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Dispersal distance and achene quality of the rare anemochorous species *Arnica montana* L.: implications for conservation

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SUMMARY

In The Netherlands, *Arnica montana* (Asteraceae) is a rare plant species. Future survival in The Netherlands depends on its ability to disperse between source populations and habitats, newly created by man. Plumed Asteraceae achenes are often considered to disperse over large distances. Therefore, these species are expected to establish easily during vegetation restoration. In this paper, the flying capability of plumed achenes is investigated in a wind-tunnel experiment. An effort is made to establish the correlation between seed quality and flying ability. It was shown that *A. montana* achenes are inefficient dispersers. Pappus size is significantly, but weakly, positively correlated with achene mass. Heavier achenes, therefore, stay closer to the point of release than lighter ones. There was a positive correlation between achene weight and both germination and seedling quality. Consequently, germination and seedling quality declined considerably with increasing flying capability of the achenes. It seems that *A. montana*, despite its plumed achenes, is adapted to an environment where moderate dispersal distances are required, up to several metres. Only low-quality achenes reach larger distances. Since large distance dispersal is a prerequisite of establishment of new populations, establishment of this species on isolated sites the Dutch landscape will depend on transport by human activity.

Key-words: Arnica montana, wind dispersal, seedling quality, species conservation.

INTRODUCTION

Dispersal strategy should optimize offspring numbers and fitness in plant species (Harper 1977; Howe & Smallwood 1982). It is therefore hypothesized that dispersal strategy is correlated with safe site density in the species' habitat. Optimizing safe site colonization dispersal contributes to maintaining population size, numbers and genetic diversity (Silvertown & Lovett Doust 1993). All plant species have their own ecological demands. Consequently, there are considerable differences in dispersal strategy between species, including the formation of seed banks (Thompson & Grime 1979; Bakker *et al.* 1997).

Within a species' natural habitat, dispersal pattern is considered to be correlated with seedling performance (Harper 1977; Augspurger & Kitajama 1992). Dispersal may, for instance, counteract deleterious effects of seedling density, maternal competition, density dependent predation or inbreeding (Howe & Smallwood 1982). Specific dispersal ability may be effective in this way. However, for maintaining metapopulations in a fragmented landscape, or invasion of new or restored sites, dispersal distances may be insufficient (Hansson 1991; With & Crist 1995; Strykstra *et al.* 1996). For the conservation of endangered plant species it is therefore necessary to know their dispersal strategy and their invasive ability. Applying proper management for maintaining or founding new populations and performing successful reintroductions depends on the availability of this knowledge (With & Crist 1995; Bakker *et al.* 1997).

When its role in vegetation regeneration is analysed there are two important components of seed dispersal. First there is dispersal distance which for most of the seeds, dispersing from a seed source, can be determined reasonably well using dispersal models or field experiments (Willson 1993; Strykstra *et al.* 1996). Secondly there is dispersule quality, depending mainly on embryo weight, which is correlated with seed weight or fruit weight (Howe & Smallwood 1982; Augspurger & Hogan 1983). It has been shown that in the field seed weight is correlated positively with the chance of establishment (Cycidian & Malloch 1982; Morse & Schmidt 1985; Leishman & Westoby 1994).

Especially for wind-dispersed plant species, seed weight may counteract dispersibility of seeds. For plumed achenes or seeds, for instance, increasing weight is expected to be negatively correlated with dispersal ability. A proportional increase in the dimensions of dispersal structure and embryo will enlarge the surface of the plume quadratically but its weight cubically (Sheldon & Burrows 1973). This results in a higher wing loading. The individual fitness of a seedling is positively correlated to its weight, but may also have an optimum at a certain dispersal distance (Augspurger & Kitajama 1992). This means that optimization of the investment in embryo weight and dispersal structure is to be expected. The distance of optimal dispersal for a species will be reflected in the relative investment in embryo and dispersal structures that are different between species (Sheldon & Burrows 1973; Ganeshaiah & Uma Shaanker 1991).

