

# Pollen dispersal by *Artemisia tridentata* (Asteraceae)

S. C. Laursen · W. A. Reiners · R. D. Kelly ·  
K. G. Gerow

Received: 26 July 2006 / Revised: 12 January 2007 / Accepted: 22 January 2007 / Published online: 17 February 2007  
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**Abstract** While the biophysics of anemophilous pollen dispersal is understood in principle, empirical studies for testing such principles are rare, particularly in native ecosystems. This paper describes mechanisms underlying the dispersal of *Artemisia* pollen in a Wyoming sagebrush steppe. The relationships between meteorological variables and pollen flux were defined during the 1999 *Artemisia* flowering season, and detailed processes at the individual plant level were experimentally tested in the field in 2000. Results indicated that *Artemisia* pollen presentation is continuous but with early morning maxima. Atmospheric pollen concentrations and potential dispersal rates are controlled at diurnal time scales by individual flower development together with characteristic changes in temperature/humidity and wind speeds, at multi-day scales by

frontal weather patterns, and at week-long scales by flowering phenology.

**Keywords** Aerobiology · Anemophilous · *Artemisia tridentata* · Pollen dispersal · Pollination ecology

## Introduction

Atmospheric transport of biological particles, particularly pollen, is a vital aspect of population, evolution, conservation, landscape and ecosystem ecology, of biogeography, and of allergology and plant pathology (Isard and Gage 2001). Whereas transport of diploid disseminules, both plant and animal, is important for demographic and distributional processes, transport of haploid pollen is vital to the maintenance of genetic heterogeneity and avoidance of inbreeding depressions within local populations across a plant species' range. A thorough knowledge of the effects of the scale, timing, duration, and intensity of micro-meteorological factors is critical to understanding the gene flow mediated by pollen dispersal. While the physics of anemophilous pollen dispersal is understood in principle, empirical studies for testing such principles are rare, particularly over diurnal intervals (but see: Ogden et al. 1969; Janaki Bai et al. 1981; Subba Reddi and Reddi 1984; Di-Giovanni et al. 1996) and especially in native ecosystems. Di-Giovanni and Kevan (1991) offer an extensive review of pollen dispersal within natural conifer stands and seed orchards. Many dispersal principles outlined in their review are equally appropriate to vegetation structures within a broad range of ecosystems.

Wind dispersal of airborne plant disseminules like pollen is a function of biological development of the disseminules, vegetation structure, turbulence, mean wind speed, topo-

S. C. Laursen (✉) · W. A. Reiners  
Department of Botany, Dept. 3165,  
University of Wyoming,  
1000 E. University Avenue,  
Laramie, WY 82071, USA  
e-mail: sclausen@earthlink.net

R. D. Kelly  
Department of Atmospheric Science, Dept. 3038,  
University of Wyoming,  
1000 E. University Avenue,  
Laramie, WY 82071, USA

K. G. Gerow  
Department of Statistics, Dept. 3332,  
University of Wyoming,  
1000 E. University Avenue,  
Laramie, WY 82071, USA

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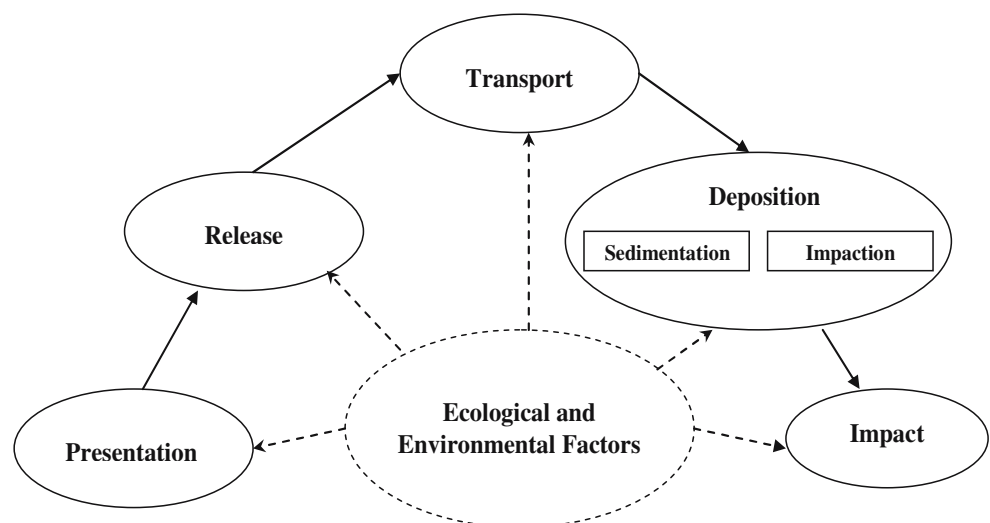
S. C. Laursen  
Wildlife Expeditions of the Teton Science Schools,  
P.O. Box 7580, Jackson, WY 83002, USA

graphic surface characteristics, and large-scale atmospheric motion systems. In this paper, “dispersal” refers to all the process leading to and resulting in movement of pollen. An inclusive “aerobiological process model,” applicable to the full range of aerobiota, consists of five stages (preconditioning, takeoff and ascent, horizontal transport, descent and landing, and impact), each of these being affected differently by multiple physical and biological factors (Edmonds 1979; Isard and Gage 2001). In the specific case of passively dispersed aerobiota like pollen, the stages are renamed as follows: presentation, release, transport, deposition, and impact (Fig. 1). “Presentation” is the point in floral development at which an anther dehisces and pollen grains are fully exposed to transport by wind or other vectors. “Release” (i.e. entrainment) is the removal of pollen grains from positions of rest by physical forces. “Transport” is the mass movement of pollen grains from a source area to a depositional locus (Isard and Gage 2001). “Deposition” includes the processes by which particulates are removed from the atmosphere to land or water surfaces. Deposition occurs through either sedimentation or impaction. Sedimentation is essentially gravitational settling (Chatigny et al. 1979; Di-Giovanni and Kevan 1991), while impaction results when a moving pollen grain strikes and is retained onto a stationary object (Di-Giovanni and Kevan 1991). “Impact” involves the evolutionary implications of species recognition and pollen tube growth when a viable pollen grain is deposited on an intraspecific stigmatic surface, resulting in successful fertilization. Alternatively, impact may involve the pollen grain’s role in nutrient cycling if it is not deposited on an intraspecific stigmatic surface or is unsuccessful in fertilization. Forces can re-entrain resting particles back through the stages of the aerobiological process model.

*Artemisia tridentata* Nutt. is an abundant native species within the sagebrush steppe ecosystem that characterizes much of the intermountain West. Covering  $44.8 \times 10^6$  ha, sagebrush steppe once occupied more area in North America than any other semidesert vegetation type (West and Young 2000). In spite of its geographic and ecologic importance, and the fact that it is an aeroallergen, little empirical data exist on pollen dispersal mechanisms in this genus, particularly within native ecosystems. Von Wahl and Puls (1989, 1991) observed diurnal patterns of pollen dispersal in *Artemisia vulgaris* in an urban setting surrounded by farmland. Munuera Giner et al. (1999) recorded *Artemisia* pollen concentrations from the top of a building in an urban setting far from pollen sources. Through novel methodology, the present study examines the factors controlling *Artemisia* pollen dispersal in its native habitat—an extensive area of sagebrush steppe.

The objective of this study was to determine the biological and meteorological factors controlling the presentation, release, transport, and deposition of *Artemisia tridentata* subsp. *wyomingensis* (Beetle and Young) pollen grains across a sagebrush steppe in central Wyoming, USA. More specific objectives of this research were to resolve the timing and magnitude of presentation events over diurnal periods and to determine if diurnal patterns of pollen release, transport, and deposition exist in the basin. Sagebrush steppe is an ideal system for this research because it features: (1) relatively simple and homogeneous vegetation for continuous canopy aerodynamic, pollen release, and deposition properties; (2) relatively flat terrain for adequate aerodynamic fetch requirements; (3) a copious source of pollen emanating from the vegetation over a defined time frame; and (4) a characteristically strong wind field.

**Fig. 1** The aerobiological process model for passively-dispersed biota. *Solid circles* enclose the five consecutive stages. *Boxes* represent the two modes by which deposition occurs. The *dashed circle* represents various factors affecting all stages. Adapted from Isard and Gage 2001



## Materials and methods

### Site description

The study site is located in the west-central portion of the Shirley Basin in south-central Wyoming (42°18'43–46"N, 106°33'25–28"W) at 2,200 m elevation. The site is on an erosion surface of Eocene alluvium. Featuring an extensive (10 km N–S, 30 km W–E), gently rolling surface having a maximum relief in the order of tens of m. Prevailing westerly winds traverse 16 km of flat, homogeneous terrain before reaching the study site.

