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 (±1.81 SE) in rain treatments and 0.23 cm (±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

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...
via hydrochoric 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 ombrhydrochorous 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 erosion, it can thereby increase the importance of dispersal during snowmelt by rain and thereby is unlikely to result in ombrhydrochorous 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.

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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) μmol m⁻² s⁻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 a | Seed volume b (mm³) | Seed shape          | Seed weight c (g 1000⁻¹) | Seed number d (0·1 g⁻¹) | Germination (%)    |
|-------------------------|------------|---------------------|---------------------|--------------------------|------------------------|-------------------|
| *Betula pubescens*      | 47         | 1·25                | Flat, wings         | 0·28 ± 0·01               | 174 ± 17·2             | 48·23             |
| *Festuca ovina*         | n.a.       | 3·35                | Cylinder            | 0·60                      | 167                    | 48·23             |
| *Filipendula ulmaria*   | 17         | 7·81                | Twisted cylinder    | 0·63 ± 0·01               | 154 ± 3·8              | 1·37              |
| *Lepidium sativum*      | n.a.       | 4·36                | Cylinder            | 2·10                      | 48                     | 52·15             |
| *Prunella vulgaris*      | 0          | 2·17                | Cylinder            | 0·96 ± 0·01               | 108 ± 1·3              | 6·47              |
| *Solidago virgaurea*    | 0·3        | 1·52                | Cylinder            | 0·42 ± 0·004              | 237 ± 2·4              | 8·49              |

a 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).
b Obtained from the digital seed atlas. http://seeds.eldoc.ub.rug.nl/ (last visited March 2016).
c 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.
d Average of five batches of 0·1 g ± SE Lepidium sativum and Festuca ovina are based on the Kew database.
e Seed origin: Svenska Skogsplantor, Hallsberg, Sweden.
f Seed origin: Econova Garden AB, Åby, Sweden.
g Seed origin: Jelitto staudensamen GmbH, Schwarmstedt, Germany.
h Seed origin: Nelson Garden AB, Tingsryd, Sweden.
considering the different seed mats as replicates. The number of seedlings per seed mat was performed, and the distances of the granules from the rain and snow treatments, an independent t-test on total numbers. 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.

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.

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,
\[ F = 40.8, \ P = 0.008; \ \text{weight d.f.} = 1, \ F = 12.8, \ P = 0.037). \]

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 (±8.15 SE) (and 0.34 cm ± 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 (±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
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 *Erodiophyllum 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.

| Type | Mat angle | Type × mat angle | R² |
|------|-----------|------------------|----|
| **Overall mean** | 0·452 | 0·009 | 0·007 | 81·7 |
| *Betula pubescens* | 0·489 | 0·032 | 0·023 | 75·4 |
| *Festuca ovina* | 0·843 | 0·013 | 0·007 | 77·6 |
| *Filipendula ulmaria* | 0·09 | 0·132 | 0·009 | 56·1 |
| *Lepidium sativum* | 0·501 | 0·364 | 0·201 | 51·2 |
| *Prunella vulgaris* | 0·747 | 0·151 | 0·199 | 46·7 |
| *Solidago virgaurea* | 0·155 | 0·003 | 0·009 | 85·7 |

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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 bythisocracy 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 extend 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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REFERENCES

Alsos IG, Eidesen PB, Ehrich D, Skrede I, Westergaard K, Jacobsen GH, Landvik JY, Taberlet P, Brochmann C. 2007. Frequent long-distance plant colonization in the changing Arctic. Science 316: 1606–1609.

Andersson E, Nilsson C, Johansson ME. 2006. Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. Journal of Biogeography 27: 1095–1106. DOI:10.1046/j.1365-2699.2000.00481.x.
Liu Z, Waebers S, Lexer C, Sedlacek J, Wheeler JA, van Kleunen M, Bossdorf O, Hoch G, Rixen C, Wipf S, Karrenberg S. 2014. Small-scale patterns in snowmelt timing affect gene flow and the distribution of genetic diversity in the alpine dwarf shrub Salix herbacea. Heredity 113: 233–239. DOI:10.1038/hdy.2014.19.