Arnica montana L. is a target species in Dutch nature conservation policy for which it would be important to know its dispersal capability. Only about 60 populations of the species are still found, mainly in the northern part of the country. The species is bound to weakly acidic (pH 5–6) and oligotrophic soils (Pegtel 1994) with Nardo–Galion or Genisto–Callunetum communities (Westhoff & Den Held 1975; Schwabe 1990; Pegtel 1994). In the past the species was threatened by direct habitat destruction through agricultural intensification. Recently, indirect habitat deterioration by soil acidification and eutrophication through atmospheric deposition is thought to affect the remaining populations negatively (Fennema 1992; Dueck & Elderson 1992; Pegtel 1994). Most populations of *A. montana* are very small (5–50 individuals) and are threatened with extinction. The distance between populations is often very large.

To counteract habitat deterioration, measures such as local topsoil removal and sod-cutting next to existing populations are recommended for areas where the species still occurs. Occasionally, liming of such areas is carried out experimentally. In this way new areas, which are presumably suitable for the species, may also be created. Re-establishment of the species depends entirely on its capability to colonize, since *A. montana* has no persistent seed bank (Thompson *et al.* 1997). *A. montana* has achenes that are adapted to wind dispersal; the achenes have a plume. However, to maintain contact between existing populations or to colonize new areas, large distances between source populations and suitable sites have to be crossed.

There are three questions we would like to answer in this paper related to the dispersal strategy of *A. montana*:

1. How well are *A. montana* achenes adapted to wind dispersal: what can be concluded from achene geometry and the correlation between the morphological components of the achenes?
2. What is the correlation between dispersal distance and achene quality in this species?
3. Is it likely that *A. montana* has the capability to colonize isolated restoration areas?

METHODS

Achene collecting

For the experiments, several thousands of achenes were collected from a large population (>500 individuals) of *A. montana* near Tynaarlo in the province of Drenthe in the Northern part of the Netherlands (53°4′N, 6°37′E). To obtain a sample reflecting the average properties of *A. montana* achenes within the population, several hundreds of entire capitulae with ripe achenes were collected from hundreds of individuals and mixed carefully, avoiding damaging the pappus hairs.

Experiment 1

To assess the distribution of achene weights, 250 achenes were drawn from the achene pool and weighed individually. To establish the relation between achene weight and germination, the achenes were sown in Petri dishes on moistened filter paper overlying hydrophilic rockwool. The achenes were kept for 1 week in darkness at 5°C to synchronize germination. The achenes were allowed to germinate at an alternate daily temperature regime of 25/15°C (16 h/8 h), the photoperiod coinciding with the high temperature (Pegtel 1988). The light was provided by fluorescent tubes. After germination, the weight of coat, pappus and embryo were established. For assessing the correlation between achene weight and seedling quality, the fresh weight of the resulting seedling was established after three weeks of development in a similar Petri dish.

Experiment 2

In order to find any correlation between achene weight and achene geometry, 150 achenes were drawn from the pool and weighed individually. Because pappus openness may influence dispersal efficiency, the angle between the pappus hairs and the rest of the achene were measured.

Subsequently, the achenes were released in a wind tunnel at 35 cm height at a wind speed of 6·5 m/s. The achenes were trapped on a glued, smooth surface and their trapping distances were measured. After trapping the achenes, the maximal length of the pappus hairs was measured. This was most convenient because the hairs stuck together.

Experiment 3

For direct correlation of germination and trapping distance, 250 achenes were drawn from the pool. They were released in the wind tunnel following the procedure of Experiment 2. After collection of the achenes, they were rinsed to wash off the glue and germination was established following the procedure of Experiment 1.

