Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) above the forest canopy

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Abstract

An outbreak of the mountain pine beetle, *Dendroctonus ponderosae* Hopk., in central British Columbia, Canada, has reached an unprecedented size and intensity, and has been spreading to the northeast. The ability of this insect to spread over large distances is known, but has not been studied directly. The 2005 emergence and subsequent flight of mountain pine beetle in central British Columbia was studied using direct observation of emergence, radar imagery, and aerial capture. Doppler weather radar was used to remotely observe the daily flight of beetles above the forest canopy. To verify that the daytime, clear-air radar returns seen during this period were indeed generated by airborne mountain pine beetles, aerial sampling in the area covered by the radar was performed using a drogue capture net towed by a single-engine light aircraft. Results from the aerial sampling verify that airborne mountain pine beetles are being detected by the Doppler radar, and that during the emergence period significant numbers of mountain pine beetles can be found at altitudes up to more than 800 m above the forest canopy. A conservative estimate of transport distance indicates that mountain pine beetles in flight above the forest canopy may move 40 to 100 km in a single day. Estimates of the instantaneous density of mountain pine beetles in flight above the canopy on flight days in 2005 indicate an average (maximum) density of 4950 (18 600) beetles per hectare.

Résumé

Une infestation de dendroctones du pin ponderosa, *Dendroctonus ponderosae* Hopkins, dans le centre de la Colombie-Britannique, au Canada, a atteint une taille et une intensité sans précédent et se propage vers le nord-est. La capacité de cet insecte à se propager sur de longues distances est connue mais n'a jamais été précisément étudiée. L'émergence de 2005 et la propagation consécutive du dendroctone du pin ponderosa dans le centre de la Colombie-Britannique ont été étudiées au moyen de l'observation directe, de l'imagerie radar et de photographies aériennes. On a utilisé le radar météorologique Doppler pour observer à distance le vol quotidien des dendroctones au-dessus du couvert forestier. Pour vérifier que les échos radar relevés le jour et dans des conditions dégagées pendant cette période ont vraiment été générés par des dendroctones en vol, on a échantillonné la zone aérienne couverte par le radar en utilisant des filets de capture tirés par un aéronef léger monomoteur. Les résultats de l'échantillonnage aérien confirment que le radar Doppler a détecté les ravageurs en vol et que, durant la période d'émergence, on peut trouver un nombre significatif de dendroctones à des altitudes allant jusqu'à 800 m au-dessus du couvert forestier. Une estimation prudente de la distance de transport indique que les dendroctones en vol au-dessus du couvert forestier peuvent parcourir de 40 à 100 km en une seule journée. Les estimations de la densité instantanée des dendroctones du pin en vol au-dessus du couvert forestier pendant les jours de vol en 2005 annoncent une densité moyenne de 4950 (densité maximale : 18 600) dendroctones par hectare.

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Introduction

The mountain pine beetle, *Dendroctonus ponderosae*, Hopk., is a native insect to the forests of western North America, and plays an important role in the dynamics of many pine ecosystems (Raffa 1988). While mountain pine beetles will attack most western pine species, its primary host throughout much of its range is lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.). In western Canada, where there is an abundance of lodgepole pine, the range of the mountain pine beetle is restricted by climate, and is confined by the mean -40 °C isotherm of the minimum annual temperature (Safranyik and Linton 1998). Consequently, populations in western Canada have historically been restricted to the southern half of British Columbia and southwestern Alberta. Over the past decade, a substantial shift in climatically suitable habitats for mountain pine beetle has been observed, and this shift has been followed by an expansion of populations northward and toward higher elevations (Carroll et al. 2004, Taylor et al. 2006). In British Columbia, the expansion of climatically suitable habitat, together with the change in natural stand conditions that have resulted from forest management practices, have contributed to populations reaching unprecedented epidemic levels in recent years. Mortality to lodgepole pine due to mountain pine beetles has doubled yearly in British Columbia since 1999, and during 2001 and 2002 both the rate of spread and the attack intensity increased (BC Ministry of Forests 2003, 2004; Westfall 2006) (Fig 1). The epicentre of the current outbreak, which stretched across an area of 8.4 million hectares as of 2005, is located in the west-central interior of British Columbia (Westfall 2006). There is a growing concern that climate change will allow the mountain pine beetle to move into the vast expanses of jack pine (*Pinus banksiana* Lamb.) west of the Canadian Rockies, and lodgepole pine in northern Canada (Ayres and Lombardero 2000, Logan et al. 2003, Carroll et al. 2004).

The movements of mountain pine beetle (and other bark beetles) associated with host finding below the forest canopy has received considerable attention (e.g., Chapman 1962, Gray et al. 1972, Byers 1988, 2000; Safranyik et al. 1989,1992; Turchin and Thoeny 1993). Movement above the canopy, while being recognized as a potentially important component to landscape level patterns of infestation, especially during epidemics, has not been as well studied. In the present study, the movement of mountain pine beetles above the canopy in the central interior of British Columbia was investigated using aerial capture and doppler weather radar.

The mountain pine beetle is a univoltine species with a relatively well-defined period during which maturation of new adults, emergence and flight occur. The onset of the emergence and flight period is generally preceded by warm, dry weather (Safranyik et al. 1999). Emergence in a region normally occurs over a 7- to 10-day period, and field observations have shown that the greatest catches of flying beetles typically occur when the daily average temperature is greater than 20°C for at least three consecutive days (Safranyik and Linton 1993). In British Columbia, peak emergence and flight usually occur in mid-July to early August. Mountain pine beetles are able to fly at speeds of up to 2 $m\ s^{-1}$ (Rudinsky 1963), which would limit dispersal to only a few kilometers, unless their flight is aided by wind. It is believed that convection, which predominates during fair weather conditions typical of the emergence and flight period, may carry some beetles above the forest canopy to be passively transported over long distances by the mean wind within the atmospheric boundary layer (Safranyik et al. 1989, Furniss and Furniss 1972). Evidence for this includes anecdotal accounts of the fallout of mountain pine beetles over lakes (L. Safranyik, personal communication 2005) and the observation by a helicopter pilot of mountain pine beetle at 1500 m above sea level (approximately

900 m above ground level) over the central interior of British Columbia (K. White, personal communication 2005). Further evidence includes the work of Furniss and Furniss (1972) who collected scolytids, including mountain pine beetles, in snowfields high above the timberline in Oregon and Washington, many kilometers from the nearest host trees. During an outbreak in southeastern British Columbia, southwestern Alberta, and northern Montana in the 1980s, mountain pine beetles were found 200 to 300 kilometers downwind of the infestation location over the prairies in residential and park pine trees (Cerezke 1989). In Norway, Nilssen (1984) used a different approach by deploying decoy logs in the landscape far removed from sources and found bark beetles attacking logs from 10 km to as far as 86 km away from spruce hosts. Safranyik and Carroll (2006) postulate that the mountain pine beetle attack discovered in the Peace River region of northeastern British Columbia in the early 2000s was likely the result of long-range transport from the areas of central British Columbia undergoing the current epidemic, several hundred kilometers away. Aukema et al. (2006) analysed the spatiotemporal development of the present infestation in British Columbia. They found that the eastward spread of the epidemic from the North Tweedsmuir Park across the center of the province was consistent with dispersal, presumably by long-range transport. They did not, however, discount the potential importance of the buildup of localized populations, especially in southern British Columbia. Taken together, these observations suggest that mountain pine beetles are able to undergo long-range transport, aided by the wind.