Egawa C, Tsuyuzaki S. 2013. The effects of litter accumulation through succession on seed bank formation for small- and large-seeded species. Journal of Vegetation Science 24: 1062–1073. DOI:10.1111/jvs.12037.

Emmerson L, Facelli JM, Chesson P, Possingham HP. 2010. Secondary seed dispersal of Erodiothyllum eldi, a patchily distributed short-lived perennial in the arid lands of Australia. Austral Ecology 35: 906–918. DOI:10.1111/j.1442-9993.2009.02097.x.

Gurnell A, Thompson K, Goodson J, Moggridge H. 2008. Propagule deposition along river margins: linking hydrology and ecology. Journal of Ecology 96: 553–565. DOI:10.1111/j.1365-2745.2008.01585.x.

Hampe A. 2010. Extensive hydrochory uncouples spatiotemporal patterns of seedfall and seedling recruitment in a `bird-dispersed' riparian tree. Journal of Ecology 92: 797–807. DOI:10.1111/j.0020-5766.2009.02078.x.

Hassler M, Schmitt B. 2007. Flora der Alpen. Updated 20.9.2015. http://worldplants.webarchiv.kit.edu/alpen last accessed 1.10.2010.

Huang HQ. 2010. Reformulation of the bed load equation of Meyer-Peter and Muller in light of the linearity theory for alluvial channel flow. Water Resources Research 46: W09533. DOI:10.1029/2009WR008974.

Klein DR, Bruun HH, Lundgren R, Philipp M. 2008. Climate change influences on species interrelationships and distributions in high-Arctic Greenland. Advances in Ecological Research 40: 81–100.

Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M, Poschlod P, van Groenendael JM, Klimes L, Klimesova J, Klotz S, Rusch GM, Hermy M, Adriaens D, Boedeltje M, Schlegelmilch J, Steendam HJ, Tackenberg O, Wilmann B, Jackel AK, Kuhn I, Kunzmann D, Ozinga WA, Romeramm C, Stadler S, Schlegelmilch J, Steendam HJ, Tackenberg O, Wilmann B, Cornelissen JHC, Eriksson O, Garnier E, Peco B. 2008. The LEDA Traitbase: a database of life-history traits of the North European flora. Journal of Ecology 96: 1266–1274. DOI:10.1111/j.1365-2466.2008.01430.x.

Kleyheeg E, van Leeuwen CHA, Morison MA, Nolet BA, Soons MB. 2015. Bird-mediated seed dispersal: reduced digestive efficiency in active birds modulates the dispersal capacity of plant seeds. Oikos 124: 899–907. DOI:10.1111/oik.01894.

Liu Z, Zhu J, Deng X. 2012. Arrival vs. retention of seeds in bare patches in the semi-arid desertified grassland of Inner Mongolia, northeastern China. Ecological Engineering 49: 153–159. DOI:10.1016/j.ecoleng.2012.08.030.

Milbau A, Graae B, Shevtsova A, Nij S, 2009. Effects of a warmer climate on seed germination in the subarctic. Annals of Botany 102: 287–296. DOI:10.1093/aob/mcp117.

Moles AT, Ackerly DD, Webb CO, Tweddle JC, Dickie JB, Pitman AJ, Westoby M. 2005. Factors that shape seed mass evolution. Proceedings of the National Academy of Sciences of the United States of America 102: 10540–10544. DOI:10.1073/pnas.0501473102.

Nilsson C, Brown RL, Jansson R, Merritt DM. 2010. The role of hydrochory in structuring riparian and wetland vegetation. Biological Reviews 85: 837–858. DOI:10.1111/j.1469-185X.2010.00129.x.

Ozinga WA, Romemcann C, Bekker RM, Prinzing A, Tamis WLM, Schaminée JH, Hennekens SM, Thompson K, Poschlod P, Kleyer M, Bakker JP, van Groenendael JM. 2009. Dispersal failure contributes to plant losses in NW Europe. Ecology Letters 12: 66–74. DOI:10.1111/j.1461-0248.2008.01261.x.