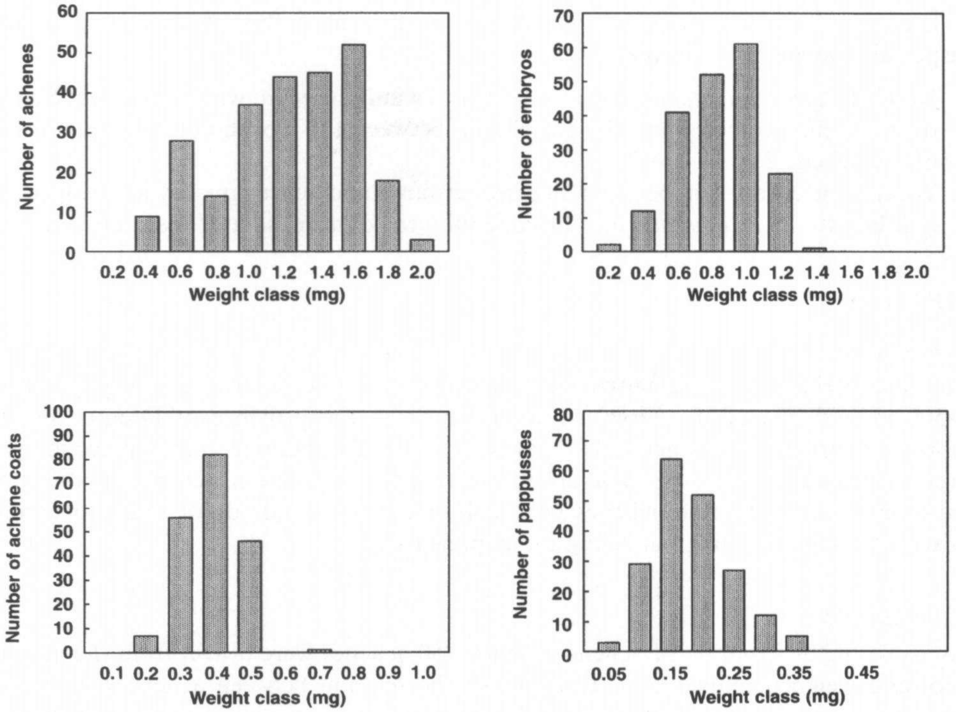

Fig. 1. Distribution of total achene weights, embryo weights achene coat weights, and pappus weights in Experiment 1.

Experiment 4

For direct correlation of seedling weight and trapping distance, 350 achenes were drawn from the pool. For reason of efficiency, the achenes were preselected for viability by eye and by probing individual achenes by pressing softly. They were released in the wind tunnel following the procedure of Experiment 2. After collection of the achenes they were rinsed in demineralized water to wash off the glue and germination and seedling fresh weight was established following the procedure of Experiment 1.

Data analysis

Linear regressions and logistic regressions were calculated with SPSSPC version 5·1.

RESULTS

Achene weights, achene component weights, germination and seedling weight (Experiment 1)

The distribution of the achene weights was skewed to the left (Fig. 1, $P<0{\cdot}05$). Embryo weight, achene coat weights and pappus weights were nearly symmetrically distributed. The embryo weight was about 60% of the total achene weight. Achene coat weight accounted for about 30% and pappus weight was only 10% of the total achene weight.

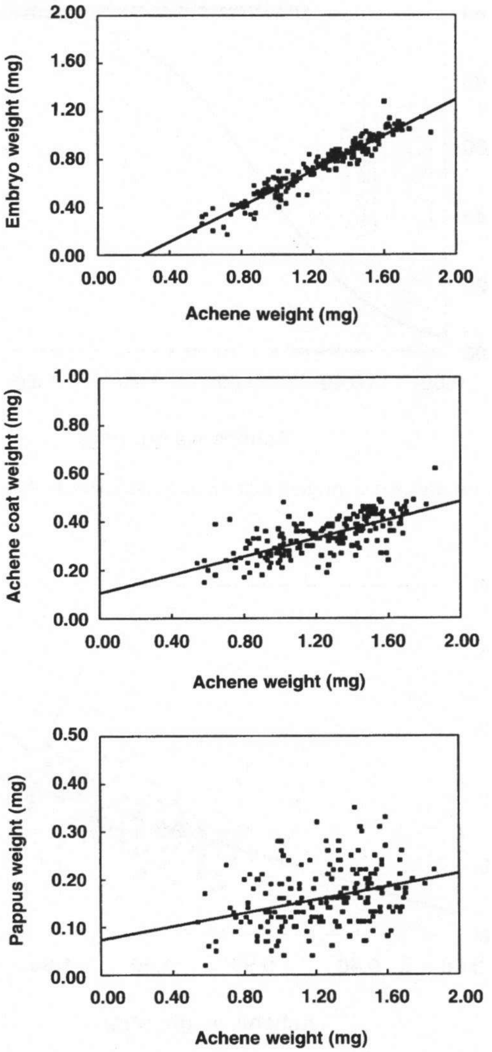

Fig. 2. Correlation between total achene weight and embryo weight ($r^2=0{\cdot}91^{***}$) , total achene weight and achene coat weight ($r^2=0{\cdot}47^{***}$) and total achene weight and pappus weight ($r^2=0{\cdot}1^{***}$) in Experiment 1.