Glick (1939) was an early researcher to mount nets on airplanes, but in 1007 hours of flight, he caught only 62 scolytids over forested areas in Louisiana. At the time, according to Furniss and Furniss (1972), Glick's captures, along with two specimens caught in kite traps by Terrell (1934), constituted all bark beetles that have been captured in flight high above a forest. Safranyik et al.

(1992) attempted to trap mountain pine beetles above the canopy using a tethered balloon and a marked release/capture approach in a natural forested setting. However, beetles were only captured below the dominant crown height. Based on the vertical distribution of captured beetles, they estimated that 0.2% and 2.4% of marked and unmarked beetles, respectively, were dispersing above the canopy; however, since no beetles were actually captured above the canopy, the result relies on extrapolation and is, therefore, somewhat uncertain. Their estimate was for a small population under non-epidemic conditions. The fraction dispersing above the canopy under the current epidemic conditions would likely be larger as the availability of local host trees is depleted. Forsse and Solbreck (1985) had similar experiences in attempts to capture *Ips typographus* L. in flight above the canopy and used extrapolation to estimate that roughly 10% of the population may fly above the forest canopy.

Since the first introduction of radars to the field of operational meteorology, echoes from the clear-air atmosphere, i.e., free of cloud and precipitation, have been observed. It has been determined that insects are the primary cause of boundary layer clear-air returns and entomological radars have since been developed to exploit this property. For example, Chapman et al. (2005) used elevated ground-based traps and entomological radar to document the mass aerial migration of the carabid beetle *Notiophilus biguttatus* over agricultural land in the UK – a species previously regarded as having poor dispersive abilities. The authors hypothesise this may be a recent adaptation to an increasingly fragmented habitat. Nieminen et al. (2000) used Doppler weather radar in combination with tow nets as well as suction and light traps and trajectory analysis to study the mass-migration of aphids in Finland. They found that the Doppler weather radar was very useful in determing the movement of insects during migrations. Little is still known about bark beetle dispersal above forest canopies, since they are very small, and therefore difficult to observe over long distances. The use of radar may offer an excellent tool for studying long-range bark beetle dispersal.

Immediately prior to the summer of 2004, the addition of a Doppler weather radar to Environment Canada's weather radar network near the epicentre of the current bark beetle outbreak in British Columbia, provided an opportunity to look for evidence of mountain pine beetles undergoing wind-borne movements above the canopy. During the beetle emergence period of 2004, the observation of daytime clear-air (i.e., non-meteorological) radar returns characteristic of insect plumes led to the current project. The purposes of our study were: 1) to determine whether the clear-air returns observed on the meteorological radar during the mountain pine beetle emergence period were indeed generated by airborne bark beetles; 2) to verify that, as indicated by the radar returns, mountain pine beetles fly well above the forest canopy during the emergence period; and 3) to determine the vertical distribution of mountain pine beetles above the forest canopy. The data gathered during the current study will also be used as input to numerical models of mountain pine beetle long-range movement being developed in concurrent projects.

Materials and Methods:

Emergence observations

Eight lodgepole pine trees infested by the mountain pine beetle were selected from a forest stand in Prince George near the University of Northern British Columbia (UNBC) (53° 53' 36" N latitude, 122° 48' 53" W longitude) (Fig.1). Four of the trees were within the forest and four were at the forest edge. Each group comprised trees clustered within approximately 10 m of each other. To facilitate the observation of mountain pine beetle emergence holes, a patch of white outdoor latex paint, 125 cm high by 20 cm wide, was painted on the east and west sides of each tree. The patch on the east side of the tree was situated to maximize exposure to sunlight and daytime heating. Starting on 18 June 2005, new mountain pine beetle emergence holes were counted and marked on a daily basis, usually during the evening hours when emergence activity was low. The daily emergence counts were continued throughout the 2005 mountain pine beetle emergence period, ending on 8 August 2005.

Radar

The Prince George Doppler Radar is located approximately 40 km southwest of Prince George, on a volcanic plug named Baldy Hughes, approximately 425 m above the surrounding terrain of the central interior plateau of British Columbia at 53° 37’ N latitude, 122° 57’ W longitude (Fig.1). The radar was installed in the late winter of 2004. It is a 250 kW C band radar that transmits from 5450 to 5825 MHz from a 5.5 m antenna with a nominal beam width of 1.1 degrees. The radar transmitter operates in continuous scanning mode, rotating continually in azimuth with the beam elevation angle changing after each horizontal scan. The radar is designed to detect hydrometeors, and using the Doppler capabilities it computes the radial wind velocity for the purposes of weather warning and forecasts. During periods without precipitation, clear-air returns usually associated with insects or birds can be detected.

The radar data used are from a nominal 0.5 degree elevation angle plan position indicator scan. Since the emitted radar beam also curves to partially follow the curvature of the earth due to temperature changes with height in the atmosphere, the radar beam is at the following approximate heights above the radar: 200 m at 20 km distance, 500 m at 40 km distance, 800 m at 60 km distance, 1 100 m at 80 km distance and 1500 m at 100 km distance. The radar data are available at 10-minute intervals and constitute a very large dataset which can be difficult to interpret and present. In order to summarize and synthesize the radar clear-air returns over the mountain pine beetle emergence and flight period, all of the daytime radar images (between 0700 and 2100 PST) during the mountain pine beetle emergence period from late June until early August were viewed. The clear-air return radar intensity for each day was subjectively categorized onto a three-point scale as low (1), moderate (2), or high (3). The categorization was based on a combination of the following factors: the strength of the radar reflectivity signal, the altitudinal extent of the clear-air returns, and the length of time during the day the clear-air returns persisted. The factors tended to be correlated: clear-air returns lasting a long time also tended to have high signal strength and altitudinal extent. The purpose of the categorization was to be able to compare the synthesized radar data with mountain pine beetle emergence, capture, and weather data to see whether any associations are apparent.

