small, light-seeded species moved over longer distances than species with bigger, heavier seeds (Figure 3b; volume *d.f.* = 1,

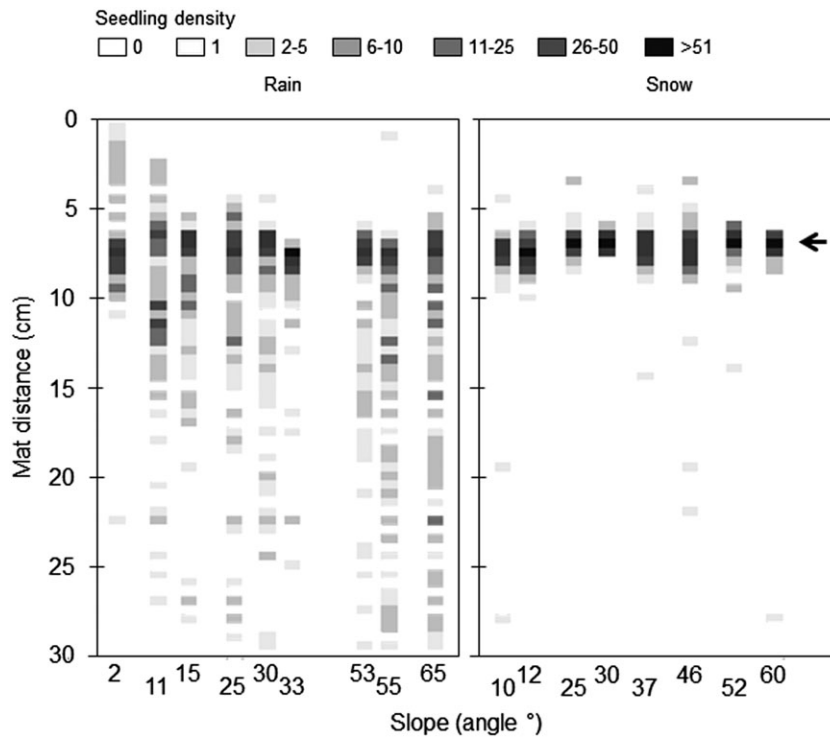


Figure 2. Density distribution of seedlings on the seed mats with different angles for rain and snow treatments. The arrow indicates the distance at which seeds were sown.

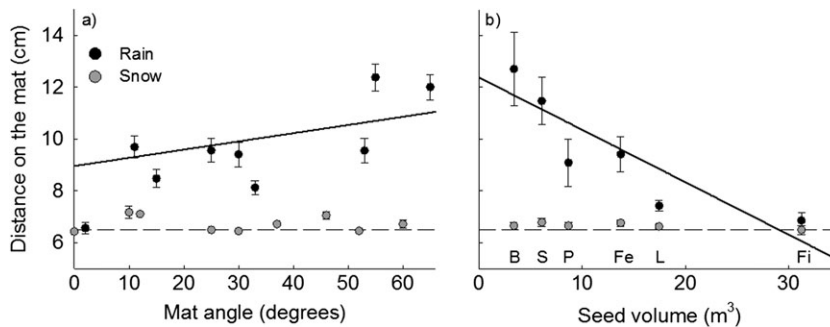


Figure 3. Average dispersal distances by rain and snow (a) on the seed mats with different angles and (b) for the different species and their seed volume ( $n = 9$ ). Solid lines indicate significant relations. Dashed line indicates sowing distance on the see mat. Letters below the points indicate species B, *Betula*; Fe, *Festuca*; Fi, *Filipendula*; L, *Lepidium*; P, *Prunella*; and S, *Solidago*.

$F = 40.8$ ,  $P = 0.008$ ; weight  $d.f. = 1$ ,  $F = 12.8$ ,  $P = 0.037$ .  
The final model  $R^2$  was 96.3%.

#### Outdoor snow dispersal

Measurements of the small plastic granules buried below the snow at ten locations showed that snow potentially can disperse seeds over long distances (max observed 105 cm) but, on average, the granules moved 6.4 cm ( $\pm 8.15$  SE) (and 0.34 cm  $\pm 0.23$  SE when the longest distance was removed). Granules placed on top of the snow (five locations) moved further from their deposition point, on average 2.9 cm ( $\pm 0.70$  SE).

## DISCUSSION

#### Dispersal capacity of snow and rain

In line with the first hypothesis, both snow and rain were able to disperse seeds over small distances. However, average distances were small and close to zero for melting snow, but no overall effect of precipitation type was observed. Yet in the rain simulations, seeds moved over larger distances on steepest slopes, while in the snow simulations, dispersal distances were limited on all slopes. In fact, both the indoor and outdoor experiments showed that snowmelt barely moves seeds. In the outdoor

Table II. *P*-values of the main effects of the general linear models.