Vegetation at the research site is dominated by *Artemisia tridentata* subsp. *wyomingensis* (Wyoming big sagebrush) (West and Young 2000; Knight 1994; Willson 1999). *Artemisia tridentata* subsp. *wyomingensis* has an average canopy height of 22 cm, and comprises the most significant roughness component within the vegetation canopy (Willson 1999). Numerous works describe the biology and ecology of big sagebrush (De Puit and Caldwell 1973; Campbell and Harris 1977; Doescher et al. 1990; Evans and Black 1993; Knight 1994; Laursen 2001). Other species among the sagebrush shrubs near the site are *Poa cusickii*, *Poa secunda*, *Koeleria macrantha*, *Phlox hoodii*, *Astragalus miser*, *Sedum lanceolatum*, *Mertensia humilis*, *Haplopappus acaulis* and *Elymus* spp. Botanical nomenclature follows Dorn (2001).

Average January high and low temperatures at this site are  $-1.7^{\circ}\text{C}$  and  $-15.7^{\circ}\text{C}$ , respectively; average July high and low temperatures are  $26.4^{\circ}\text{C}$  and  $7.4^{\circ}\text{C}$ , respectively. (Western Regional Climate Center, Shirley Basin Station 488192, (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wyshir>). The average high and low temperatures during the *Artemisia* September flowering season are  $20.3^{\circ}\text{C}$  and  $1.5^{\circ}\text{C}$ , respectively.

The average annual precipitation at the Shirley Basin WRCC site is 27.3 cm, with an average annual snowfall of 1.4 m. More than 40% of the basin's annual precipitation falls from December through May. Summer precipitation is rarely effective in recharging the soil profile to depths that significantly contribute to vascular plant growth (West and Young 2000), so that water availability becomes a limiting factor for plant processes in mid- to late summer (Knight 1994).

Wind data collected from 24 August to 20 October 1999 and 3 May to 11 October 2000 indicated prevalence of westerly winds over multi-day timescales, while highly variable wind directions and velocities associated with sharp fronts occasionally occurred for approximately 24-h periods. Daytime wind speeds over summer and early fall ranged over 3–12 m/s. Evening wind speeds were quite variable, often decreasing to less than 1 m/s on calm nights.

### Measuring pollen release, transport, and deposition

A pollen sampling array was constructed during the 1999 pollination season, 10 m away from an associated micrometeorological tower, to examine natural pollen concentrations over vertical gradients in association with meteorological variables during the flowering season. The array consisted of a primary tower 3.2 m high, and three, shorter validation towers, under 3 m in height, located at 30-m intervals along a N–S axis from the primary tower. This line of towers was perpendicular to prevailing winds.

### Sampling array

The micrometeorological tower was a 3-m mast bearing a microbarograph (Vaisala, Woburn, Mass., USA) at 1.0 m above ground, two thermocouples (Omega, Stamford, Conn., USA) at 0.8 and 3.2 m, a temperature and relative humidity probe (Campbell Scientific, Logan, Utah, USA) at 3.0 m, a wind vane (Met One Instruments, Grants Pass, Ore., USA) at 3.4 m, and four anemometers (Met One Instruments) at 0.8, 1.3, 2.1, and 3.2 m. A Rebs net radiometer (Campbell Scientific) was located SSW of the tower at 1.0 m above ground. These instruments logged meteorological data hourly during three diurnal sampling periods of 1999. For longer term site characterization, micrometeorological data were collected continuously from 24 August to 20 October 1999, providing pressure (1.0 m), net radiation (1.0 m), temperature (3.0 m), relative humidity (3.0 m), wetness (2.6 m), and wind speed (3.2 m) at 30-min intervals.

To determine *Artemisia* pollen concentrations, Rotorod samplers were used during sampling periods (Perkins 1957; Grinnell et al. 1961; Sampling Technologies, Minnetonka, Minn., USA). The sampling rate of each Rotorod was calibrated with a tachometer prior to field use; all performed within the manufacturer's specifications for sampling accuracy.

Measurement height was critical for estimating the height profile of pollen flux. The tallest sagebrush near the research site was 0.35 m to the top of its flowering stem, while the bulk of the vegetation was only 20 cm tall. Following guidelines from Mathias et al. (1990), the lowest meteorological sensors and pollen collectors were set at just over twice the maximum value for vegetation canopy height (0.8 m) in order to avoid the roughness sublayer (Isard and Gage 2001; Mandrioli 1998; Driese and Reiners 1997; Laursen 2001). This height was judged adequate considering the significant spacing between individual *Artemisia* plants and the minor disruption of airflow from the reproductive portion of the sagebrush.

Three Model 40 and two Model 20 Rotorod samplers were mounted to the primary pollen tower at heights of 0.8,

1.3, 2.1, 2.8, and 3.2 m. All Rotorod models were programmed to sample identically. Four of these Rotorods (0.8, 1.3, 2.1, and 3.2 m) were mounted at heights identical to the wind speed sensors on the nearby micrometeorological tower. In addition, the top and bottom Rotorod samplers in the pollen profile were mounted at heights identical to the temperature sensors. The three validation towers each held one Rotorod sampler, at 0.8 m, 2.1 m, and 2.8 m, respectively, corresponding to three of the sampler heights on the primary tower.

#### *Pollen measurements over diurnal periods in 1999*

In 1999, *Artemisia* began flowering at the site about 2 September and was in full bloom at the site by mid-September. Pollen and meteorological data were collected over three 24-h periods on 11–12, 17–18, and 25–26 September, representing early, mid-, and late periods within flowering season, respectively. For most of the experiment the Rotorods samplers operated 45 min out of each hour for each sample, allowing time to change pollen collection rods and record hourly concentrations. During the third sampling period, exposure times were varied from 20 to 105 min to ensure adequate sampling in varying wind speeds. For each sampling period, all the primary and validation rods had identical exposures over a given hour.

*Artemisia* pollen grains on the rotorods were counted under a compound microscope at 400× magnification, and the concentrations were calculated with standard methods, assuming collection efficiencies of 100% (Brown et al. 1993; Laursen 2001).

#### *Statistical methods*

Wind speed, temperature, relative humidity, and net radiation were considered as predictors in a multiple regression model, with  $\ln(\text{pollen concentration})$  as the response. We treated each pollen tower as an independent experimental unit for this exercise. For each sampling period, the data comprised hourly pollen concentrations from the primary pollen tower and each validation tower, with corresponding hourly values of wind speed, temperature, relative humidity, and net radiation from the micrometeorological tower. It was assumed that relative humidity and net radiation changed very little within the vertical and horizontal extent of the sampling area. A regression model was fitted separately to each tower and the resulting coefficients were considered as measurements on the experimental units. Means and standard errors of these across the four pollen towers were then calculated, treating the coefficients as measurements taken independently on each tower (i.e. in the usual “single sample of data” style). With this simple approach, observed variation among the

coefficients implicitly includes all sources and obviates the need to treat the temporal autocorrelation directly. See Allen et al. (1983), Allen (1983) and O’Brien (1981) for discussion of this approach in the analagous (measurements collected across time on independent subjects) context of analyzing growth curves. Since these predictors attend to different dimensions of pollen dispersal (wind speed to physical factors, temperature to biological, etcetera), we also report simple correlations (averaged across towers) for these predictors. All analyses were conducted using Mini-tab software, Version 13.1.

#### *Measuring pollen presentation and release*

##### *Sampling array*

Morphological development is a critical determinant of pollen availability for physical transport through the atmosphere. The 1999 field measurements were inadequate for evaluating anther development and dehiscence, since local wind speeds at plant surfaces depart from speeds recorded by anemometers only a few meters away. The 2000 field season was devoted to experimentally determining when anthers from individual plants expose pollen grains to the environment and their consequent rate of pollen exposure under varying environmental conditions.

To control for diurnal variation in ambient wind velocity and the coincident levels of turbulence, a physical apparatus was erected over individual plants having robust flowering stems and about half of their floral buds still closed. This ensured that the specimen had progressed well into flowering and would exhibit further bud opening. A three-sided sampling box (1.2 m high  $\times$  1.5 m  $\times$  1.5 m) was centered flush with the ground over plants with the open end facing downwind.

A 4-amp Dayton blower (1030 RPM; Electric Motor Warehouse, Burton, Mich., USA) was attached to an adjustable port so that it delivered a wind field directly to the plant in a downwind direction concordant with the ambient wind. The adjustable port was positioned 8 cm from the test plant and at an angle such that airflow directly impacted the reproductive shoots. The blower itself was enclosed to prevent ambient turbulence from entering the fan’s incoming air source.

The fan delivered a wind velocity of 18.3 m/s in the laboratory with a standard deviation of 0.12 when placed 8 cm from a wind speed sensor. This velocity was 2 m/s stronger than the highest wind speed recorded in the long-term 1999 micrometeorological data set. By delivering a stronger airflow than normally encountered in the field, the fan provided enough air velocity to entrain exposed pollen grains from the anthers upon completion of presentation.

To measure the entrainment of pollen grains into the generated wind field downstream of the test plant, a Rotorod sampler was positioned 16 cm downwind of the selected plant with rods rotating at the height of the flowering stems. An “ambient” Rotorod sampler was positioned 7 m crosswind of the chamber at 1.8 m above ground. Data from this ambient sampler determined whether the chamber was simply recording ambient pollen passing through the fan and the timing of local *Artemisia* pollen release.

The same meteorological variables as described for 1999 were recorded at appropriate heights. Precipitation was logged at 30 min intervals by a tipping bucket rain gauge (Meteorology Research, Altadena, Calif., USA).