Parolin P. 2006. Ombrohydrochory: Rain-operated seed dispersal in plants – with special regard to jet-action dispersal in Aizoaceae. Flora 201: 511–518. DOI:10.1016/j.flora.2005.11.003.

Pufal G, Ryan KG, Garnock-Jones P. 2010. Hydrochory capsule dehiscence in New Zealand alpine Veronica (Plantaginaceae). American Journal of Botany 97: 1413–1423. DOI:10.3732/ajb.1000066.

Sarneel JM. 2013. The dispersal capacity of vegetative propagules of riparian fern species. Hydrobiologia 710: 219–225. DOI:10.1007/s10750-012-1022-3.

Sarneel JM, Beltman B, Buijze A, Groen R, Soons MB. 2014. The role of wind in the dispersal of floating seeds in slow-flowing or stagnant water bodies. Journal of Vegetation Science 25: 262–274. DOI:10.1111/jvs.12074.

Singh P, Wu QJ, McCool DK, Dun S, Lin CH, Morse JR. 2009. Winter hydrologic and erosion processes in the US Palouse Region: field experimentation and WEPP simulation. Vadose Zone Journal 8: 426–436. DOI:10.2136/vzj2008.0061.

Soomers H, Sarneel JM, Patberg W, Verbeek SK, Verweij PA, Wassen MJ, van Diggelen R. 2011. Factors influencing the seed source and sink functions of a floodplain nature reserve in the Netherlands. Journal of Vegetation Science 22: 445–456. DOI:10.1111/j.1654-1103.2011.01261.x.

Sukhanovskii YP. 2008. A physically based model of soil erosion during snow melting. Eurasian Soil Science 41: 890–901. DOI:10.1134/s10642930808115.

Sukhanovskii YP. 2013. Probabilistic approach to the calculation of soil erosion loss. Eurasian Soil Science 46: 431–437. DOI:10.1134/s1064293013040133.

Tekiela DR, Bamey JN. 2013. Quantifying Microstegium vimineum seed movement by non-riparian water dispersal using an ultraviolet-marking based recapture method. Plos One 8. DOI:10.1371/journal.pone.0063811.

Travis JMJ, Delgado M, Bocedi G, Baguette M, Barton K, Bonte D, Boulangeat I, Hodgson JA, Kubisch A, Penterian V, Saastamoimen M, Stevens VM, Bullock JM. 2013. Dispersal and species' responses to climate change. Oikos 122: 1532–1540. DOI:10.1111/j.1600-0706.2013.00399.x.

van Leeuwen CHA, Sarneel JM, van Paassen J, Rip WJ, Bakker ES. 2014. Hydrology, shore morphology and species traits affect seed dispersal, germination and community assembly in shoreline plant communities. Journal of Ecology 102: 998–1007. DOI:10.1111/j.1365-2745.12250.

Walck JL, Hidayati SN. 2007. Ombrohydrochory and its relationship to seed dispersal and germination strategies in two temperate North American Oenothera species (Onagraceae). International Journal of Plant Sciences 168: 1279–1290. DOI:10.1086/521691.

Williams KS, Tarboton DG. 1999. The ABC’s of snowmelt: a topographically factorized energy component snowmelt model. Hydrological Processes 13: 1905–1920. DOI:10.1002/(sici)1099-1085.199909013.12<1905::aid-hypp890>3.0.co;2-8.

Wong M, Parker G. 2006. Reanalysis and correction of bed-load relation of Meyer-Peter and Muller using their own database. Journal of Hydraulic Engineering-Asce 132: 1159–1168. DOI:10.1061/(asce)0733-9429(2006)132:11(1159).

Woolhiser D, Lieggett JA. 1967. Unsteady 1-dimensional flow over a plane–rising hydropgraph. Water Resources Research 3: 753–771. DOI:10.1029/WR003i003p00753.

Zwanepeol A, Roovers P, Hermy M. 2006. Motor vehicles as vectors of plant species from road verges in a suburban environment. Basic and Applied Ecology 7: 83–93. DOI:10.1016/j.baae.2005.04.003.