Boundary Layer Characteristics

In order to assess the characteristics of the atmospheric boundary layer that the mountain pine beetles were emerging into and being transported by, data from afternoon (approximately 1530 PST) radiosonde observation of Environment Canada’s Prince George Aerological station were used. The Prince George Aerological station is located at 53° 54’ N latitude, 122° 48’W longitude in the city of Prince George with a base elevation of 601 m above sea level. The radiosonde data are balloon-borne measurements of temperature, humidity, pressure, altitude and wind that are collected twice daily for weather forecasting purposes.

Aerial sampling apparatus

Following the method of White (1970), a drogue-net apparatus was constructed and attached to a Cessna 172 aircraft and used for the aerial capture of insects. The net apparatus comprised a 110 cm long conical nylon net attached at its open end to a 38 cm diameter steel ring. The ring and net were attached to the aircraft's right-hand-side wing strut with a 244 cm length of 3.2 mm aircraft cable (Fig. 2). The net could be deployed and retrieved in flight through the passenger door using a nylon cord attached to the net ring. Before the net was deployed, a sheet of letter size (8 ½” x 11”) writing paper, loosely crumpled into a ball, was placed into the net to provide the captured insects with shelter from the airstream, thus minimizing damage to the collected specimens.

Based on drag measurements and momentum analysis of different nets, the sampling efficiency of the drogue-net used was estimated to be 82%, i.e., 82% of the incident airstream passed through the net material, with the remainder diverted around the outside. This efficiency was used to estimate the airborne insect density given the amount of air sampled and the number of insects caught.

Aerial sampling procedure

The aerial capture flights were planned to take place during the annual peak emergence period, which typically occurs in mid-July to early August. Information from the concurrent emergence monitoring was used to determine more exactly when the 2005 mountain pine beetle emergence had begun. Since emergence appears to be triggered by specific patterns of maximum daily temperature and barometric pressure (Safranyik and Carroll 2006), weather forecasts were used to determine the days on which the aerial capture flights would be launched.

Sampling was performed over a 35 km-long transect located approximately 25 km southwest of Prince George, BC, between West Lake, 53° 44’ N latitude, 122° 52’ W longitude and Punchaw Lake, 53° 25’ N latitude, 123° 01’ W longitude (Fig. 1). The transect had an approximate north-northeast to south-southwest orientation and was located just east of the Baldy Hughes radar site, where the Doppler radar was situated. The surface elevation below the transect varied between 700 m and 900 m above sea level. Sampling periods were 15 minutes long and were flown at true airspeeds from 108 km/hr to 126 km/hr at altitudes from 850 m to 2000 m above sea level (100 m to 1200 m above ground level). Sampling at the lowest altitude was done following the elevation of the terrain, approximately 100 m to 200 m above the forest canopy. For clarity of presentation, altitudes will generally be reported above ground level, assuming an average minimum terrain elevation of 800 m above sea level, except when elevation above sea level makes most sense – as in reporting meteorological values.

The samplng runs proceeded in the following manner. Once stabilized on altitude and airspeed, a net was deployed and the sampling transect flown for a 15 minute period. At the end of the sampling period, the net was retrieved, removed from the steel support ring, and its open end was quickly tied in a loose knot. The net was then sealed in a numbered plastic bag. The aircraft was stabilized at a new altitude and the process repeated, flying the transect in the opposite direction. Typically, sampling was started at a minimum safe altitude above the forest canopy, then it was increased in 150 m increments for each transect leg until flight was above the top of the insect layer, determined when insects were no longer being caught. The sampling altitude was then decreased in 150 m increments down to the minimum safe altitude. At the beginning of each sampling period, sampling altitude, outside air temperature, indicated airspeed, time-of-day, and sample bag number were recorded. The recorded altitude represents an average, as up- and down-drafts caused the aircraft to fluctuate considerably (up to ± 100 m) around the nominal altitude. Following each flight, the captured insects were removed from the nets and stored in a freezer until counted and identified.

Results

Observed Emergence and Radar Intensities

The observed mountain pine beetle emergence from the eight representative lodgepole pine trees during the summer of 2005 is shown in the top panel of Fig. 3 along with a subjective categorization of radar intensity. The beetle capture rate on each flight day, observed maximum daily temperature, average daily sea-level pressure and 500 hPa heights during that period are also shown. These data indicate a well-defined mountain pine beetle emergence period between 17 July and 4 August, with the three most significant emergence days on 17, 22, and 26 July. Radar intensity tends to be in the "high" category on days of peak emergence (i.e., intensity level 3 in Fig. 3). The data also confirm the correlation between the mountain pine beetle emergence and peaks in the air temperature, decreasing mean sea level pressure and the presence of a mid-tropospheric (500 hPa) ridge across the area indicated by peak values in 500 hPa height in the bottom panel of Fig. 3.

The clear-air radar returns believed to be of biotic origin and of interest to us can be easily differentiated from precipitation returns. Specifically, the insect returns are concentrated near the center of the radar image (i.e., at lower altitudes), and do not display organized large-scale movement since they represent reflection of the radar beam from insects within the volume of air sampled by the radar beam. The insects exist up to a certain altitude in the atmosphere that is indicated by the radial distance from the radar location since the radar beam altitude increases with radial distance. This can be seen in Fig. 4, which depicts mountain pine beetle radar signatures on the five aerial flight dates on which mountain pine beetles were captured.

Visual inspection of all the radar imagery over this period indicated two distinct peaks of clear-air returns typically occured in the daily cycle, one during daylight hours (samples of which are shown in Fig. 4) and one at night (not shown). The nighttime cycle typically developed between 2000 PST and 0600 PST, and we assumed that these were generated by nocturnal insects. The strength of these returns was not as great, and maximum altitudes not as high, as those seen during the daytime period. This would be expected, since the atmospheric boundary layer is shallower and more stable at night. The typical radar signatures believed to be generated by airborne mountain pine beetles during daylight hours were seen on radar images starting at 0900 PST, peaking at 1300 PST, and ending around 1700 PST.