#### *Pollen measurements over diurnal periods*

Two 30-h runs were conducted early and midway through the *Artemisia* flowering season (19–20 August and 2–3 September 2000). The same sampling and counting methods were used as in 1999, with all the samples being 45-min exposures for each hour.

## Results

Results of regional pollen release, transport, and deposition experiments in 1999

Typical fair weather diurnal cycles occurred before, during, and after the first sampling period (Fig. 2). This sampling period was, therefore, used as the base case scenario for the study site. Pressure steadily increased during the sampling period, precipitation was absent, and cloud cover was sparse during daylight hours. Net radiation, temperature, and wind speed values increased during daytime hours and decreased in the evening, while relative humidity displayed the opposite pattern. Wind speeds consistently increased logarithmically with height (Fig. 3a).

During the second and third sampling periods, fair weather diurnal cycles were interrupted by the passage of cold fronts (Figs. 4 and 5), presenting meteorological contrasts with the base scenario exemplified by the first sampling period. Atmospheric pressure remained fairly steady throughout most of the second sampling period and then dipped (Fig. 4a). While cloud cover was minimal during daylight hours on 18 September, net radiation was low throughout the following day indicative of cloud cover associated with the cold front (Fig. 4b). Temperature and relative humidity followed a typical diurnal pattern until passage of the front (Fig. 4c,d), when both temperature and pressure dropped sharply (Fig. 4c,a) and relative humidity jumped (Fig. 4d). Relative humidity remained near 100%

and temperature remained low over the next day and a half (Fig. 4d,c). Light rain occurred from 1930 to 2005 hours, about 2 h after the passage of the cold front. Wind speed increased throughout the sampling period, indicative of control by the frontal passage rather than by diurnal heating patterns (Fig. 4e).

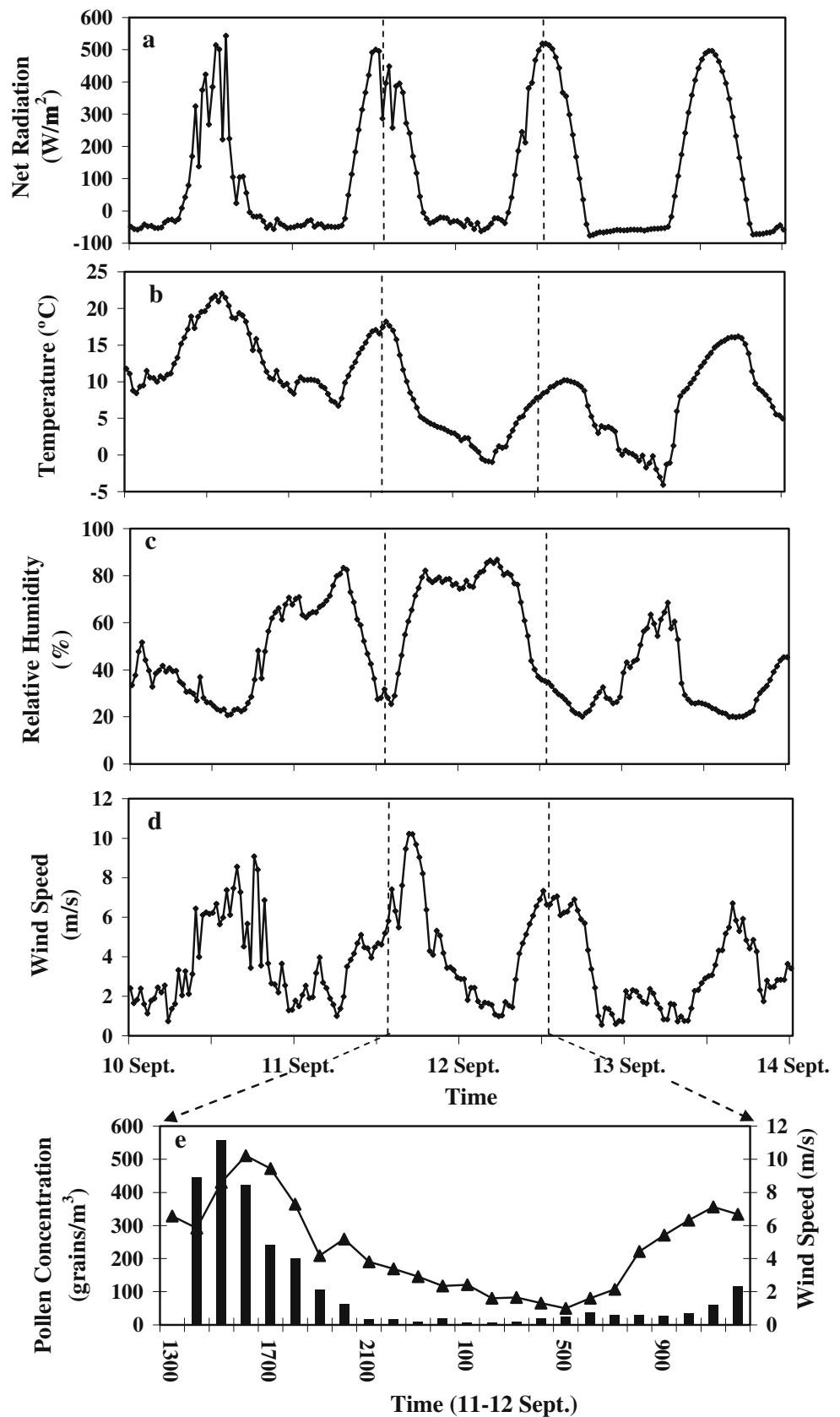
Likewise, a cold front passed through the site during the third sampling period at 2100 hours on 25 Sept. (see pressure trace in Fig. 5a), providing a second contrast with the fair weather conditions observed in the first sampling period. Temperature followed a typical diurnal pattern until the dramatic temperature drop at the arrival of a cold front and then remained low for 2.5 days before returning to pre-frontal values (Fig. 5c). Relative humidity followed a pattern inverse to temperature with a dramatic increase coinciding with the cold front passage superimposed on diurnal fluctuations (Fig. 5d). The higher relative humidity also remained for two and a half days following the termination of the sampling period. Wind speed followed a diurnal pattern similar to temperature, decreasing in the late afternoon, remaining low in the evening, and increasing only minimally the next morning (Fig. 5c). Wind directions were erratic after the frontal passage. Light snow fell from 1000 hours to 1118 hours and from 1243 hours to 1255 hours on 26 September, 12 h or more after the cold front passage.

During the continuous fair weather conditions of the first sampling period, hourly pollen concentrations at the primary profile tower varied diurnally (Fig. 2e; Laursen 2001), a pattern duplicated at all validation towers (Laursen 2001). Pollen concentrations were relatively high at the start of the sampling period, increased, then dramatically decreased into the evening hours. The concentrations remained low throughout the rest of the evening and into the next morning. By late morning and early afternoon pollen concentrations again began to increase.

As afternoon pollen concentrations increased on 11 September, the pollen height profile displayed an increasingly stronger positive vertical gradient (Fig. 3b), consistent with the wind speed profile (Fig. 3a). The strongest vertical gradient in pollen concentration was reached at 1600 hours on 11 September, and then decreased as pollen concentrations diminished into the evening, until there was essentially no vertical gradient by 0200 hours on 12 September. A vertical gradient in the pollen profile remained absent into the early morning hours, at the same time that concentrations decreased overall. The average vertical gradient again became slightly positive after dawn as concentrations also began to rise.

Statistical analysis of this first sampling period revealed that wind speed and temperature together formed the best model (by best-subsets analysis, using adjusted- $R^2$  and  $C_p$  criteria); the interaction of these two variables was then

**Fig. 2** 30-min averages of **a** net radiation, **b** temperature, **c** relative humidity, and **d** wind speed, during the 4 days around the first 1999 sampling period, 11–12 September, which is denoted by dashed bars. Tick marks on the *abscissa* denote 0000 and 1200 hours LT (local time; Mountain Standard Time), with day labels at 0000 hours LT. The lowest graphic (**e**) displays hourly pollen concentrations (*bars*) at 3.2 m from the primary pollen tower and hourly wind speeds (*line*) at 3.2 m from the micrometeorological tower during the first sampling period, 11–12 September 1999. Pollen data are missing for 1300 hours on 11 September. During each of the three sampling periods in 1999, pollen concentrations at 0.8 m, 1.3 m, 2.1 m, and 2.8 m on the primary pollen tower recorded very similar patterns to that observed at 3.2 m (Laursen 2001)



added to the final model. The equation (all coefficients averaged across the four pollen towers) is

$$\ln(\text{PC}) = 2.756 + 0.0924W + 0.0602T + 0.0193W \times T; \text{adjusted } R^2 = 77.5\%,$$

$$(0.181) \quad (0.044) \quad (0.022) \quad (0.007) \quad (2.23\%)$$

where PC = pollen concentration, W = wind speed, T = temperature, and standard errors are in parentheses.