Embryo weight had a strong positive linear correlation with achene weight (Fig. 2, $r^2=0{\cdot}91$, $P<0{\cdot}001$). A significant positive linear correlation was found between achene weight and achene coat weight ($r^2=0{\cdot}47$, $P<0{\cdot}001$) and between achene weight and pappus weight ($r^2=0{\cdot}10$, $P<0{\cdot}001$). A logistic regression between achene weight and germination chance was calculated and found to be significant (Fig. 3, r-logistic$\,=0{\cdot}44$, $P<0{\cdot}001$). A significant positive linear correlation was found between achene weight and seedling weight (Fig. 4, $r^2=0{\cdot}32$, $P<0{\cdot}001$).

Achene geometry, achene weight and flying ability (Experiment 2)

Hair length and hair angles were symmetrically distributed (Fig. 5). No significant correlation was found between achene weight and hair angle (Fig. 6), but there was a

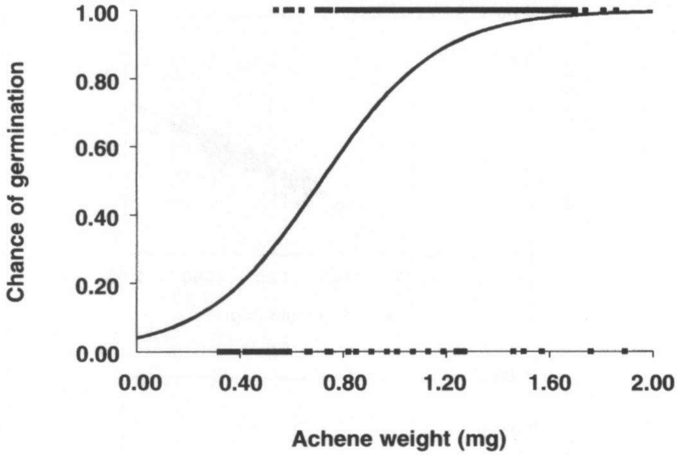

Fig. 3. Logistic curve representing chance of germination in Experiment 1, dependent on achene weight (*r*-logistic = 0·44***).

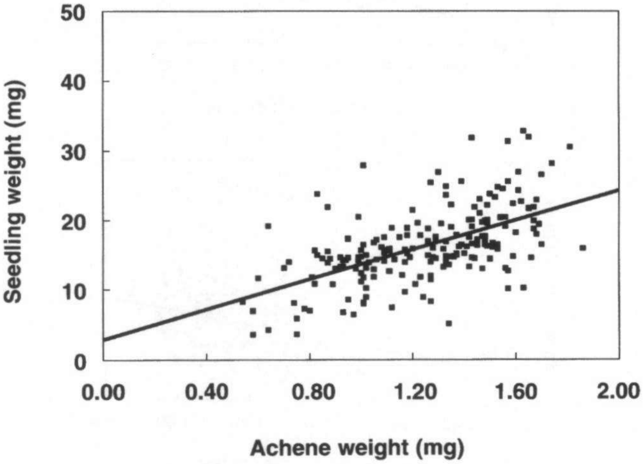

Fig. 4. Correlation between achene weight and seedling weight in Experiment 1 ($r^2 = 0{\cdot}32^{***}$).

significant positive correlation between achene weight and hair length (Fig. 6, $r^2 = 0{\cdot}16$, $P < 0{\cdot}001$). The distribution of the trapping distances was skewed to the right (Fig. 7). The median of the trapping distance corresponds to a falling velocity of 1·44 m/s.

Flying ability and germination (Experiment 3)

A significant negative logistic correlation was found between germination and trapping distance (Fig. 8, *r*-logistic = 0·29, $P < 0{\cdot}001$).