Inspection of the original radar backscatter images for the entirety of each of the daytime cases (samples are shown in Fig. 4) revealed two types of non-meteorological radar returns: the first type were relatively low intensity returns that were mostly of uniform intensity and clustered around the radar, indicating a relatively shallow altitudinal extent. These returns are most clearly associated with insects. The second type were less homogeneous with narrow bands of relatively strong returns woven throughout the overall area of radar returns and occuring at a further distance from the radar and therefore at higher altitudes. Several of these bands of stronger returns appeared to be related to convergence zones due to the interaction between the synoptic wind field and topographic features, mostly to the west and south of the radar site. This can be clearly observed on 3 and 4 August (bottom panels of Fig. 4), and it seems that those returns were either caused by localized convergence or swarming of mountain pine beetles, or possibly by some other particle or aerosol being carried aloft by the horizontal wind convergence in those zones, which are quite high in the atmosphere. At a horizontal range of over 60 km they are over 800 m above the radar. Since the radar is at 1128 m above sea level, this places those higher returns at approximately 2000 m above sea level where temperatures on August 3 and 4 were about 10 ^{o}C, and about 6 ^{o}C on 2 August. These are lower than the temperatures at which any mountain pine beetles were captured.

The radar returns that were more uniformly distributed and therefore more obviously caused by insects, tended to be below about 300 to 600 m above the radar elevation, or 1400 to 1750 m above sea level. The terrain elevation in the area covered by the Baldy Hughes radar varies between 600 m to 900 m above sea level, indicating the possibility that, during their emergence, mountain pine beetles can be found as high as 1150 m above the forest canopy. Based on the radiosonde data, temperatures at these maximum altitudes of insect return consistently ranged from 12.5 to 14.3 ^{o}C, with warmer temperatures below these heights. The aerial capture data were consistent with the radar data – mountain pine beetles were found as high as 876 m above ground level, verifying the radar indications of mountain pine beetle presence at those altitudes. There were no insects captured above the maximum altitudes of clear-air returns determined from the radar images. The 2 August aerial capture date had the lowest number of mountain pine beetles captured. The radar indicated insect returns at the lowest maximum altitude on this date (530 m above ground level where the temperature was 12 ^{o}C), and this also corresponded with the coldest temperatures based upon the radiosonde data.

Atmospheric Boundary Layer

The wind, temperature and humidity characteristics below 2500 m above sea level are presented in Fig. 4, along with the aerial capture and radar data for each of the five capture dates. It can be seen from the temperature profile each day that the atmosphere is convective. This can be inferred from the atmospheric lapse rate which is “dry adiabatic”, cooling at about 9.8 ^{o}C per km increase in altitude. Under these conditions the lower part of the troposphere is well-mixed by thermal plumes, which are driven by intense solar heating of the surface. The mixing on most days occurs through much of the troposphere, well above the 2500 m above sea level height displayed in Fig. 4. The wind speeds within the layer in which mountain pine beetles were captured ranged from 3 to 10 m s^{-1} with typical values of 5 m s^{-1}. Wind directions were typically from southerly through westerly, although low level winds on 4 August (Fig. 4e) were easterly.

Aerial Capture

Aerial capture flights, totalling 19.5 hours of sampling time, were conducted from 13 July 2005 to 4 August 2005. Flights that captured mountain pine beetles occurred on 17 July, 26 July, 2 August, 3 August and 4 August, with the average beetle capture rate on each day summarized in the second panel of Fig. 3. In total, 115 mountain pine beetles were captured over all flights, in addition to approximately 20 other insects as well as parts of insects that could not be identified as mountain pine beetles.

The altitude distributions of mountain pine beetle density captured in flight are presented with corresponding atmospheric characteristics and radar images from the flight times in Fig. 4. The mountain pine beetle density is the number of mountain pine beetles caught at a given altitude, sometimes over more than one sampling period, divided by the total volume of sampled air, and is expressed as the number of mountain pine beetles per gigaliter (1 gigaliter equals 10^6 m^3). The volume of sampled air is calculated from the true airspeed, inlet area of the net, estimated net efficiency, and sampling period. Fig. 5 shows relationships between the absolute and relative density of mountain pine beetles captured with elevation, temperature and time of day. While there is considerable variability, it can be seen that, on average (Fig. 5b), the density of mountain pine beetles captured is highest close to the canopy top and decreases with altitude above the canopy. The highest altitude at which mountain pine beetles were captured was at 876 m above the nominal ground elevation of 800 m (Fig. 5 a, b). The density of mountain pine beetles caught tended to decrease with temperature (Fig. 5 c, d), with the highest density in a given flight occurring at the warmest temperature for that flight. The 3 August flight was the only exception to this, having the highest capture at the third highest temperature and third lowest altitude. For the 2005 flights, the highest average capture rate was for temperatures between 18 and 19 °C – although this is biased by the large capture on 26 July. There were no mountain pine beetles caught at temperatures lower than 11 °C. Since the atmospheric temperature decreases with altitude (Fig. 4), this is consistent with the decreasing mountain pine beetle density with altitude discussed previously. The highest capture rate and mountain pine beetle densities tended to occur later in the afternoon (Fig. 5 e, f).

Comparing the mountain pine beetle capture data with the emergence from the eight sample trees, the maximum capture of mountain pine beetles occurred on 26 July, the day of the third largest peak in the observed emergence. Aircraft scheduling conflicts precluded a flight on 22 July, the day of the second peak emergence from the trees. The capture flight on 17 July, the day of the largest observed emergence, yielded only a small number of insects. A correlation between the density of captured mountain pine beetles and the subjective radar echo intensity is evident in the top panel of Fig. 3. However, the captured mountain pine beetle density on 26 July is an order of magnitude larger than on the other days, although that relative difference is not readily apparent in the corresponding radar images (Fig. 4b versus the other panels in this figure). The full set of radar images from 17 July shows bands of high return strength in the area near the emergence observation site, corresponding to the largest observed emergence peak at UNBC. The images from 26 July show bands of high return strength in the area of the aerial capture transect, although it is difficult to spatially compare the radar data with the aerial capture data since the radar beam altitude increases with distance from the radar and the radar beam is sampling a volume of the atmosphere that also increases with distance.

Discussion

Migration results in relocation, and perhaps also aggregation or dispersal, of a population. Insects move when their habitat is becoming unsuitable due to a lack of food resources, mating possibilities, territories and suitable domiciles, or from the need to escape the local build-up of parasites and predators (Ricklefs 1990). Migratory and vegetative movements often overlap, so that the same insect may undertake both migratory and vegetative flights (Dingle 1996). The phenomenon of wind-borne migration has evolved independently in several insect orders, and is now believed to be more prevalent than originally thought (Byrne 1999). Other bark beetles have been found to be good dispersers that can cover distances of many kilometres in flight (Botterweg 1982, Forsse and Solbreck 1985, Jactel and Gaillard 1991). It therefore seems highly likely that mountain pine beetles undergo wind-borne transport above the canopy. This is supported by the limited indirect observations for this species discussed in the introduction, and is confirmed by the direct evidence from aerial capture and from radar observations in the present study. However, it is still not clear whether these movements are behavioural, or simply the result of random meteorological interactions – insects being carried aloft by thermals. In either case, it is reasonable that the frequency of above-canopy transport would be greater during an epidemic, both because of the increased pressure on resources (behavioural), and simply because of the large number of beetles emerging across the landscape in convective conditions (random). In any case, the results of the aerial capture and radar analysis in the present study both support the theory that mountain pine beetles can undergo long-range transport, aided by wind within the planetary boundary layer.