Wind speed and temperature act synergistically; higher levels of either increase the effect of the other on pollen concentrations. Taken individually, average adjusted correlations (and SE) for each of the four predictors were wind (0.79, 0.02), temperature (0.86, 0.02), radiation (0.53, 0.03), and humidity (−0.48, 0.03).

Pollen concentrations in the second and third sampling periods deviated substantially from the fair weather pollen patterns described above. Initially, pollen concentrations in the second sampling period showed a diurnal pattern similar to that of the first sampling period except with smaller magnitude (Fig. 4e), yet then pollen concentration rapidly increased in the early evening of 18 September and remained high until the end of the sampling period. Recorded by all pollen towers (Laursen 2001), this increase

coincided with the arrival of the cold front, resulting in concentrations several orders of magnitude larger than those before frontal passage (Fig. 4). The increase was observed an hour prior to the brief precipitation event. Pollen concentrations during the third sampling period followed a pattern similar to the first sampling period until 2100 hours on 24 September, when all pollen towers recorded a significant spike in pollen concentration, coinciding with the arrival of the cold front (Fig. 5). Unlike the second sampling period, however, the higher pollen concentration was not maintained after frontal passage (Fig. 5e). Concentrations decreased with low wind speeds into the late afternoon hours on 25 September (Fig. 5e). In both the second and third sampling periods, the pollen height profiles were similar to the first sampling period with vertical gradients near zero in the evening and morning and increasingly positive profiles in the afternoon, except for periods of strong evening winds during the second sampling period (1800–2100 hours) in which positive gradients also occurred (Laursen 2001).

While it is evident that pollen concentrations at all four pollen towers correlated strongly with meteorological variables during the fair weather diurnal cycles of the first sampling period, they did not correlate strongly with the same predictor variables during the second and third sampling periods. This probably resulted from the fact that both the second and third sampling periods contained abrupt, strong bursts of pollen concentration at times when meteorological variables were also changing rapidly—too rapidly for the details of the changes to be resolved by the hourly meteorological data. Correlation coefficients were very low at all four pollen towers for all predictor variables in the second and third sampling periods, and are therefore not reported.

#### Results of pollen presentation and release experiments in 2000

During both sampling periods in 2000 (19–20 August and 2–3 September), all meteorological variables except wind speed and precipitation were very similar to the fair weather patterns observed during the first sampling period of 1999 (Fig. 6). Wind speed gradually declined during the first sampling period excepting a slight decline in the early evening hours (19–20 August; Fig. 6d).

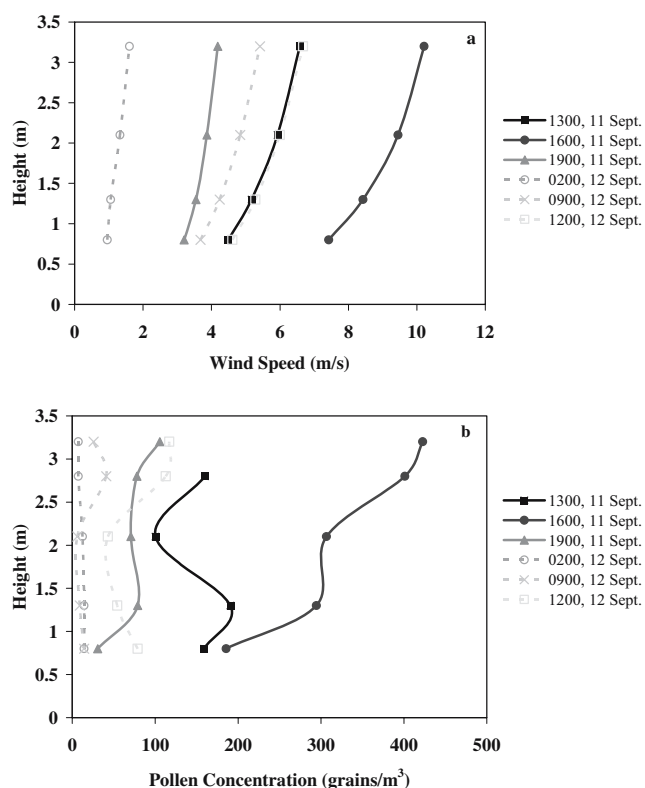


**Fig. 3** Wind profiles from the micrometeorological tower (a) and pollen profiles from the primary pollen tower (b) during the first sampling period, 11–12 September 1999

**Fig. 4** 30-min averages of **a** atmospheric pressure, **b** net radiation, **c** temperature, and **d** relative humidity during the 4 days around the second 1999 sampling period, 17–18 September, which is denoted by solid bars. Dashed bars denote the initiation (1800 hours) of the increase in pollen concentration. The lowest graphic (**e**) displays hourly pollen concentrations (bars) at 3.2 m from the primary pollen tower and hourly wind speeds (line) at 3.2 m from the micrometeorological tower during the second sampling period, 17–18 September 1999

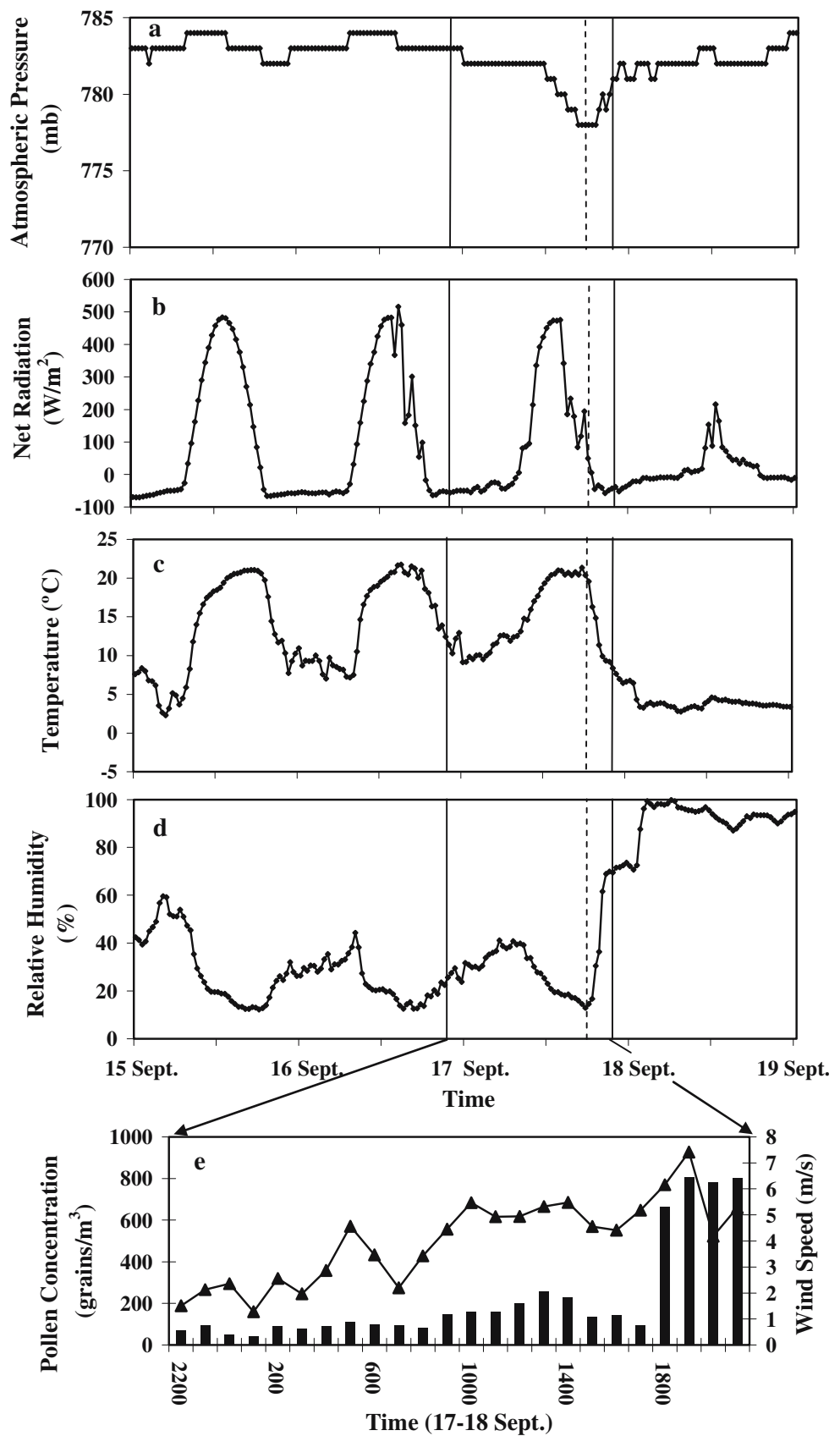


**Fig. 5** 30-min averages of **a** atmospheric pressure, **b** net radiation, **c** temperature, and **d** relative humidity, during the 4 days around the third 1999 sampling period, 25–26 September, which is denoted by *solid bars*. *Dashed bars* denote the hour (2100 hours) in which a spike in pollen concentration occurred. The lowest graphic (**e**) displays hourly pollen concentrations (*bars*) at 3.2 m from the primary pollen tower and hourly wind speeds (*line*) at 3.2 m from the micrometeorological tower during the third sampling period, 25–26 September 1999. Pollen data are missing for the 1900 hours on 25 September