	Type	Mat angle	Type × mat angle	<i>R</i> <sup>2</sup>
Overall mean	0.452	0.009	0.007	81.7
<i>Betula pubescens</i>	0.489	0.032	0.023	75.4
<i>Festuca ovina</i>	0.843	0.013	0.007	77.6
<i>Filipendula ulmaria</i>	0.09	0.132	0.009	56.1
<i>Lepidium sativum</i>	0.501	0.364	0.201	51.2
<i>Prunella vulgaris</i>	0.747	0.151	0.199	46.7
<i>Solidago virgaurea</i>	0.155	0.003	0.009	85.7

experiment, only a few seeds dispersed further, over ~20 cm and even up to 1.05 m, indicating that longer dispersal by snowmelt can occur, although with a much lower frequency. Seeds on top of the snow dispersed slightly further. Given that the roughness of snow is very low, seeds dispersed on top of the snow may be subjected to wind gusts, which may continue to disperse them, if the seeds are light. In this way, snow could aid dispersal, for light seeds, but the used experimental granules were probably too heavy to be dispersed by wind. As total numbers of seedlings did not differ between the seed mats, there are no strong indications that many seeds moved out of the seed mat or that differences between snow and rain simulations are due to differences in viability. The low dispersal capacity of snow is in line with the minimal erosion because of snowmelt observed in non-tillage plots by Singh *et al.* (2009) but in apparent contradiction with the calculated erosion by snow by Sukhanovskii (2008). However, the latter included soils that were tilled and subjected to quite large volumes of water.

A few outdoor studies and anecdotal observations confirm our observation that rain events can provide a (secondary) dispersal agent especially on steeper slopes. For instance, Tekiela and Barney (2013) tracked *Microstegium vimineum* seeds using ultraviolet dye and observed them to disperse on average 21 cm with a maximum of 2.4 m. Also, the seed heads of *Erodiohyllum elderi* were found to disperse on average 30 cm by rain (Emmerson *et al.*, 2010). In these outdoor experiments, the quantity of the rainfall correlated positively with dispersal distance (Tekiela and Barney, 2013) and to slope. Egawa and Tsuyuzaki (2013) reported that after 1 year, almost all seeds of all species disappear from 10 × 10 cm plots with bare soil, whereas increasing litter depth and seed size drastically decreased dispersal probability (to 0% for some species) in their Japanese peatlands. They attribute their observed seed movement to snowmelt, which would indicate average dispersal distances of >5 cm, which was larger than in this study. The results of the studies mentioned earlier indicate also that soil roughness (e.g. by litter, plant cover or soil type) is also a critical modifying factor for dispersal distances by both forms of precipitation (Sukhanovskii, 2008, 2013).

Comparatively, the mean dispersal distance of 3 cm and of 5.5 cm at the steepest slopes in the rain simulations is relatively low, given the intensity of the rain treatment. During a rain event or snowmelt, some of the water infiltrates in the soil, thereby loosing the ability to disperse seeds, although it may aid seed bank formation. The limited dispersal in this study may therefore be attributed to the relatively high roughness of the artificial soil and easy infiltration of water into the soil compared with, for instance, peat, clay or sandy soils used in the outdoor experiments reported in literature (Emmerson *et al.*, 2010). Generally, this infiltration will be less during snowmelt compared with rain as soils are frozen. Such interaction may stimulate the dispersal in outdoor conditions. It should be noted, however, that although the dispersal during one event may be small, the eventual distance after a whole rainy season could be considerable. Both rain and snowmelt dispersal may therefore provide a reasonable likely dispersal mechanism next to or after other dispersal vectors.

#### *Effects of slope*

In line with the second hypothesis, increasing slope increased dispersal distances. This was only true in the rain treatment. In the treatments with a ramp angle of 0°, dispersal distances were equal between snow and rain treatments. Interestingly, there was already a substantial increase in dispersal distances in very gently sloping seed mats, with angles that can occur frequently in most field situations. Given the difference in dispersal distances invoked by small slope differences, it is likely that in the field, microtopographical differences rather than height gradients on larger spatial scales may be important (Hampe, 2004).

