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Long-distance dispersal of spruce budworm (*Choristoneura fumiferana* Clemens) in Minnesota (USA) and Ontario (Canada) via the atmospheric pathway

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ABSTRACT

Dispersal can play an important role in the population dynamics of forest insects, but the role of long-distance immigration and emigration remains unclear due to the difficulty of quantifying dispersal distance and direction. We designed an agent-based spruce budworm flight behavior model that, when interfaced with temperature, wind speed, and precipitation output from a high-resolution atmospheric model, produces detailed flight trajectories and deposition patterns over large landscapes. Rules and relationships describing budworm adult (moth) lift-off, ascent, horizontal flight, and descent were parameterized using a detailed empirical study of budworm dispersal behavior and corresponding meteorological conditions during a 1970s outbreak in New Brunswick, Canada. Simulated moth landings were assumed to be dependent in part on the availability of suitable host tree species. We applied the model to a 6.4 million ha landscape at the border between northern Minnesota (USA) and Ontario (Canada) during an eight-day flight window in late June 2007. Specimens collected during and after this flight window indicated moths emerging from an inland source of outbreak populations dispersed over 150 km to trap sites near the north shore of Lake Superior, where localized cooling was predicted to have delayed emergence of locally-produced budworm moths. Simulations suggested immigration of moths to lakeshore sites from the outbreak source was plausible on three of eight dates within the flight window, but the relatively narrow deposition footprints implied immigration occurred on different dates across lakeshore sites. Apart from wind speed and direction, precipitation and low temperatures limited dispersal to substantially shorter distances for a few dates within the simulated flight window. Key uncertainties limiting our understanding of atmospheric transport of spruce budworm include behavioral responses to vertical heterogeneity in the air temperature profile, the precipitation threshold required for the forced descent of moths from the air column, and search mechanisms affecting host and/or mate location during long-distance flight.

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1. Introduction

The ability to disperse long-distances is fundamental to the population ecology of most economically-important insect pests (Isard and Gage, 2001). Yet the role of long-distance dispersal in the spread, synchrony, and persistence of insect outbreaks remains unclear due to the difficulty of quantifying dispersal and its impacts on populations (Royama, 1979, 1984; Royama et al., 2005). For Lepidopteran forest defoliators, dispersal has been indirectly inferred by examining egg to moth ratio, which can indicate exodus by dispersers from heavily defoliated areas (Nealis and Régnière, 2004; Royama, 1984; Royama et al., 2005). Theoretical models testing dispersal parameters have produced spatial covariance estimates of populations matching observed defoliation patterns (e.g., Williams and Liebhold, 2000). In these models, dispersal was usually represented as a stationary process (i.e. parameters are equal over the entire landscape); however, mounting evidence suggests that dispersal is not stationary (Keyghobadi et al., 1999, 2006). Spatial factors affecting insect movement may include landscape structure (Cooke and Roland, 2000; Nathan et al., 2005), vegetation phenology (Gage et al., 1999), temperature (Sanders et al., 1978), and the direction and speed of air currents (Anderson and Sturtevant,

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2011; Greenbank et al., 1980; Onstad et al., 2003). However, the actual influence of dispersal on spatiotemporal patterns of insect outbreaks is a hotly contested area of research (e.g., Royama et al., 2005) and will remain so until dispersal processes can be quantified more precisely.

Most forest and agricultural pests either actively or passively use wind to enhance their dispersal (e.g., Greenbank et al., 1980; Onstad et al., 2003; Riley et al., 1991; Westbrook and Isard, 1999). Aerobiology – the science of the atmospheric transport of biota – requires understanding of ecology, life history, behavior, meteorology, and the multiple scales at which these factors interact (Gage et al., 1999). To date aerobiology has been most often applied to understand the passive transport of biota, particularly pollen (Bohrerova et al., 2009; Schueler and Schlunzen, 2006) and pathogen spores (Isard et al., 2005, 2007; Waggoner and Aylor, 2000). Actively dispersing insects, including many economically important pest species (Strand, 2000), add complexity by introducing behaviors during ascent, horizontal transport, and descent stages of the atmospheric dispersal pathway. Empirical observations of flight behaviors from field studies (Greenbank et al., 1980), radar (e.g., Chapman et al., 2010; Greenbank et al., 1980; Riley et al., 1991; Westbrook and Isard, 1999), and laboratory experiments (Lu et al., 2007; Vogt et al., 2000; Wu et al., 2006) may be used to empirically estimate key flight behaviors such as time of ascent, flight duration, velocity parameters, thermal and energetic constraints for a variety of flying insects. Such studies may be used to parameterize flight models that can interface with high-resolution weather models to produce accurate patterns of insect deposition and identify source populations of immigrants (Achtemeier, 1996; Scott and Achtemeier, 1987). Coupled atmospheric-behavior models have been applied to understand avian flight behavior (Mandel et al., 2008, 2011; Sapir et al., 2011; Shamoun-Baranes et al., 2010), but only rarely applied to examine active insect dispersal through the atmospheric pathway (e.g., gypsy moth, Fossberg and Peterson, 1986; Isard and Gage, 2001).