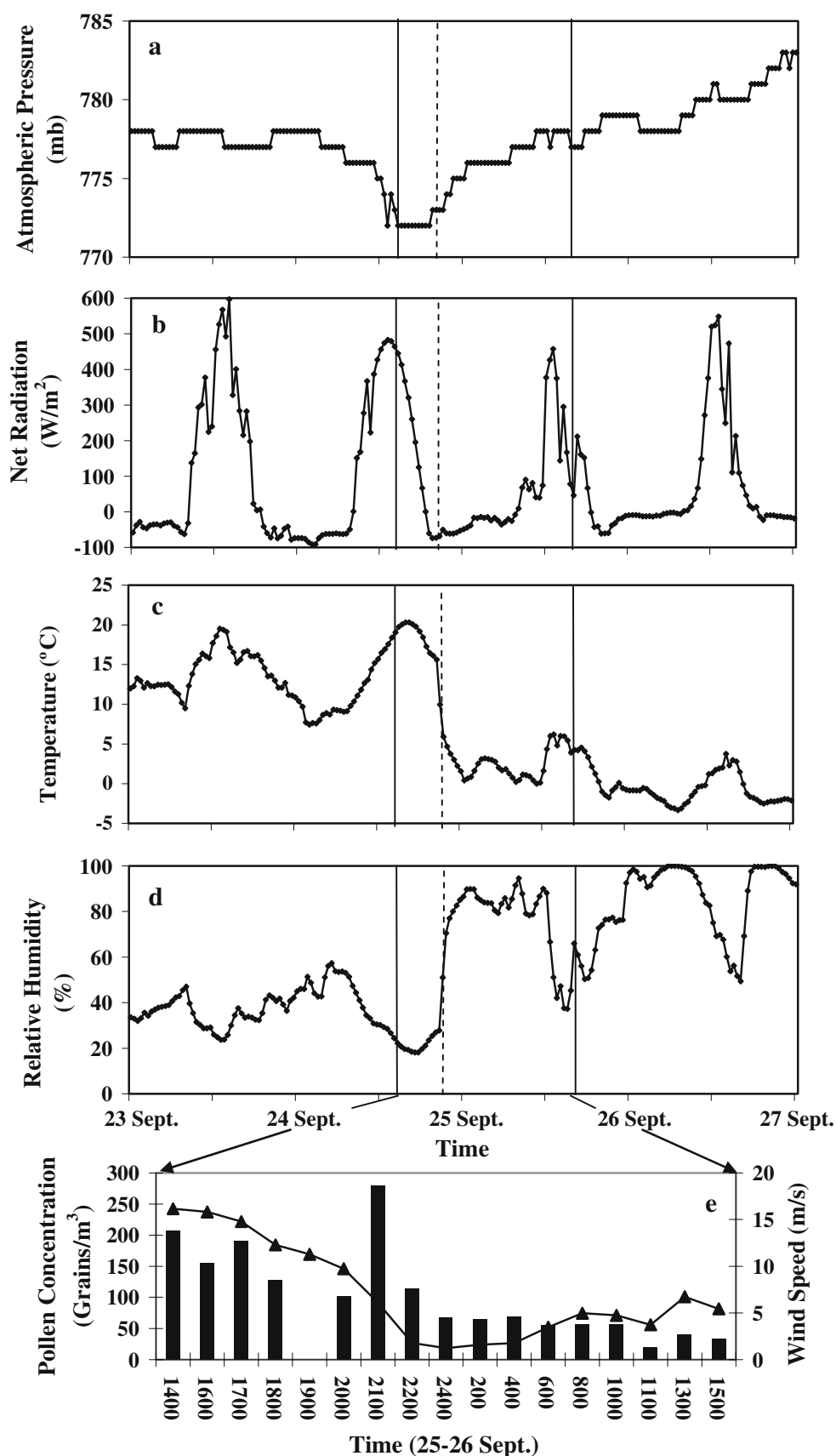
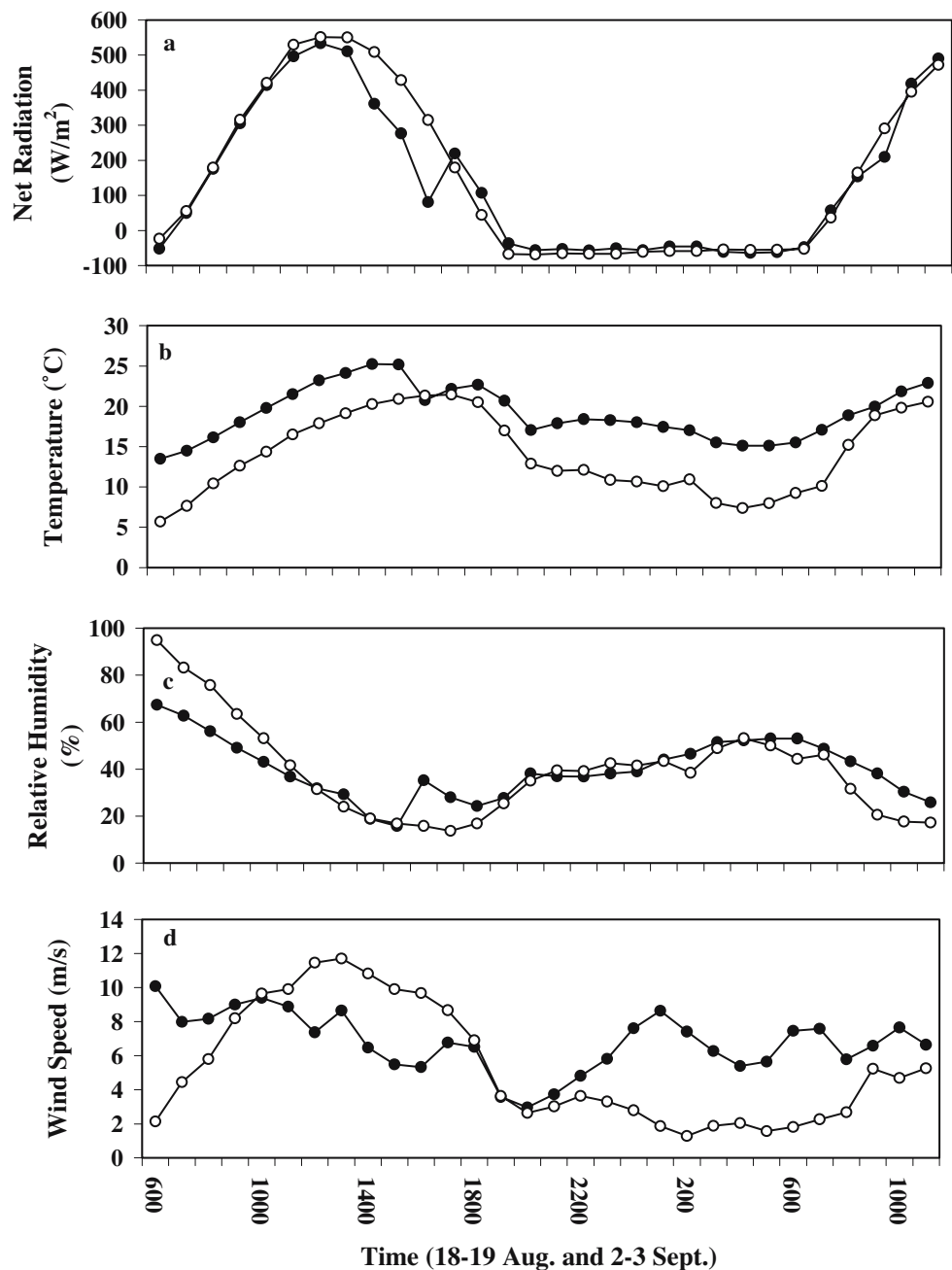


**Fig. 6** Hourly averages of **a** net radiation, **b** temperature, **c** relative humidity, and **d** wind speed, during the first 2000 sampling period, 18–19 August (*closed circles*) and the second 2000 sampling period, 2–3 September (*open circles*)