Our emergence monitoring from eight lodgepole pine trees at UNBC corresponded well with the aerial capture data, with the exception of 17 July when, based upon the emergence peak on this date, we would have expected a higher aerial capture rate. Since the trees used to observe the mountain pine beetle emergence were approximately 25 km distant from the location of the aerial capture transect, it is possible that local variations in peak emergence timing may account for the disparity. It is also likely that insects caught flying in the atmospheric boundary layer would have originated from even further away from the emergence monitoring location so that variations in peak emergence timing would be even greater.

During periods of mountain pine beetle emergence and flight (i.e., warm summer afternoons), the atmospheric boundary layer is typically well-mixed and convective – in other words, it is conditioned by atmospheric instability and “thermals” arising when intense solar radiation warms the surface. Typical depths of this layer under these conditions range from 1000 to 3000 m above ground level, depending mostly on the background atmospheric stability and intensity of the surface solar heating. Under these conditions, it is expected that passive particles would be well-mixed in this layer. If mountain pine beetles are carried into this layer, and fly with sufficient vigor to behave as neutrally buoyant particles, they too should be uniformly distributed within the layer. However, this is not what the present study has found: mountain pine beetles were observed, both by direct capture (Figs. 4 and 5) and with radar (Fig. 4) to concentrate in the (warmer) layers closer to the canopy. This may be due to a response to temperature. Most observations of mountain pine beetle flight within the tree canopy indicate a preference for flight when temperatures are between 22° C and 32° C (Safranyik 1987). The present study also found generally increased capture of mountain pine beetles with warmer temperatures (Fig. 5 d). Since the atmosphere cools with height at the dry adiabatic lapse rate (9.8° C km^{-1}) under convective conditions, and mountain pine beetle flight and activity has been found to be related to air temperature (e.g., Safranyik and Linton 1993), it seems likely that mountain pine beetles may limit their maximum altitude through a sensitivity to temperature by folding wings and dropping to lower and warmer altitudes when conditions become too cold. Recent work by Geerts and Miao (2005), who studied the vertical flight behaviour of other insects in the convective atmospheric boundary layer using Doppler radar, revealed that insects do not passively ride updrafts, but rather oppose them at a rate proportional to the updraft strength. This could result in insects “riding” the updrafts but maintaining an approximately constant altitude while they are advected by the mean wind. It therefore seems likely that mountain pine beetles are responding to temperature by dropping to lower altitudes when updrafts move them to temperatures which are too low, as was hypothesized by Geerts and Miao (2005) of other insects.

Flight mill studies of the European spruce bark beetle *Ips typographus* indicate that this species is able to fly up to 6 hours and 20 minutes, although 90% of the beetles flew for less than 2 hours and

30 minutes (Forsse and Solbreck, 1985). Atkins (1961) found that strong individuals of the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopk.) flew up to 8 hours uninterrupted and the southern pine beetle (*Dendroctonus frontalis* Zimm.) up to 6 hours. It seems likely that beetles undergoing passive transport in the midst of updrafts from thermals would expend less energy than beetles on a flight mill and so should be able to remain airborne for longer periods. It is also possible that mountain pine beetle flight is interrupted by periods of rest that would therefore extend the total duration of flight. In the absense of specific information on the flight duration for mountain pine beetles undergoing passive transport, we assumed an average flight duration of 4 hours with a standard deviation of 2 hours for illustrative purposes. We also used the average wind speed between 900 and 1500 m above sea level (approximately 100 to 700 m above ground level) from the five cases shown in Fig. 4 of 4.8 m s^{-1} with a standard deviation of 1.3 m s^{-1}. By multiplying the flight duration by the speed, an estimate of the flight distance is 69 km with a standard deviation of 39 km for the 2005 cases. Since the wind direction is predominantly from the southwest to the west, the wind would move most mountain pine beetles flying above the canopy in an easterly to northeasterly direction between 30 and 100 km (mean distance ± 1 standard deviation). The transport distance could be even greater on days with stronger winds than those found in 2005, and if mountain pine beetles are able, on average, to fly for longer than 4 hours. This transport distance is consistent with Hodgkinson (2005) who reported that between 1996 and 2001 the mountain pine beetles in the Vanderhoof forest district west of Prince George were dispersing approximately 65 km per year.

Based on the aerial collection data, it is possible to estimate the flux of mountain pine beetles undergoing passive transport in the atmospheric boundary layer as the density of beetles times the volume flux of air. In all cases except the 4 August case (Figure 4e in which one mountain pine beetle was caught above this height), mountain pine beetles were only caught below 1525 m above sea level, and assuming an average terrain height over the flight transect of 875 m above sea level, this results in a conservative flight depth of 650 m. The average wind speed in this zone for the five cases sampled is 4.8 m s^{-1} and the mean observed mountain pine beetle density is 761 mountain pine beetle per gigaliter (Figs. 4 and 5). An estimate of the flux of beetles per hour per 100 m of distance perpendicular to the wind direction can be calculated as:

F = 761 beetles/10^6 m^3 x 4.8 m/s x 650 m x 100 m/ 100 m x 3600 s/hour

F = 850 000 beetles per hour per 100 m distance perpendicular to the wind.

By using the 26 July data (the largest catch), with an average windspeed of 6.3 m s^{-1} and mountain pine beetle density of 2854 mountain pine beetles per gigaliter, the flux of beetles per hour per 100 m of distance perpendicular to the wind direction is estimated as 4.2 million. Another way of expressing the quantity of mountain pine beetles found to be undergoing transport above the tree canopy would be to consider the number of beetles per hectare of land surface that are undergoing long-range transport. For the average (maximum) cases, this can be calculated as 4950 (18 600) beetles per hectare. Given that approximately 40 beetles per square meter of bark (Raffa and Berryman 1983) are needed to successfully attack a pine tree and assuming a mean attack height of 17 m and a mean diameter of 27 cm (based on data collected near Norman Lake, British Columbia), approximately 577 beetles need to successfully attack a tree to induce mortality. If there are 4950 (18 600 maximum) beetles per hectare undergoing long-range transport at any given time, then this corresponds to 8.6 (32) trees of potential mortality per hectare. This is not a large number given that typical susceptible pine stands are at densities of approximately 700 stems per hectare. However, if one considers the possibility of aggregation of mountain pine beetles and concentration of them in time in a given area of forest by either pheromone-seeking activity or atmospheric convergence, then this number could be much larger. For example, if one assumes a mean wind speed of 4.8 m s^{-1} (6.3 m s^{-1} for the peak case) as above, there would be enough beetles to kill 1473 (7300) trees per hour per 100 m line perpendicular to the wind. If the average stand density of pine is 700 stems per hectare, then there would be enough beetles crossing a 100 m line to kill all the trees extending 210 (1040) m downwind (i.e., 2.1 (10.4) ha of pine) each hour. It needs to be emphasized that these are conservative upper limits, and assume that all mountain pine beetles will successfully take part in attacking a host tree.