Flying ability, achene weight and seedling weight (Experiment 4)

A significant linear correlation was found between viable achene weight and trapping distance (Fig. 9, $r^2 = 0{\cdot}15$, $P < 0{\cdot}001$). At shorter distances, both heavy and light seeds

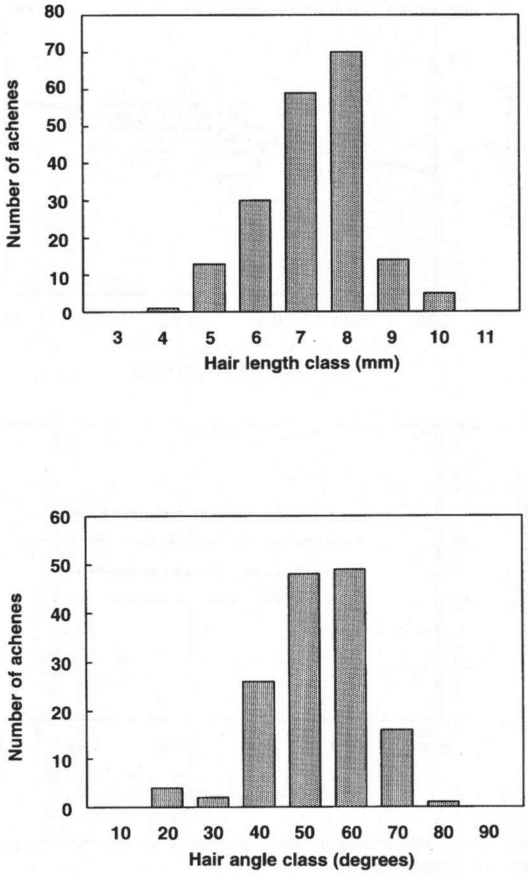

Fig. 5. Distribution of hair length and hair angles in Experiment 2.

were found. At larger distances the proportion of heavier achenes declined rapidly. Heavier achenes tended to have shorter primary trajectories than most of the lighter achenes (Fig. 9, top right panel). A similar pattern was found in the correlation between seedling weight and trapping distance. Linear correlation was low ($r^2=0{\cdot}11$, $P<0{\cdot}001$), but the proportion of heavier seedlings declined rapidly with increasing trapping distance. Heavier seedlings tended to derive from achenes that had shorter trapping distances (Fig. 9, bottom right panel).

DISCUSSION

Differences in achene weight are the most important factor determining differences between the trapping distance of individual achenes of *A. montana* (cf. Van Andel & Vera 1977). This dependence is based on the low correlation between pappus size and total weight of the achene, which is largely composed of embryo weight. This may reflect that the pappus is formed early in the development of the achene, at least before embryo development. A correlation between achene weight and the position of the achene in the capitulum is found in many Asteraceae (Heywood *et al.* 1977). Differences

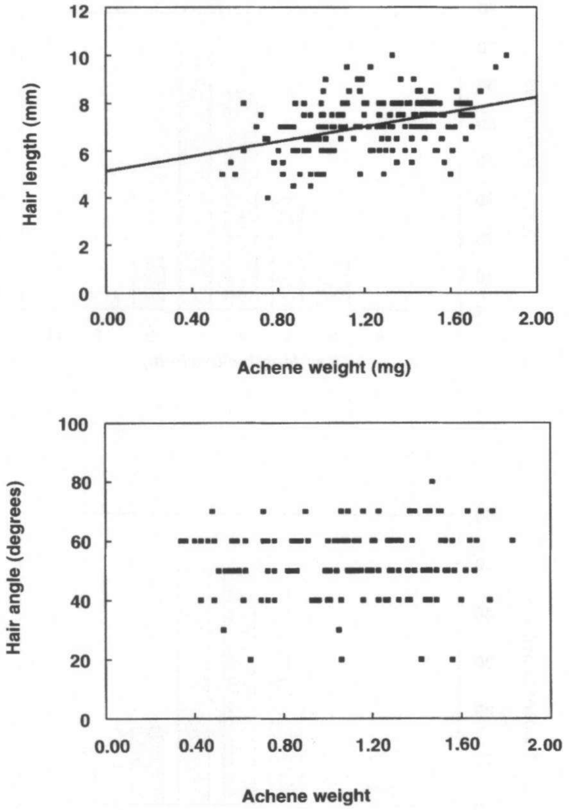

Fig. 6. Correlation between total achene weight and hair length ($r^2=0{\cdot}16^{***}$) and total achene weight and hair angles (non-significant) in Experiment 2.