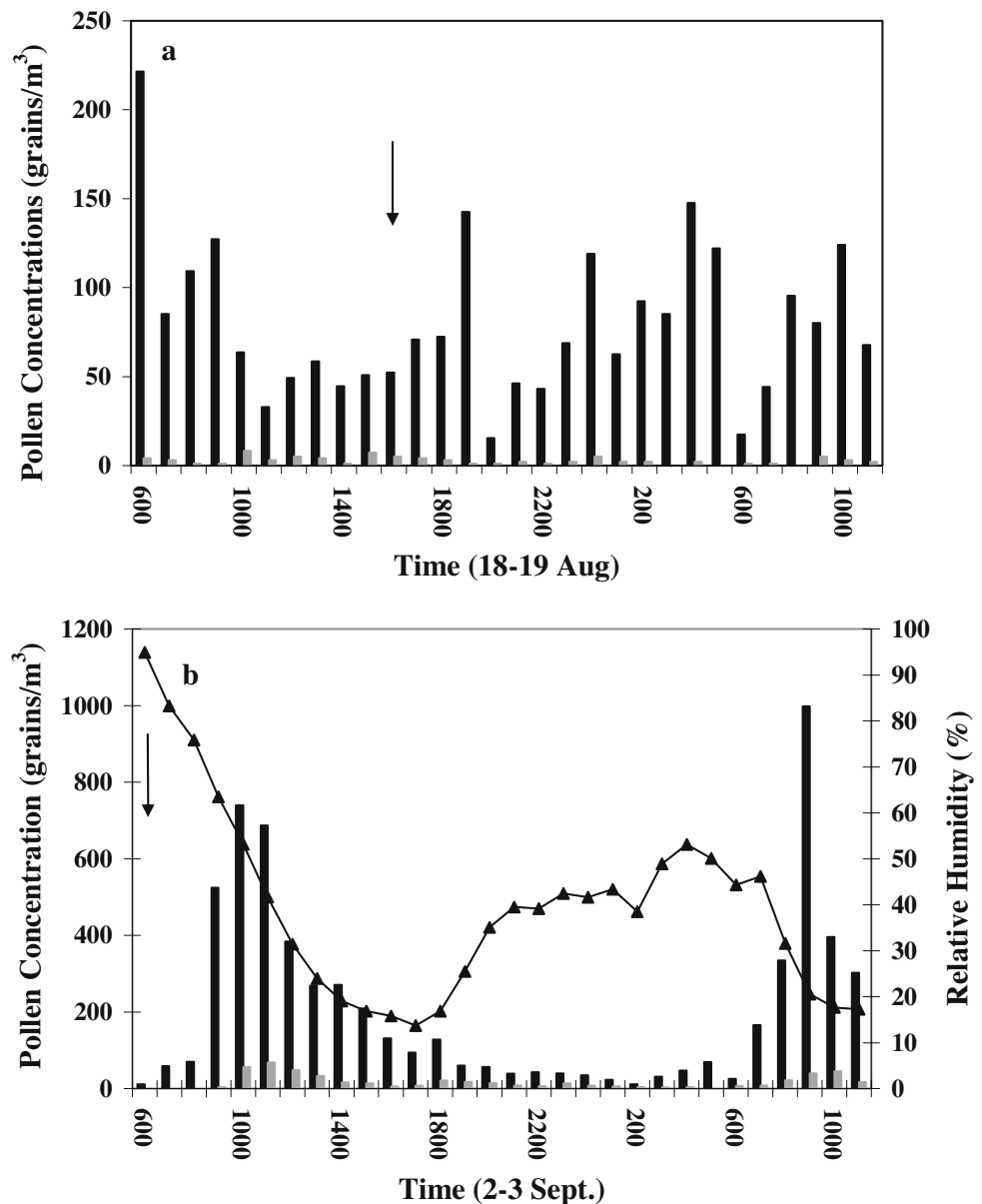


A light and brief shower (0.27 mm of rain, 5 min) occurred at 1605 hours during the first sampling period, although rain water could not have reached even the shallow root system of the test plant. Relative humidity was less than 40% in the hour of this rain event and was less than 30% in hours prior and afterward. A larger precipitation event occurred prior to the second sampling period (0.9 mm, 15 min) at 0540 hours to 0555 hours on 2 September. The humidity was 95% during this shower and remained at 70% for the subsequent 2 h.

During the first sampling period, ambient pollen concentrations were very low ( $<10$  grains/ $\text{m}^3$ ), exhibiting

neither a diurnal pattern (Fig. 7a) nor a change in pollen release in response to the light precipitation event at 1600 hours (Fig. 7a). Pollen concentrations in the chamber were 10–200 times higher than the ambient values (Fig. 7a), and their relative continuity suggested continuous presentation of pollen from the test plant over the entire 30-h period without any significant diurnal pattern. There was no evidence for an increased pollen presentation signal in the hours following the light precipitation event. Chamber concentration fluctuations did not follow ambient concentration fluctuations, indicating that the chamber sampler recorded the general pattern of pollen “presentation”

**Fig. 7** Hourly pollen concentrations from the Rotorod within the sampling chamber (black bars) and the ambient Rotorod (gray bars) during the first chamber sampling period, 19–20 August 2000 (**a**) and the second chamber sampling period, 2–3 September 2000 (**b**). Hourly relative humidity (line) is additionally displayed in the second sampling period (**b**). Arrows denote rain events



from the test plant, rather than simply recording ambient atmospheric pollen concentrations pushed through the chamber fan.

During the second sampling period (2–3 September), ambient pollen concentrations followed a very subtle diurnal pattern (Fig. 7b), varying by a magnitude of only around 70 grains/m<sup>3</sup>. During the 2 h following the rain event (0600–0800 hours), ambient concentrations were very low, not increasing until after 0900 hours, to a maximum value at 1100 hours, then returning to the low, early morning values by 1600 hours. At 0800 hours on the second day of this sampling period, the ambient sampler recorded a second pollen increase, reaching a maximum by 1000 hours.

In contrast with the ambient data, the chamber concentrations showed a marked diurnal cycle, with low values

during late evening and early morning hours within the sampling period and high values in the late mornings (Fig. 7b). A marked increase in pollen concentrations in the chamber suggested that dehiscence was enhanced within the test plant's florets (Fig. 7b) by either meteorological conditions or the precipitation event that occurred 4 h earlier. A similar morning pollen pulse began at 0700 hours on the second day, diminishing by 1000 hours.

Both morning chamber presentation pulses were concurrent with increasing temperature and decreasing relative humidity (Figs. 7b, 6b,c) and were also similar in magnitude, just as both morning ambient pulses were similar in magnitude (Fig. 7b). The similar timing and magnitude of both morning presentation events suggest little if any effect from the brief rain shower in the first

morning. The large difference in magnitude between ambient and chamber concentrations indicated that the experimental apparatus successfully separated pollen presentation from single chambered plants, rather than simply recording ambient atmospheric pollen concentrations pushed through the chamber's fan.

## Discussion

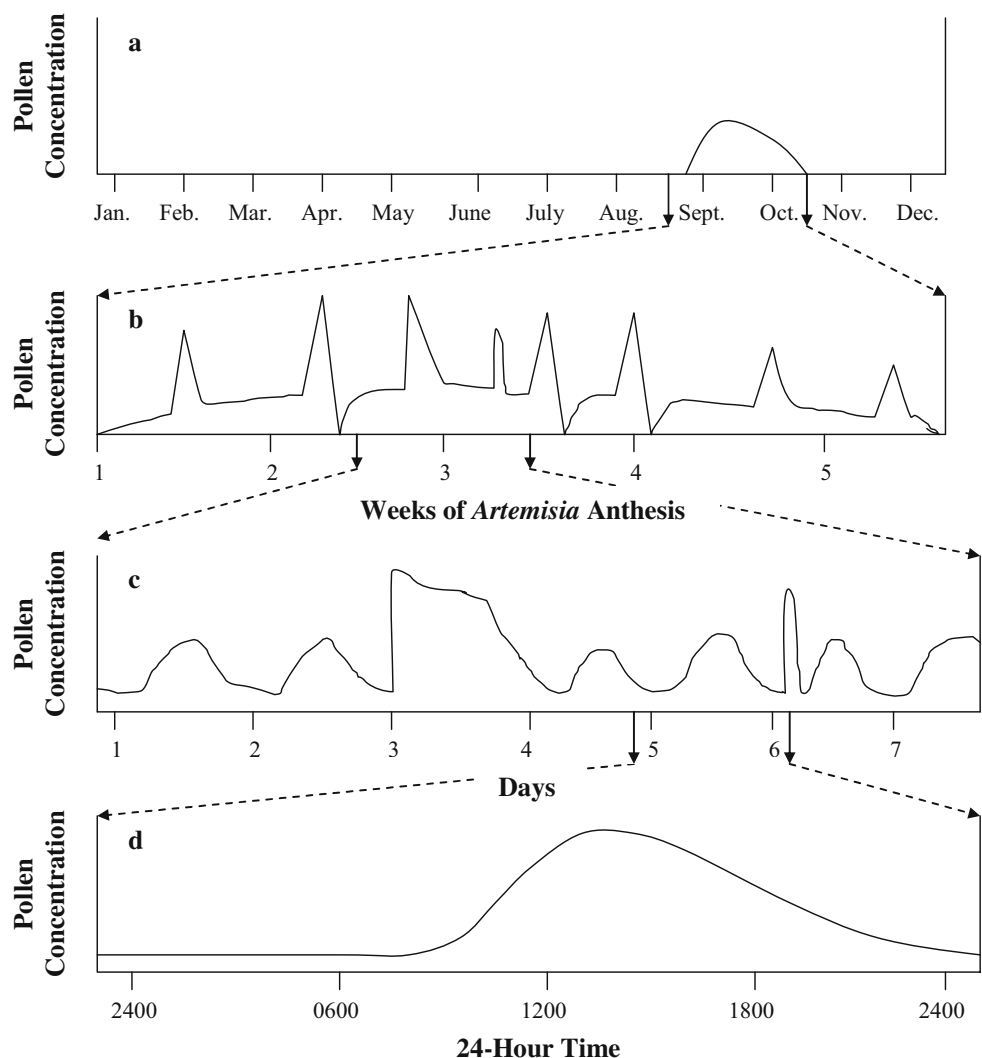
This research documents how wind dispersal of pollen involves interactions of meteorology with phenology at multiple scales (Fig. 8). Morphogenesis and phenology are genetically controlled, while the expression of these can be altered in amount and timing by the weather, extending as much as a year in the past (Akers et al. 1979). In the case of *Artemisia tridentata*—a dominant and widespread species of the intermountain West—long-term observations prior to this research have indicated that the degree of flower production is modified by weather for periods of a week to

two or three months (Fisser 1984). This study suggests that the actual degree and timing of anther development and dehiscence are modified by diurnal variations in temperature and humidity. These are issues of pollen presentation. Weather dominates the processes of release, transport, and deposition, mainly through diurnal and frontal variations in wind speed. This discussion reorganizes the field evidence in terms of controls on presentation, release, transport, and deposition, all of which involve processes occurring at multiple scales.