Conclusions

A major conclusion of this research is that during mountain pine beetle emergence events, airborne beetles are present in the atmospheric boundary layer up to 800 m or more above the forest canopy. There they are exposed to relatively strong and consistent winds which facilitate long-range transport. Both the estimated heights from the radar returns as well as actual captures of mountain pine beetles at these altitudes verify this. We also showed that Doppler weather radar can be used to detect airborne mountain pine beetles during their emergence period. Since relatively few other species of insects were caught during the capture flights, it is reasonable to conclude that airborne mountain pine beetles were the major source of the daytime, clear-air radar returns we observed. The returns generally corresponded with the mountain pine beetle emergence periods observed from infested lodgepole pine trees. Conservative estimates of the likely distance of mountain pine beetle movement above the tree canopy indicate that typical movement distances of 30 to 100 km in a day are plausible. Estimates of the flux of mountain pine beetles indicate that the numbers are sufficiently high to be able to induce considerable tree mortality, making long-range transport a viable mode for the spread of the mountain pine beetle epidemic. Based on this, long-range transport should be considered in constructing decision support tools to evaluate mountain pine beetle spread.

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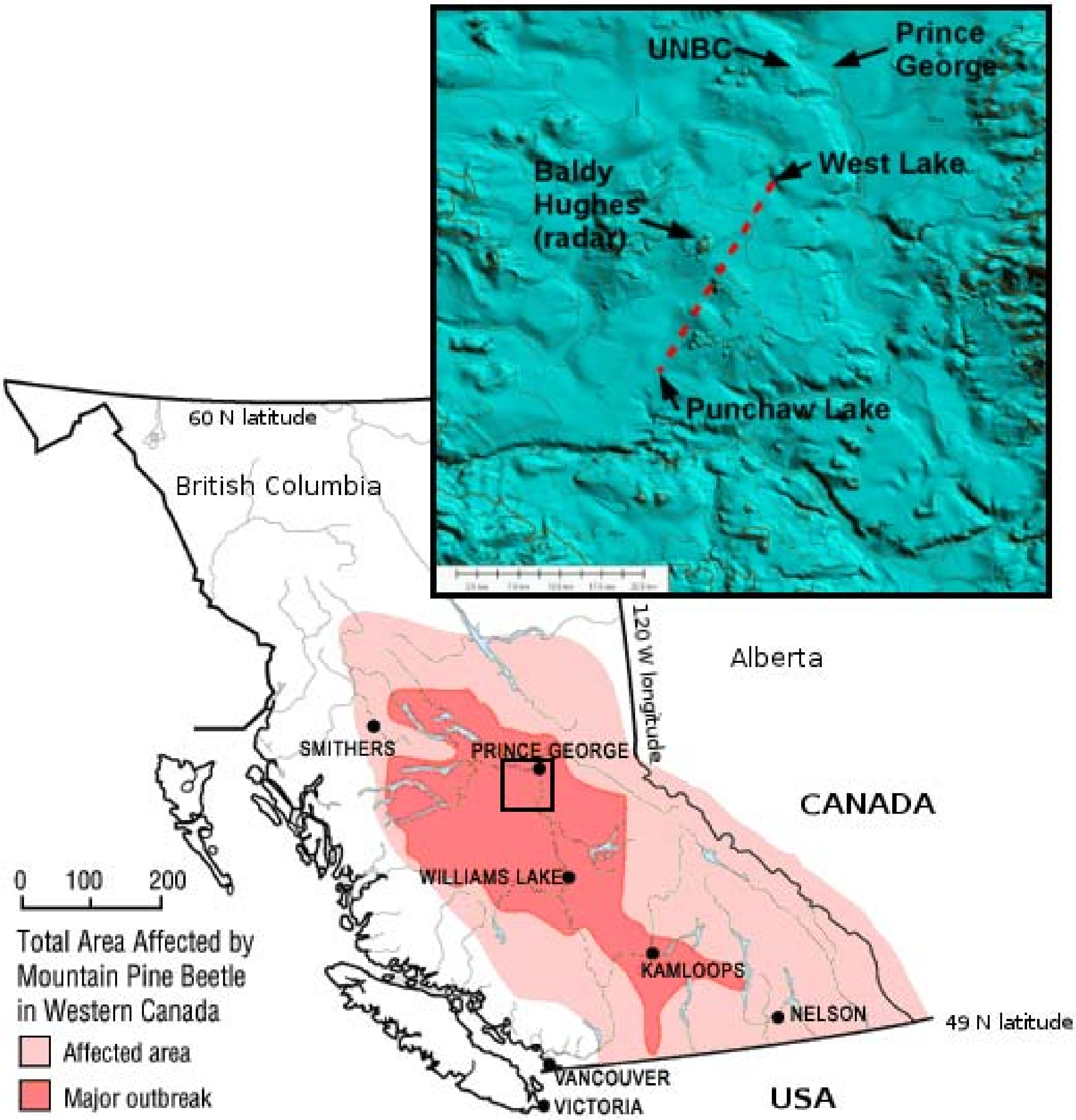

Figure 1. Mountain pine beetle infestation area in British Columbia. The rectangular area is shown in more detail in the enlarged inset map, which depicts topography as shaded relief with the dashed line indicating the flight track for aerial mountain pine beetle sampling. Infestation area map is from Natural Resources Canada, February 2005 at http://mpb.cfs.nrcan.gc.ca/images/mpbi-map_450_e.gif.

Figure 2. Deployed mountain pine beetle aerial capture net with mountain pine beetle killed “red” trees in the background.

Figure 3. SEE NEXT PAGE. 2005 Mountain pine beetle daily emergence hole count (number per 0.25 m^2) with subjective daily radar intensity (top panel). Aerial capture rate (number of beetles per hour of flight averaged over each flight day) is indicated by a histogram with the daily maximum temperature in the second panel. Sea level pressure and 500 hPa height are shown in the lower panels.