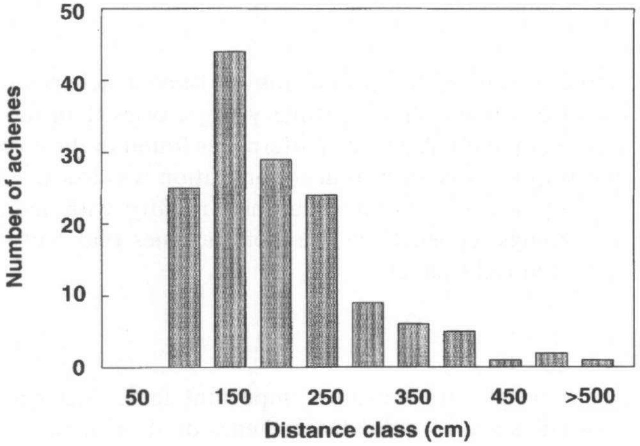

Fig. 7. Trapping distances of individual achenes in Experiment 2.

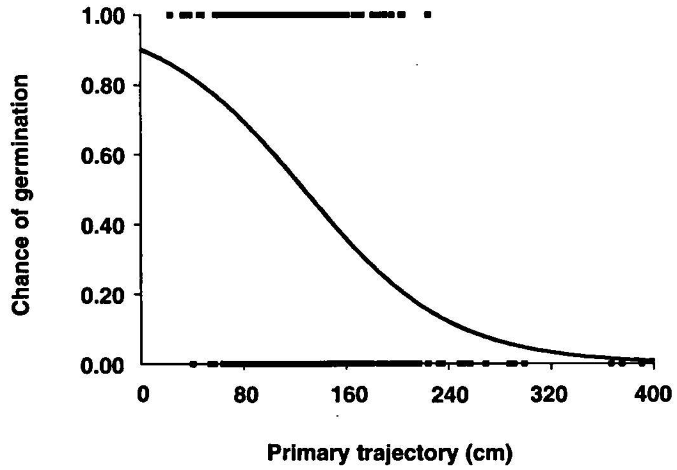

Fig. 8. Logistic curve representing chance of germination in Experiment 1, dependent on trapping distance in Experiment 3 (*r*-logistic = 0·29***).

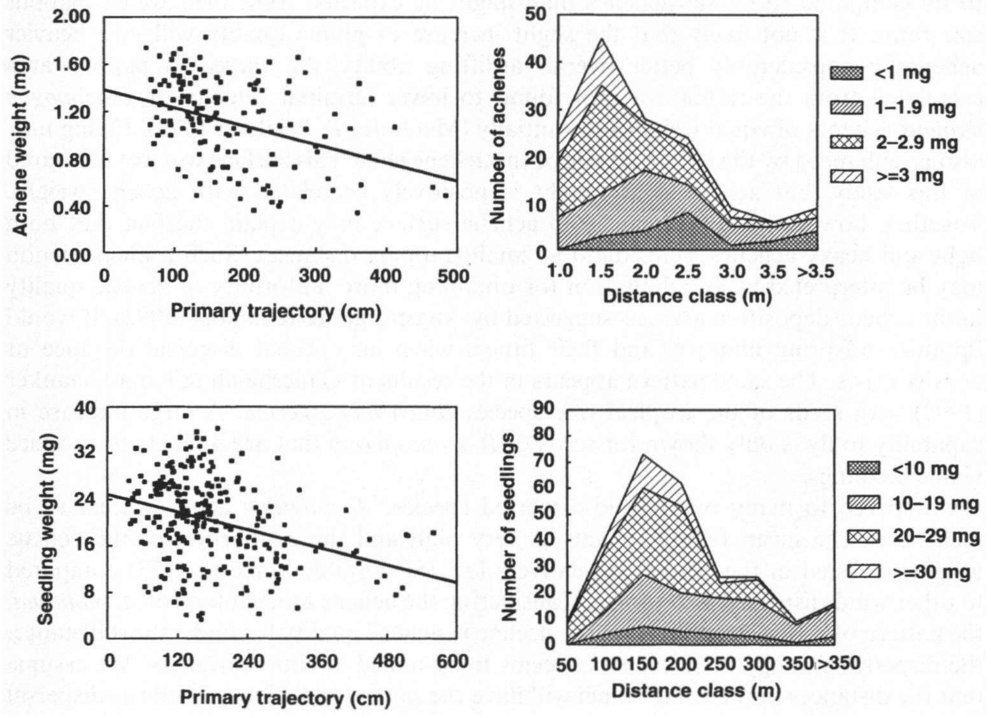

Fig. 9. Correlation between trapping distance and achene weight (r^2=0·15***) and trapping distance and seedling weight (r^2=0·11***).

in this position, which lead to unevenness in resource supply to the developing achenes may not affect pappus size as much because of its early development and relatively lower cost. Although this was not studied for *A. montana*, the existence of such unevenness in development could also explain the skewness of the distribution of the achene weights to some extent. In Asteraceae species the situation of achenes on the capitulum may relate to their size: the outer achenes are mostly heavier and larger than the inner ones and, by the nature of their position in concentric circles, relatively more numerous (Heywood *et al.* 1977).

