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Release thresholds strongly determine the range of seed dispersal by wind

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Abstract

The effect of the seed abscission process on the dispersal distance of seeds has never been studied explicitly and is often ignored in studies that aim to estimate the seed shadows of species. To examine the importance of the abscission process for the seed shadow we used a seed trajectory model that keeps track of the release threshold dynamics of the individual seeds on mother plant. We defined the release threshold as the critical wind speed that induces a mechanical force that is just large enough to release a seed from its mother plant. The model used real wind speed sequences and seed appearance over time on the mother plant.

Several calculations were performed to investigate the effect of release thresholds dynamics on seed shadow of two herbaceous species with contrasting terminal velocity values (V_t): *Centaurea jacea* ($V_t = 4.1\,\mathrm{m\,s^{-1}}$) and *Hypochaeris radicata* ($V_t = 0.49\,\mathrm{m\,s^{-1}}$).

Release thresholds were responsible for a two-fold increase of median dispersal distances in both species. Tails of the seed shadows, the fraction of seeds that travel furthest, were even more sensitive and increased with a factor 4.5 for *Centaurea* and 7.0 for *Hypochaeris*. Our work indicates that the abscission process appears to be very important and suggests that dispersal distance of plants is currently severely underestimated, which, in turn, has major consequences for our current understanding of the distribution, metapopulation dynamics and survival of plant species.

Keywords: Anemochory; Dispersal; Herbaceous plants; Mechanistic model; Seed abscission; Seed shadow; Turbulence

1. Introduction

Seed dispersal is a crucial process in the life cycle of plant species (Nathan and Muller-Landau, 2000; Wang and Smith, 2002). It plays a key role in their distribution, metapopulation dynamics and survival (Cain et al., 2000; Schippers et al., 2001, Schippers and Joenje,

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2002; Johst et al., 2002; Higgins et al., 2003; Wang et al., 2003; Favier et al., 2004). Many herbaceous species rely on wind as their most important dispersal vector (Van der Pijl, 1982; Van Dorp et al., 1997).

Many studies have been performed to quantify seed dispersal that involved seeds being released artificially (Van Dorp et al., 1996; Strykstra et al., 1998; Murren and Ellison, 1998; Jongejans and Schippers, 1999; Jongejans and Telenius, 2001; Tackenberg, 2003). Seed shadows obtained through these methods do not take the effects of natural abscission into account. When a seed ripens on a plant, the connection between seed and mother plant gradually weakens (Elgersma et al., 1988; Whalley et al., 1990; Van Dorp et al., 1996; Ferrándiz, 2002; Roberts et al., 2002). The seed is released when the wind speed is higher than or equals a critical wind speed, the wind speed that creates just enough mechanical power to break the connection between plant and seed (Burrows, 1986). We call this wind speed the 'release threshold'. The release threshold dynamics of a species might be a major factor that determines the shape of the seed shadow because seeds with a release threshold encounter faster wind speeds (Greene and Johnson, 1992; Emig and Leins, 1996; Nurminiemi et al., 1998; Wagner et al., 2004). Although the possible importance of this phenomenon has been recognised (Elgersma et al., 1988; Greene and Johnson, 1992; Van Dorp et al., 1996; Greene and Johnson, 1996; Nathan et al., 2000, 2001) recent important studies ignore this process (e.g. Nathan and Muller-Landau, 2000; Nathan et al., 2002; Tackenberg, 2003). This raises the question of how important are release threshold dynamics for seed dispersal and how will it affect the plant's seed shadow?

It is difficult to investigate the effects of seed release threshold dynamics in herbaceous species systematically because: (1) the small seeds are difficult to trace and many seeds are needed to obtain a reliable seed shadow, (2) it is very time consuming because one has to wait until seeds of different flowers are released naturally which might take about half a year and (3) it is extremely hard to measure the tail of seed shadow curves of far travelling seeds because of the low probabilities of seed arrival per m^2 at larger distances. These experimental problems could be overcome by using an explanatory model that includes the appearance of ripe seeds over time, release threshold dynamics and dispersal by wind. Therefore, the trajectory model of Jongejans and Schippers (1999) was extended with routines that describe seed appearance on the mother plant and release threshold dynamics. We choose this trajectory model because it judged to be the best seed dispersal model evaluated by Andersen (1991), it worked very well in wind tunnel experiments (Jongejans and Schippers, 1999) and was the best model evaluated by Tackenberg (2003) if we consider flat landscape conditions. The extended model was used to evaluate the importance of seed release processes for seed dispersal of two herbaceous species with contrasting seed properties: *Centaurea jacea* and *Hypochaeris radicata*.

2. Model description

We used an individual-based model that keeps track of the number and release thresholds of seeds attached to the mother plant. A seed appearance function determined the addition of just ripened seeds to this number. These just ripened seeds had a certain initial release threshold that gradually decreased over time. When a seed that is attached at the mother plant encountered a wind gust that exceeded its present release threshold, the seed was abscised. Measured maximum wind speeds were used to determine the seed abscission and finally the dispersal distance of the released seeds was determined by a seed trajectory model.

2.1. Seed appearance over time

The seed appearance function that describes the addition of just ripened seeds on the mother plant over time was estimated from flower phenology data observed in The Netherlands (Hartemink et al., 2004). A probability distribution function that was able to describe the flower phenology of our species over time was:

$$f(t) = \left(\frac{1}{A}\right)^2 (t - S)\mathrm{e}^{-(1/A)(t-S)} \quad \text{and} \quad f(t) \geq 0 \tag{1}$$

in which: $f(t)$ is the probability density (day^{-1}), t is the time expressed in day of the year, S is the start day of seed ripening, A is the scaling parameter that represents the time from S to the maximum of the curve (day). We calibrated the cumulative function. The cali-