Figure 4. SEE FOLLOWING PAGES. Mountain pine beetle capture, meteorological and radar data for five flight dates in 2005 on which a significant number of beetles were caught. Each panel shows the vertical distribution of captured mountain pine beetle density (number per gigaliter), vertical profiles of wind, temperature and humidity from the Prince George radiosonde station (valid at 15:30 PST) and a radar backscatter intensity plot at a similar time. The mountain pine beetle density is from several capture flights on the same afternoon. Note that in b) the mountain pine beetle density scale has a much larger range than for the other days.

Figure 5. SEE FOLLOWING PAGES. Relationships between mountain pine beetle density and altitude, temperature and capture time for all of the flights in 2005 on which beetles were captured. The plots on the left (a,c,e) have absolute values of mountain pine beetle density in number per gigaliter, while the plots on the right (b,d,f) have relative mountain pine beetle density – the density divided by the sum of all densities for a given flight. Panels a,b show altitude above ground versus density. Altitude above ground is found by subtracting an average minimum terrain height of 800 m from the altitude above sea level. Panels c,d show the relationship between density and temperature. Panels e,f show the relationship between density and time of capture (Pacific Standard Time). The histograms shown in panels d and f indicate the capture rate (# of mountain pine beetles per hour) for the given temperature or time averaged across all flights.

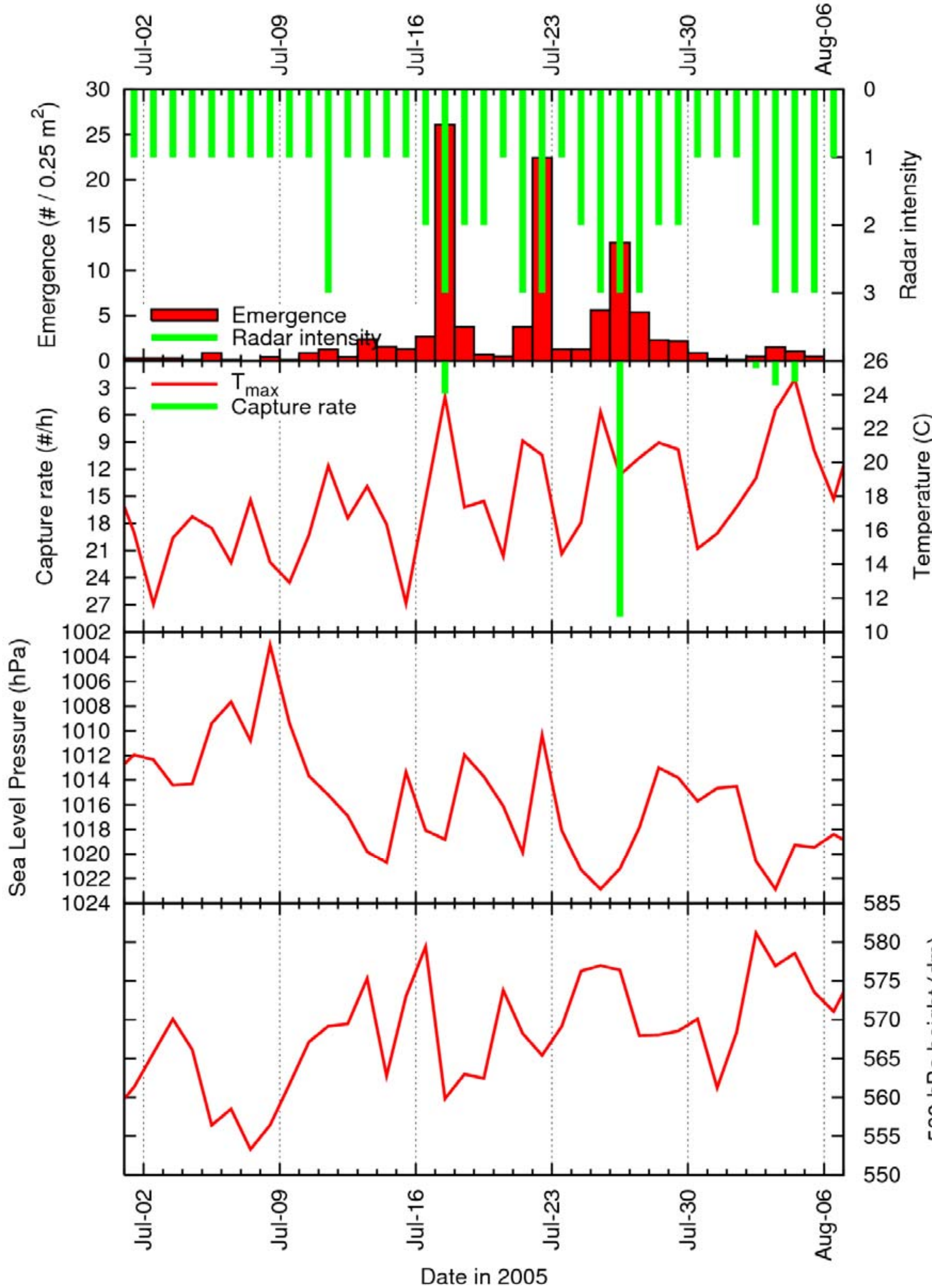

Figure 3. (see caption on previous page)