There are several stages of overland flow recognized (Woolhiser and Liggett, 1967), which were also observed in the rain simulation. First, there is the impact of a rain drop or rain beat, which may have caused some of the uphill seed movement especially on the most gentle sloping seed mats. Second, thread flow and sheet flow occur where raindrops integrate and flow around or above surface grains, respectively. This occurs when force of overland flow (depending on soil slope, water quantity) exceeds the resistance of the surface (depending on vegetation cover, soil type, etc.). I did not observe the next stages in the precipitation experiments: rill and gully flow, which occurrence also depends on slope and soil friction. These stages may be most effective in seed dispersal, as seeds may start to float and are therefore less affected by soil roughness, but only by water quantity and flow speed (which in turn depends on slope). The behaviour of seeds followed erosion patterns of increased erosion with increasing slope (Sukhanovskii, 2008), with the effect of slope being species specific, as not all species showed significant effects of slope on their dispersal



distances. Virtually, all sediment transport equations include the effect of slope as it is considered a major determinant for displacement of soil particles (Wong and Parker, 2006). That is, increasing slope will increase water velocity and the shear stress acting on soil and thereby increase the displacement energy available to move particles. When the shear stress exceeds a critical shear value, a particle will start moving (Huang, 2010). The critical shear is determined by particle density and shape, which is in line with our finding of seed volume and weight determining seed displacement. However, erosion equations are dependent on empirical and experimental data, which make it impossible to derive a direct seed displacement models from them (Wong and Parker, 2006) and call for experiments (Emmerson *et al.*, 2010; Tekiela and Barney, 2013). Direct comparisons are further hampered as erosion or bed load is usually expressed as mass per hectare or in volume per time unit, rather than in distances. Yet finding the same factors that govern them indicates that the processes that govern them are the same.

#### *Species traits*

In line with the third hypothesis, seed shape and weight were important for dispersal distances. Smaller seeds dispersed further than big seeds but again only in the rain treatment. This is partly in line with observations of Egawa and Tsuyuzaki (2013) that observed smallest seeds to move most frequently in sown plots compared with bigger seeds, which they contributed to snowmelt. Seed volume was the strongest predictor, which therefore adds to an increasing body of work showing that seed volume is a better proxy for dispersal via various dispersal vectors (e.g. by wind and ducks) than seed mass *per se* (Liu *et al.*, 2012; Egawa and Tsuyuzaki, 2013; Kleyheeg *et al.*, 2015). This study did not incorporate extremely complex seed shapes such as with hooks or plumes, which could decrease seed dispersal distances by rain compared with seeds with similar size and weight but without those appendages.

#### *Range expansion in cold climates*

Given the high abundance of small seeds in cold environments, rain-mediated bythisochory may be a very common and additive dispersal mechanism in those habitats. Taking the alpine flora as an example for species present in cold environments (Hassler and Schmitt, 2007), ~44% of species has small seeds (<1 mg), and still 36% of the species has seeds <0.5 mg, whereas only 20% has big seeds (>5 mg), based on the species present in the LEDA trait base (Kleyer *et al.*, 2008). Although small seeds are generally seen as an adaptation to disperse via wind (Moles *et al.*, 2005), this research now indicates that the occurrence of relatively small seeds could be an adaptation

to dispersal via rain, especially in sloping habitats. Increased rainfall (e.g. due to climate change) could lead to increased dispersal distances, especially for light-seeded species on sloping habitats. Yet to what extent dispersal by rain can contribute to the already observed shifts in colonization rates in cold environments (Alsos *et al.*, 2007; Klein *et al.*, 2008) remains to be elucidated. For instance, in cold climates, climate warming is thought to increase germination rates, by which recruitment processes as a whole will be accelerated, which can also attribute to faster spread of species (Milbau *et al.*, 2009). In addition, more rain and less frozen soil may further impact dispersal distances, as seeds in mud more easily stick (and hence are dispersed) by mobile vectors such as animals and vehicles compared with seeds in frozen soils during snowmelt (Zwaenepoel *et al.*, 2006). Likewise, it can be assumed that climate change will affect many other dispersal vectors, clonal expansion, tropic interactions and timing of rain events. Such complex interactions, among which the (additive) effects of rain and snowmelt on dispersal, may drive shifts in geographic distribution ranges or species invasions (Ozinga *et al.*, 2009; Travis *et al.*, 2013).

## CONCLUSIONS

From the results of this study, it can be concluded that rain and melting snow have limited dispersal capacity and that, for light seeds on sloping soils, rain is more efficient as a dispersal vector compared with melting snow. For rain-mediated dispersal, increasing slope and decreasing seed volume and weight increase dispersal distances. This implies that rain-mediated dispersal could provide an additional dispersal vector.

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