The spruce budworm (SBW) is a native Lepidopteran that periodically defoliates balsam fir (*Abies balsamea*) and spruce species (*Picea* spp.) in the boreal and sub-boreal forests of North America. Pupation occurs between mid-June and late July, where the specific phenology is dependent on ambient temperature (Régnière and You, 1991). Adults emerge approximately 10 days after pupation with female emergence lagging a few days behind males. Adult dispersal occurs in the evenings and is dependent upon meteorological conditions (Greenbank et al., 1980; Régnière and Nealis, 2007), and levels of host defoliation (Nealis and Régnière, 2004; Royama, 1984). Both sexes emigrate together with similar exodus characteristics, though the sex ratio of emigrants is biased toward females (Greenbank et al., 1980). Adult females select either spruce or fir for oviposition, but do not indicate preference between spruce and fir species (Régnière and Nealis, 2007). Adults are strong fliers and can easily disperse 20 km with a maximum recorded dispersal distance of 450 km (Greenbank et al., 1980).

In this paper we describe the design and application of an atmospheric transport model for SBW adult (moths). SBW is one of the few species for which aerobiological parameters have been empirically estimated in situ under outbreak population conditions (Greenbank et al., 1980). We applied the SBW transport model to an eight-day flight window in northern Minnesota and adjacent Ontario corresponding with budworm adult male capture data from a large spatial network of pheromone traps. We evaluated model behavior by addressing the question: What is the prospect that budworm adults emerging from a localized outbreak in northern Minnesota dispersed to moth collection sites over 150 km to the east on the lakeshore of Lake Superior, where SBW phenology is generally delayed due to lake-effect cooling? This question was evaluated by the relative proximity of simulated moth landings relative to six lakeshore trapping sites, and by quantifying the flight properties (i.e., distance, direction, relative landing success etc.) of simulated moths over the flight period.

2. Methods

2.1. Model description

2.1.1. Lagrangian trajectory model

The SBW atmospheric transport model is an agent-based model of budworm flight, where each agent is representative of an insect or group of insects with the same flight characteristics, assigned behavioral parameters based on probability distribution functions corresponding to the timing of liftoff, relative flight strength, and descent rules (see Section 2.1.2). The Lagrangian trajectory model calculates a step-by-step location of the SBW agent flight through a four-dimensional wind field simulated by a numerical meteorological model. The trajectory model is diagnostic in that trajectories are calculated from meteorological model output as opposed to embedding the agent within the meteorological model during its production run. Meteorological model outputs used to construct the trajectories consist of a time series of simulated temperature, wind speed, wind direction, and precipitation concentration for regularly spaced point locations on a horizontal grid and vertically spaced sigma levels subject to compression in the surface layer with the compression being relaxed with height. In our specific application we applied the Weather Research and Forecasting Model (WRF v3, Skamarock et al., 2005) to produce outputs for a 6.5 million ha study area at hourly intervals at grid points spaced at 4 km in the horizontal and 50 vertically stretched sigma levels below 3000 m above ground level (AGL), with 33 of the levels packed within the lowest 1000 m AGL (see Section 2.2.1). The input map consists of a bitmap image file, referred to thereafter as the “study map”, with three cell types corresponding with source habitat, host target habitat, and the remaining matrix.

Each segment of the agent trajectory from launch to landing (or transport out of the grid domain) is calculated through a “predictor-corrector” method for streamlines (Achtemeier, 1979) adapted for trajectories (Scott and Achtemeier, 1987). The construction of a trajectory segment of an agent located at $P(x_0,y_0,z_0,t_0)$ through a time and space-varying wind field to a new spatial and temporal location $P(x,y,z,t)$ ($t = t_0 + \Delta t$) proceeds along the following steps. The current position $P(x_0,y_0,z_0,t_0)$ is enclosed by two square cuboids each defined by eight corner points of the meteorological grid and enclosing the hour interval of the weather model output that bounds t_0. Thus 16 points are involved in the construction of the trajectory segment. While passage of the trajectory segment through the side of the cuboid or past the weather time step complicates the mathematical bookkeeping, the methodology is the same. Each of the 16 corner points carries the components of the vector wind for its three-dimensional location and weather output interval. The values for wind vector components at x_0,y_0,z_0,t_0 are calculated by linear interpolation of the components at the 16 corner points to construct the vector wind V_0 at $P(x_0,y_0,z_0,t_0)$. The flight velocity components of the SBW adult agent, dependent on the flight stage of the insect (see Section 2.1.2), are then added to the wind vector components to construct the flight-modified wind vector V_0' components at $P(x_0,y_0,z_0,t_0)$ using the following equations:

$$u_0' = \begin{cases} (V_0 + H_i) \times \sin\left(\frac{\pi}{180} \times \alpha_0\right) & \text{ascent and horizontal flight statges} \\ V_0 \times \sin\left(\frac{\pi}{180} \times \alpha_0\right) & \text{descent stages} \end{cases} \quad (1)$$

$$v_0' = \begin{cases} (V_0 + H_i) \times \cos\left(\frac{\pi}{180} \times \alpha_0\right) & \text{ascent and horizontal flight stages} \\ V_0 \times \cos\left(\frac{\pi}{180} \times \alpha_0\right) & \text{descent stages} \end{cases} \quad (2)$$