Gone with the wind: high-resolution analysis of pine dispersal in New Zealand mountains

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Summary   Amongst the world's invasive plant species, those of the genus *Pinus* are widespread and conspicuous. In many parts of the world pine trees were planted for production purposes or erosion control, and are now spreading well outside the plantations, threatening biodiversity, ecosystem function, and landscape values. In New Zealand, this phenomenon has been observed for several decades, and the total area affected by conifers is estimated at 150,000 ha. Areas affected are mostly natural and semi-natural grasslands and scrublands, and abandoned pastures. Here we study the mechanisms that underlie the spread of pine with an innovative approach. We focus on a pine invasion at Mount-Barker (South Island, New Zealand). Starting at a shelter-belt including the wind-dispersed Corsican pine (*Pinus nigra* subsp. *laricio*), planted around 1910, the invasion has since spread to neighbouring grasslands and scrublands. We use high-resolution data collected on Mount-Barker in 2008 and 2009 to analyse the interactions between wind and pine biology in the colonisation dynamics. We show that (1) wind turbulence, (2) wind speed and (3) density-dependence play important roles in the population dynamics. This approach provides an exciting opportunity for management plans that take into account fine-scale heterogeneity in landscape, wind patterns and tree dynamics.

Keywords   Invasion biology, *Pinus nigra*, long distance dispersal, population biology.

INTRODUCTION
Invasive species cause major environmental and economic damage worldwide (Shea and Chesson 2002, Fox *et al.* 2009). Few ecosystems on the planet remain free of species introduced by humans, and introduced species can affect local ecosystems through a wide range of processes (Mack *et al.* 2000). Conifers in general, and pines in particular, are some of the most effective invaders in the world (Richardson and Rejmanek 2004). They have spread from plantations in South and North America, Europe, South Africa, and Australasia, as their traits allow them to establish and dominate a large variety of ecosystems, threatening local biodiversity (Higgins and Richardson 1998).

One key feature of pines is their wind-dispersed seeds that can travel long distances when uplifted. Rate of spread is strongly affected by long distance dispersal (Clark *et al.* 1998, Cain *et al.* 2000), but long distance dispersal is rare and difficult to predict. Indeed, many seeds travel only short distances and only a few travel much longer distances (Willson 1993, Cain *et al.* 2000). Early attempts to model population spread used models that did not take highly skewed distribution of dispersal into account, and therefore underestimated spread speeds. Recently the explosion in interest in long distance dispersal (LDD) has led to new empirical methods for quantification of dispersal (Katul *et al.* 2005), new formulations of the dispersal kernel (Chesson and Lee 2005) and new spread models that more closely approximate observed spread speeds (Neubert and Parker, 2004).

Here we study the mechanisms that underlie the spread of an invasive species with an innovative approach. We focus on Mount-Barker, in the high country of the South Island of New Zealand, where a shelter-belt including Corsican pine (*Pinus nigra* Arn. subsp. *laricio*), a wind-dispersed species, was planted around 1910, leading to invasion of neighbouring grasslands and scrublands. We use high-resolution wind and demographic data collected on Mount-Barker in 2008 and 2009 to analyse the interactions between wind and pine biology. We particularly focus on wind turbulence, which has been shown to be a key mechanism of LDD (Katul *et al.* 2005). This approach opens exciting perspectives for management plans that take into account fine-scale heterogeneity in seed dispersal in relation to landscape.

MATERIALS AND METHODS
Study species   *Pinus nigra* (black pine) occurs throughout the mountain zone of Mediterranean Europe and is reported as invasive in Australia and New Zealand (Richardson and Rejmanek 2004). There are six recognised subspecies of *P. nigra* (Quezel and Medail 2003); the data here are for *P. nigra* Arn. subsp. *laricio* (Corsican pine, hereafter referred simply as 'pine').

Study area   The study site was at 620 m elevation on a flat terrace beneath Mount Barker in the Rakaia Catchment, Canterbury, New Zealand (43°21'30"S, 171°35'15"E,). Soils are derived from a thick layer of loess over greywacke moraine till (N.J. Ledgard pers. comm., Dehlin *et al.* 2008). Annual precipitation at Lake Coleridge (1.5 km distant) is 907 mm. Pines were planted in a shelter-belt north of Mount Barker around 1910 and have since spread to the South-East over several kilometres (Buckley *et al.* 2005).