Since achene weight is positively correlated with germination chance, embryo size and seedling weight, achene weight is both an indicator of dispersal distance and of achene quality. Indeed it was found that achene weight, germination and seedling weight decreases with increasing trapping distance. Therefore it can be concluded that in *A. montana* a strong negative correlation between dispersal distance and achene quality exists. Germination is unlikely in achenes travelling more than several metres. The quality of the seedlings is also low in case they germinate.

A strong negative correlation between dispersal distance and seed quality has been found in this study. This has been reported before for other species (Augspurger & Hogan 1983; Morse & Schmitt 1985; Ganeshaiah & Uma Shaanker 1991). The ecological implications, however, are not easily understood. In this study, it was found that achene quality only drops considerably beyond a certain distance, when most of the achenes have already been trapped. It seems that heavier achenes have a slightly larger capacity to fly compared to lighter achenes than might be expected from their weight/pappus size ratio. It is not likely that the slight increase of plume quality will give heavier achenes a considerably better overall airlifting ability. An increased pappus area calculated from the radius was not found to lower terminal velocity of *Tragopogon dubious* achenes of equal weight substantially (McGinley & Brigham 1979). Flying may also be enhanced by the increased size of the achene coat. This surface was not measured in this study, but achene coat weight is positively correlated with achene weight. Together, however, a total increase in achene surface may explain the fact that both light and heavy achenes were found at small trapping distances. Such a phenomenon may be interpreted as an adaptation for obtaining more uniformity of achene quality in the achene deposition area, as suggested by Augspurger & Kitajama (1992). It would optimize offspring numbers and their fitness when an optimal dispersal distance or density exists. The same pattern appears in the results of Ganeshaiah & Uma Shaanker (1992) with seeds of the tropical tree species *Butea monosperma*. A large increase in capability to fly is only shown for seeds of *B. monosperma* that are unlikely to produce viable seedlings.

Compared to many other wind-dispersed species, *A. montana* achenes seem to be inefficient. The mean falling velocity is very high and the proportion of the achene weight, invested in the plume, is relatively low (Sheldon & Burrows 1973) compared to other wind-dispersed Asteraceae. Considering the achene morphology of *A. montana*, the pattern of achene trapping and the decline in achene quality beyond a short distance, the dispersal strategy of *A. montana* seems to be aimed at short distances. We assume that the distances in the wind tunnel will have the same order of magnitude as dispersal distances in the field. The genetic structure of *A. montana* populations also suggests that dispersal distance is limited (Luijten *et al.* 1996). The relatively low dispersal capability of *A. montana* may be related to the relative rarity of its habitat and the relatively small size of suitable locations (Quinn *et al.* 1994), which may lead to stabilizing selection for rather inefficient wind dispersal (Cody & Overton 1996).

Restricted dispersal capability is common for many threatened species. Estimations of dispersal efficiency will therefore be vital for designing a conservation strategy for such species (Klinkhamer 1988; Verkaar 1990; Bakker *et al.* 1996; Prins *et al.*1998). However, the required detailed information on specific dispersal ability is almost never available. For wind-dispersed species such as *A. montana*, modelling may help to estimate dispersal distances (Sheldon & Burrows 1973; Burrows 1973, 1975; Green & Johnson 1989, 1996; Okubo & Levin 1989; Augspurger & Franson 1991; Willson 1993). This study, however, shows that it is not enough to predict effectiveness of seed dispersal in terms of distance alone. Declining seed quality is an important additional factor.

The spontaneous founding of new populations of *A. montana* at large distances from source populations is therefore very unlikely. This presents serious implications for the species' conservation. In order to re-establish populations of *A. montana* in restoration areas, not only the abiotic conditions have to be restored. Artificial dispersal will also be necessary (Strykstra *et al.* 1998).

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