### Sagebrush pollen presentation and release

Diurnal cycles associated with fair weather represent a base case for pollen presentation and release. Variations on this base case arise with fronts, precipitation events, etc. Results from the 1999 field measurements showed that pollen concentrations varied with diurnal variations in wind speed (Fig. 2e; adj.  $R=0.79$ ) and more strongly with temperature (Fig. 2b,e; adj.  $R=0.86$ ). However, closer inspection of the

**Fig. 8** A hierarchical model of airborne *Artemisia tridentata* subsp. *wyomingensis* (Beetle and Young) pollen in the surface boundary layer at multiple temporal scales, **a** annual, **b** weekly, **c** daily, and **d** hourly



time traces revealed that pollen peaks occurred 2 h after the temperature peak and 1 h prior to the peak wind speed (Fig. 2b,e), suggesting that while release may be driven by wind speed, presentation is driven by temperature. Humidity varies more or less inversely with temperature. Evening hours of high humidity most likely promote anther development, while early morning hours of decreasing humidity most likely drive anther dehiscence. Plant developmental processes ensuing overnight, early morning dehiscence, and increasing morning release winds collectively contribute to the timing of peak pollen concentrations.

Anthers mature over daily time scales. After maturing over evening hours of high humidity, anthers decrease in turgor pressure in the first hours of light when soil–plant water potentials become lower (more negative) than in the early morning hours of darkness. Dehiscence, or presentation, is driven by an increasing water vapor deficit that ultimately ruptures the anther by mid- to late morning hours after temperatures have increased and humidity has fallen. Unlike leaves, anthers are composed of only a few cell layers and lack functional stomata and a cuticle. With essentially no adaptations for minimizing the removal of water vapor from their intercellular spaces (Mauseth 1988; Fahn 1990), anthers are easily ruptured and pollen made available for release when temperatures rise and humidity declines (Niklas 1985; Yates and Sparks 1993). Other than mid-morning pulses under ideal, fair weather conditions, pollen presentation is continuous at low levels throughout diurnal periods (Fig. 7), allowing dispersal potential at any point in which physical conditions promote pollen movement.

The field chamber experiments provide an opportunity to test this general interpretation. Diurnal patterns of ambient pollen concentrations were absent (Fig. 7a) or weak (Fig. 7b) in the 2000 experiments, suggesting that temporal patterns of release from individual plants were obscured in the well-mixed air streams of the general atmosphere. At the more detailed level of observation in the chamber, diurnal variation in pollen concentrations and a mid-morning pollen presentation peak were supported by the second experiment but not in the first (Fig. 7). The difference between these two results may have been caused by a more advanced stage of floral development during the second period than in the first period.

In contrast to the present study of a drought adapted shrub species where pollen presentation occurs at daybreak concurrent with a substantial drop in relative humidity and rise in temperature, Subba Reddi and Reddi (1984) documented evening anther maturation and dehiscence in two tropical tree species, *Cicca acida* (dehiscence from 2000 to 0200 hours) and *Emblia officinalis* (dehiscence from 1600 to 2100 hours). They also documented a pattern of early morning peak pollen release in *Cicca acida* (0600–1000 hours). However, *Emblia officinalis*, revealed an evening peak pollen release

(1800–0600 hours). In a tropical environment characterized by minimal diurnal shifts in relative humidity, atmospheric moisture may have less control over presentation than it does in arid or semidesert landscapes.

Pollen detachment is probably not linearly related with wind speed. While pollen concentrations correlate in a general way with wind, a record more detailed than the hourly ones recorded in this study would most likely show that thresholds of turbulence at the microscale are a driving factor in the release stage of biological particulates from plant and soil surfaces (Aylor 1978, 1990; Aylor et al. 1981; McCartney 1994a,b; Jackson and Lyford 1999). Only crude relationships between hourly average wind speeds at the tower with critical wind speeds experienced as gusts of seconds or less at the anther can be approximated with data collected in this study. Pollen profile data collected in 1999 indicate that mean wind speeds of less than 4 m/s during the evenings were insufficient to initiate pollen release or maintain transport (Figs. 2e, 4e, and 5e).

The 2000 data, however, indicate a lower critical wind speed. Ambient data from the second sampling period in 2000 showed an initiation of the second pollen release event occurred at 0800 hours (Fig. 7b) under an average hourly wind speed of 2.67 m/s (Fig. 6d). These relatively low wind speeds for this environment were strong enough to remove pollen from anthers in the landscape and keep them suspended for subsequent transport as winds continued to increase into the morning. Wind speeds would be expected to be less around the anther boundary layer than on the tower as an hourly average, while individual gusts might be about the same or greater than the hourly average tower value. Similarly low wind speed requirements have been reported for the release of some spores (Aylor 1975).

The difference in apparent, critical wind speeds between the 1999 pollen tower and 2000 ambient studies seem less anomalous if the limitations of hourly wind speed estimates are considered. At the initiation of the second release and transport pulse in the second 2000 sampling period (Fig. 7b), the hourly wind speed average was 2.67 m/s, but wind speeds increased into mid-morning and reached 5.23 m/s by the following hour (Fig. 6d). Winds were almost certainly increasing within the initiation hour, most likely reaching an average level greater than 4 m/s towards the end of the sampling hour. Pollen transport was, therefore, most likely maintained late in the hour, allowing atmospheric concentrations to begin increasing late in the hour as well. Had wind speeds not been increasing overall, net deposition would most likely have continued, under the same hourly average wind speed of 2.67. Our data suggest that the transport/deposition boundary occurs at wind speeds averaging 4 m/s and that release occurs under average wind speeds that are at least this strength or possibly less.

## Transport and deposition

### *Mesoscale transport winds*

Once entrained, wind-borne pollen is transported vertically and horizontally, and sometimes deposited by wind. Wind may be limiting to this process for some plants, while for sagebrush wind is a pervasive characteristic of its environment. Sagebrush pollen is transported for extended periods over the Shirley Basin due to characteristic strong convective instability, horizontal advection, and especially during frontal advances. Frontal effects are discussed separately in a later section. In fair weather, the atmospheric boundary layer typically becomes thermally destabilized after sunrise and into late afternoon (see Fig. 2 for the best example). Microscale turbulence associated with daytime instability leads to pollen entrainment in the airstream and subsequent vertical and horizontal transport during the late morning and afternoon (Figs. 2e and 3). Ogden et al. (1969) observed a similar diurnal pattern in *Ambrosia* pollen dispersal. The pollen grains released in the early morning, and at lower levels throughout the day, are transported above the atmospheric surface layer and remain entrained in the atmosphere by the strong, daytime advective wind field and strong convective circulations common in the basin during daytime hours, suspending large quantities of pollen above the surface layer (Fig. 3b).

### *Vertical pollen profiles*

The vertical direction of pollen flux can be inferred from the vertical profiles of pollen concentration (Di-Giovanni et al. 1996). These gradients were initially zero (no change with height) early in the day, became positive (increased with height) later in the day as wind speeds increased into the afternoon, and then returned to zero in the evening when wind speeds dropped to below 4 m/s (Fig. 3). These patterns suggest that as wind speed dropped overnight, pollen sedimented out of the atmosphere to the ground and reached low values at all measured heights. Then, during the day, the strong winds not only increased the pollen concentrations at all heights by pollen entrainment from the mature anthers and from vegetative and ground surfaces (Fig. 2e), but also led to higher pollen concentration several meters above the canopy than near the canopy, presumably the original source of the pollen (Fig. 3b). Two factors might account for this kind of gradient in the afternoon. The first is that most of the pollen to be released in a given day had become entrained in the wind stream by the afternoon following a mid-morning release, so that only small amounts of new pollen were available for further release late in the day. The second possibility is that pollen was being deposited from the atmosphere through impac-

tion to the vegetation surface so that a net flux from several meters above the canopy to the canopy was creating an inverse concentration gradient through turbulent deposition. The strength of such a net downward flux would seem to be slight, given the possibility of reentrainment of deposited grains back into the turbulent afternoon atmosphere.