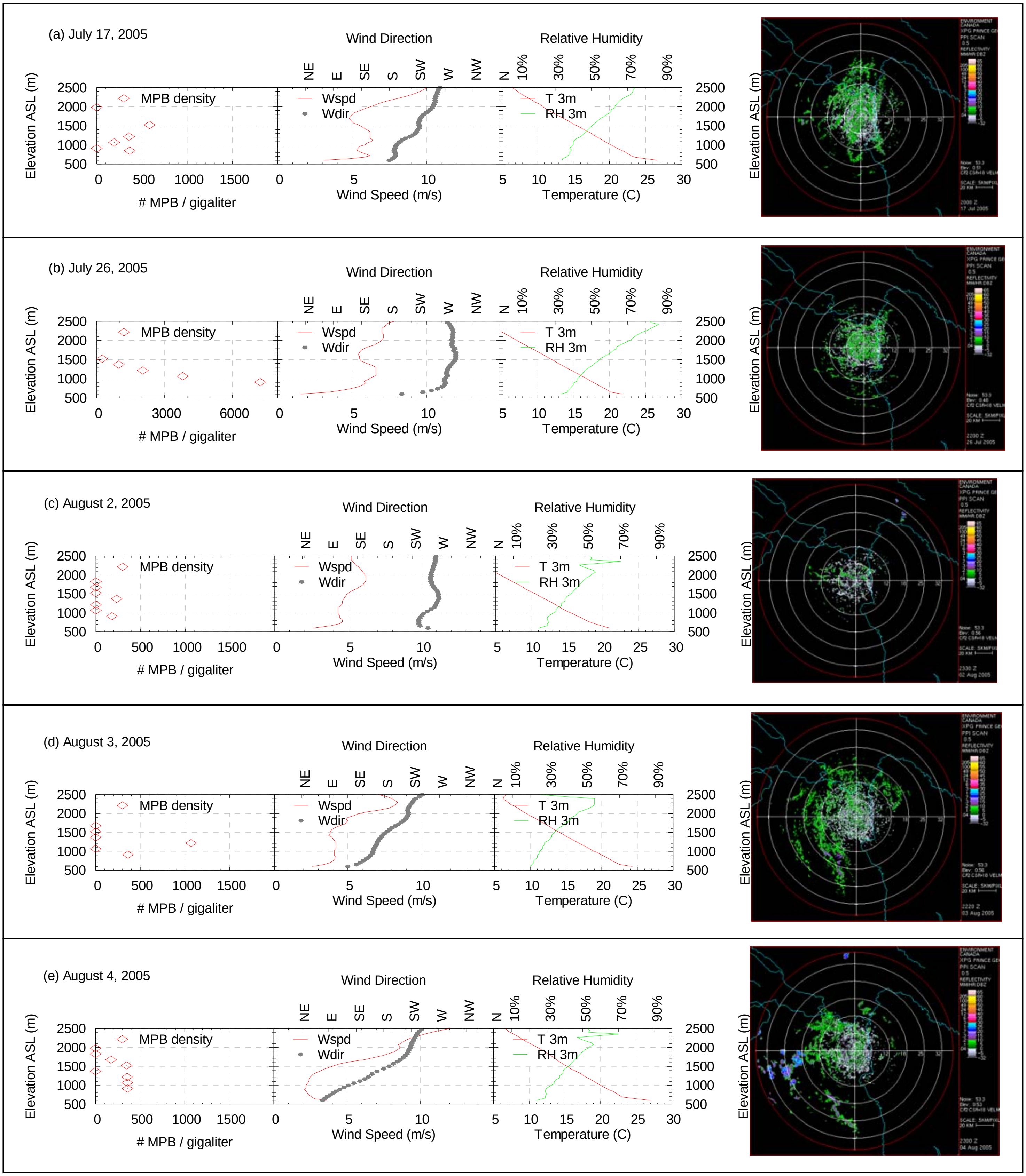

Figure 4. (see caption on previous pages)

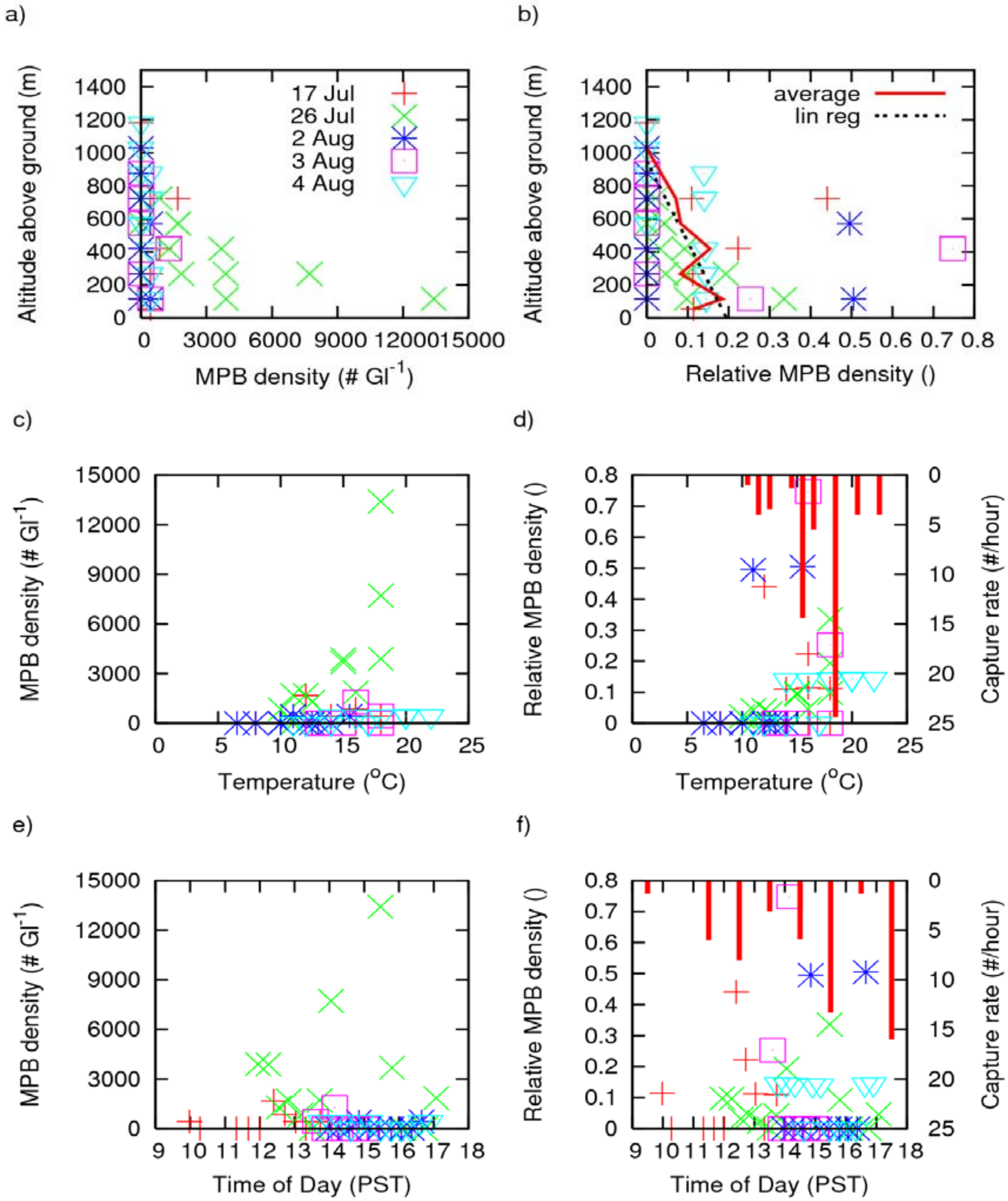

Figure 5. (see caption on previous pages)