Demographic data   In winter 2008 and 2009 we noted the presence, age, size and fecundity (through the number of cones) of adult pines in 30 × 30 m plots. Age was evaluated by counting the internodes, and cones were double counted by the same observers throughout the study. We sampled six plots of open woodland in 2008; in 2009 we sampled the same six plots and an additional eight plots of different densities (intermediate and high density). We thus compared 2008 and 2009 cone production in open woodland only, and analysed the effect of stand density on cone production in 2009 only.

Dispersal data   Campbell Scientific CSAT3 sonic anemometers placed at three different heights (3.7, 8.3 and 13.1 m) and a Campbell Scientific Logger on two towers were used to collect wind data (20 min averages and covariance of wind vectors) throughout the dispersal season (24 June to 24 September) in 2009. Site 1 was located in an area of recent pine expansion, south of Mount Barker, while site 2 was located at the bottom of Mount Barker on the north side, in the area where the spread started in the mid 20th century.

   To quantify the frequency of uplift events throughout the dispersal season we mounted at site 1 two towers equipped with height conic seed traps placed in pairs at four heights (1, 3, 8 and 12 m). The top traps were located above the canopy and were used as a way to evaluate seed uplift.

RESULTS
Pine biology   The 70 adult pines sampled in low density stands carried on average 58 and 168 cones per tree in 2008 and 2009 respectively. The age of first reproduction was 15.6 years on average, with a standard deviation of 2 years.

   In the 2009 study, cone production was negatively correlated with stand density (Figure 1), leading to cone production per area peaking at intermediate stand density (Figure 2) and decreasing at high densities. Trees in low density stands were significantly younger (average 18, standard deviation 2) than trees in high density stands (average 23, standard deviation 3).
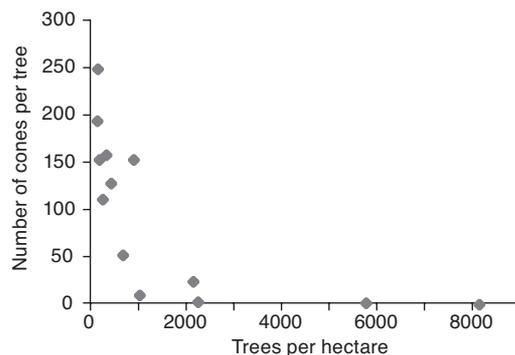

Figure 1.   Individual tree cone production in 2009 plotted against stand density in 13 plots.
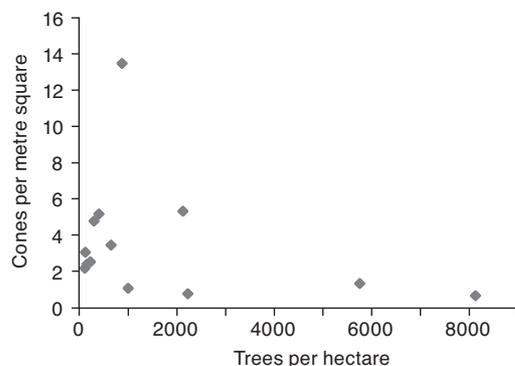

Figure 2.   Cone density (number m^{-2}) in 2009 plotted against stand density in 13 plots.

Wind and dispersal data   Wind speeds exhibited high variability throughout the season, with a 20 min average ranging from 0 to 16 m s^{-1}. North-westerlies (shown for site 1 in Figure 3) were the strongest and most frequent winds, while south-easterlies were almost absent during the dispersal season. Wind turbulence (measured as the turbulence kinetic energy) varied greatly during the season, averaging 15 m^2 s^{-2} and 8 m^2 s^{-2} on site 1 and site 2 respectively, and was correlated (Pearson coefficient of 0.65) with average wind speed on both sites.

   In total, 264 seeds were collected in the vertical seed traps (Figure 4). Most seeds were collected in the second trap (3 m high). The proportion of seeds reaching the top trap (12 m high) during five time periods was correlated (Pearson coefficient of 0.62) with turbulences but not with wind speed during the same time (Pearson coefficient 0.2).