### *The problem with positive profile gradients*

The 1999 pollen profiles never demonstrated a negative vertical gradient (higher concentrations near the ground). If shrubs are the source of pollen, pollen should be more concentrated near the canopy surface during presentation pulses and decrease with height, a negative gradient. Under conditions of fair weather during the first sampling period, the vertical gradients were near zero in the evening and early morning and increasingly positive in the afternoon (Fig. 3b). Similar patterns were observed in the second and third 1999 sampling periods, in addition to positive gradients during periods of strong evening winds (Laursen 2001).

One possible explanation for the apparent absence of negative vertical pollen concentration gradients near the vegetation canopy is the limited height gradient measured by our apparatus. With a maximum height of only 3.2 m, profile shapes will not necessarily demonstrate the direction expected. Other studies have demonstrated negative profile gradients using much taller sampling towers (Peterson 1931; Hubert 1932; Rempe 1937; Craigie 1945; Harrington 1965; Gregory 1973; Janaki Bai et al. 1981; Di-Giovanni et al. 1996). Janaki Bai et al. (1981) took vertical samples of a variety of pollen and spores from grasses, shrubs, and trees within a low level profile of up to only 5 m and found mostly negative gradients, excepting a slightly positive gradient for *Oidium* conidia. Di-Giovanni et al. (1996) reported some positive vertical pollen profiles below 50 m at some of their sampling locations for jack pine and black spruce above a seed orchard. However, their larger overall profiles, which extended up to 300 m, generally displayed negative gradients. They suggest that pollen maxima at low levels in the profile represent upwind local release, whereas profiles missing low level pollen maxima were upwind of local release and instead represented meso-scale pollen sources. Similarly, our positive profiles likely represent upwind meso-scale pollen sources from the larger basin in a well mixed surface layer that swamp the local morning release signal from sparse shrubs.

That local pollen maxima exist near the ground in the Shirley Basin over diurnal periods is indicated by the 2000 sampling data in which individual plants are clearly substantial pollen sources in mid-morning (Fig. 7b). As mentioned above, besides having a limited capacity to measure the height profile, it is possible that the local release signal may have gone undetected at a single location due to sparse

vegetation at a given point on the landscape and swamping from upwind pollen sources. Additional factors contributing to missing local release signals are possible decreased collection efficiency in the lower samplers resulting from increased microscale turbulence, hydrated pollen grains, and the initial clumping of pollen grains (Laursen 2001).

#### *Settling periods within the boundary layer*

While sedimentary deposition leads to a decrease in evening pollen concentrations, the boundary layer most likely is not completely emptied of pollen grains during a 12-h evening period. Settling velocity is a critical measurement in elucidating sedimentary deposition and is variable for a given species relative to varying pollen densities, pollen sizes, and environmental conditions. As a comparison to theoretical values of settling velocities, Di-Giovanni et al. (1995) empirically measured the variability of settling velocities amongst biota of the same species as well as the effects of clumping on settling velocities for a variety of pollen and spores. This study uses previously reported settling velocities of 1–2.5 cm/s for wind-dispersed pollen grains within *Artemisia* pollen's diameter class (20–30  $\mu\text{m}$ ; Crane 1986; Mandrioli 1998) to roughly estimate whether *Artemisia* pollen would completely sediment out of the atmospheric boundary layer by the end of a continuously stable evening. This range of settling velocities, which is more general than the small scale variability measured by Di-Giovanni et al. (1995), suggests that after 12 evening hours of calm atmospheric conditions, *Artemisia* pollen grains below 1,080 m above ground level would have sedimented to the surface. Mid-day depths of the convectively unstable atmospheric boundary layer, which would contain pollen by vertical mixing, were measured by aircraft over the research site at 800–1,500 m above ground level (R. Kelly, University of Wyoming, personal communication). Thus, even in the extreme and unlikely case of the entire boundary layer depth becoming stable immediately at sunset, there would not be enough time for the pollen to sediment out overnight, leaving small but measurable concentrations through the profile at the following sunrise, which we consistently measured (Figs. 2e, 3, 4e, 5e, and 7b).

#### Effects of meteorological fronts on pollen release and transport

Storm cells commonly accompany the arrival of a cold front. With these fronts, downdrafts caused by evaporation of precipitation, or “virga”, generate smaller scale surface gust fronts of up to 28 m/s (Ahrens 1994). During the sampling periods, very little precipitation occurred after the arrival of the cold fronts. While a light rain fell an hour after

the arrival of the 18 September front, it was not enough to empty the atmosphere of pollen through rainout or washout. Virga occurs often, however, in the dry atmosphere above the Shirley Basin. It is possible that precipitation initiated pollen rainout and washout at higher altitudes, but that evaporation near the ground effectively concentrated the pollen closer to the surface. In addition, the dramatic increase in small-scale turbulence characterizing the arrival of gust fronts could supply a force strong enough to quickly release a large proportion of the pollen presented on both vegetation and bare-ground surfaces. Gust fronts associated with large-scale cold fronts can, therefore, cause immediate increases in atmospheric pollen concentration as were recorded in this study (Figs. 4e and 5e).

Our hourly wind speed measurements could not record the arrival of gust fronts or the small-scale turbulent forcings associated with them, which is the probable mechanism behind the dramatic increases in pollen concentration from 1800 to 2100 hours on 18 September 1999 and at 2100 hours on 25 September 1999. However, we personally noted sharp changes in wind speed and direction at minute time scales at the point of front arrival during the second sampling period.

#### Evolutionary perspectives

Regal (1982) suggests that animal-pollinated plant species are prevalent in arid areas due to climatic unpredictability and intense selection for outcrossing systems. This may be true, yet at the same time, where strong, turbulent winds can occur day or night, it may be evolutionarily adaptive for the anemophilous species to provide pollen continuously for potential atmospheric gene transport. The pattern of continuous pollen presentation for *Artemisia tridentata* observed in this study may not be unique to this species, but may be shared by those shrubland species having adopted a generalist approach to pollen dispersal by wind. This behavioral pattern requires that a background level of pollen be available for release and transport day or night. Subba Reddi and Reddi (1984) also found continuous detectable levels of pollen in two exclusively anemophilous tropical tree species, suggesting a similar adaptive approach for anemophilous tropical species. Contrary to the present study, however, pollen release occurred largely in the evening under stable atmospheric conditions, maintaining high levels of local pollen to promote geitonogamy among widely spaced conspecific plants.

#### Summary: controls of anemophilous pollen dispersal, a temporal hierarchy

Our observations suggest that the production and dispersal of Wyoming big sagebrush pollen are controlled

by biotic and physical factors operating at several time scales. At the semi-annual scale, winter precipitation and weather conditions throughout the growing season (May through September), such as consistent winds, mild temperatures, and late-season rainfall, are long-term controls of sagebrush morphogenesis, phenology, and pollen production.

Whitehead (1983) outlined factors that determine whether wind pollination will be frequent in a given vegetation type. One of which is a short growing season that favors early flowering. While this scenario may hold true in general, sagebrush steppe is an exception in which the anemophilous syndrome for *Artemisia tridentata* occurs late in the growing season (late August through September), resulting in a 6-week pollen dispersal period in which pollen concentrations are initially high and gradually decrease through the flowering season (Figs. 8a, 2e, 4e, and 5e).

Over the approximate 6-week period of anthesis, the general trend of decreasing dispersal rates is interrupted by large, short-term pollen dispersal spikes resulting from large-scale frontal systems (Fig. 8b). Microscale turbulence associated with gust fronts can cause discrete pollen release or re-entrainment events at any point in a diurnal period and dramatically increase atmospheric pollen concentrations in the surface layer. Strong updrafts associated with storm cells simultaneously offer a mechanism for lifting pollen into the upper portions of the atmospheric boundary layer, increasing the opportunity for long-distance dispersal. While not observed during our sampling periods, rainout and washout from significant rain events can have the opposite effect, quickly scouring the atmosphere of pollen over similarly short time periods (Fig. 8b; Gregory 1973; Chatigny et al. 1979; Di-Giovanni and Kevan 1991; Mandrioli 1998; Isard and Gage 2001). Over a single week, frontal dispersal spikes may vary in temporal extent depending on the meteorological conditions following frontal passage (Fig. 8c). A strong, steady wind field must be sustained and/or thermal, daytime buoyancy must be high to maintain atmospheric pollen suspension after the initial spike in concentration (Fig. 8c). Finally, at the scale of a single fair weather day, there is a baseline diurnal pattern of increasing presentation, release, and transport from late morning to mid- to late afternoon (Fig. 8d), followed by deposition through sedimentation in the evening as wind speeds drop below 4 m/s. Pollen is most likely available for dispersal from anthers and vegetative and ground surfaces throughout the sagebrush steppe at all times during the pollination season and is typically airborne at low levels even during calm, early-morning hours due to strong turbulent mixing within the entire boundary layer over the previous afternoon.

**Acknowledgements** The authors gratefully acknowledge the research support provided by a grant from the Andrew Mellon Foundation. We thank the Pan-American Aerobiology Association for lending field equipment; Dr. Stephen Jackson and Dr. Robert Booth for laboratory use and microscopy support; Ted Hehn, Emily Holt, and Scott Miller for field and laboratory assistance; and Dr. Laura Perry for her review of this work as well as two anonymous reviewers.

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