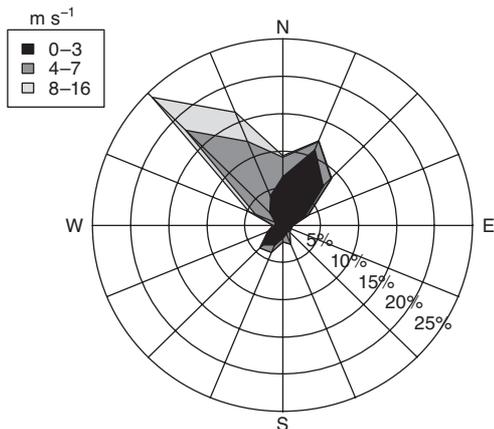Frequency of wind speed, 24/06–24/09/10, site 1, high CSAT

Figure 3. Wind-rose showing the direction and average speed of winds measured between June and September 2009 at a height of 13.1 m at site 1.
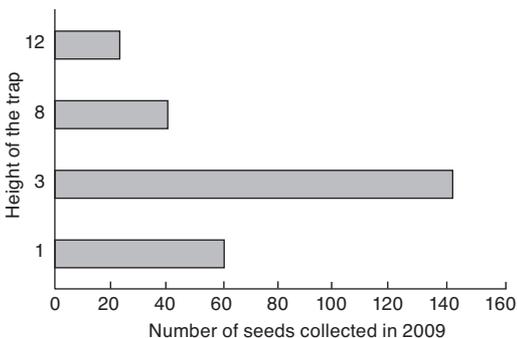

Figure 4. Distribution of seeds collected in vertical seed-traps, summed from the two towers.

DISCUSSION

Wind dispersal is a key process in the colonisation dynamics of pine trees. The objective of this study was to understand the temporal and spatial variability in wind turbulences that allow seeds to travel long distances, and to link them with the biological cycle of the pine. We revealed a combined effect of dominant winds and infrequent turbulent events on seed dispersal. The dominance of north-westerlies confirmed a strong effect of the dispersal process in creating the pattern of pine spread (which is oriented to the South-East, see Buckley *et al.* 2005). Turbulent events led to seeds uplifted above the canopy, a key element for LDD (Katul *et al.* 2005), allowing the seeds to 'catch' horizontal winds. Turbulence kinetic energy was lower at site 2 on the north side of Mount Barker (near the point of introduction), although this site was expected to be more exposed to strong winds. This could explain why the initial progression of pine was slow, while frequent uplifts on the south side of Mount Barker led to an explosive spread in the last 30 years.

Pines usually exhibit an early maturity and high fecundity, which explains their ability to be invaders (Richardson and Rejmanek 2004, Cousens *et al.* 2008). On Mount Barker, age of first reproduction was *c.* 16 years, which is earlier than reported elsewhere (Johnson 1974, Debain *et al.* 2007). We observed a large variability in cone production between 2008 and 2009, which suggests a mast seeding behaviour (Cousens *et al.* 2008) but might also be explained by maturation of the stand (fecundity increasing with age, see Debain *et al.* 2007). Cone production was characterised by a strong density dependence – high-density stands (more than 4000 trees ha^{-1}) carrying less cones per area than stands with lower tree density despite being on average older. This suggests the effect of isolated dispersal events (producing isolated clusters of trees) on population growth rate is stronger than predicted by theory (Cousens *et al.* 2008).

From these results we can make a few management suggestions. Despite the importance of turbulence events for LDD, we showed a strong pattern in dominant winds, which supports the usefulness of defining areas of sensitivity to invasion through maps of wind and seed sources (McNeill 2008). Control actions should also target isolated trees, which contribute greatly to both the population growth and the rate of spread. The low variability of age of first reproduction should facilitate identifying stands before they start reproducing. Finally, the occurrence of seed uplift several meters above the canopy calls into question strategies of planting non-spread-prone trees to act as a barrier to dispersal (Buckley *et al.* 2005), although an effect on population growth can be expected from a reduction in cone production.

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