The biomechanics of *Cornus canadensis* stamens are ideal for catapulting pollen vertically

D. L. WHITAKER,*† L. A. WEBSTER‡ and J. EDWARDS§

Physics Department, Williams College, Williamstown, MA 01267, ‡Physics Department, University of Michigan, Ann Arbor, MI 48109, and §Biology Department, Williams College, Williamstown, MA 01267, USA

Summary

1. Rapid movements in fungi and plants have evolved in different species to facilitate the dispersal of spores and seeds. The mechanisms of action can differ among species, but the effectiveness of these movements has rarely, if ever, been tested. Here we show through a quantitative biomechanical analysis that the stamens of *Cornus canadensis* L. (bunchberry) are ideal for catapulting pollen vertically at high speeds.

2. We develop a biomechanical model to describe the explosive launch of pollen from the flowers of bunchberry. The model determines the equation of motion for the stamens based only on the morphology and measurements of the parts of the stamens. To measure the motion of the stamens to compare with our model, we analysed individual frames of a video taken at 10 000 fps.

3. The thecae of adjacent stamens dehisce in bud so that the stomia face each other, retaining pollen between neighbouring anthers. As the flowers open, pollen is accelerated vertically as long as the thecae remain in contact. Pollen is released only when the anthers move horizontally and separate.

4. The observed motion of the stamens matches the results from our model through release of the pollen. The model reveals that pollen release (horizontal movement of the anthers) occurs only after the vertical speed is at its maximum. Thus, for this particular catapult mechanism, the morphology of the stamens is optimal for launching light, dry pollen straight upwards at high speed. Pollen launched vertically at high speed both enhances insect pollination by helping to making pollen stick on visiting insects, and also allows for successful wind pollination by propelling pollen into the air column. Seed set by inflorescences in pollinator-exclosure cages further supports the ability of this flower to use wind as a pollination mechanism.

Key-words: bunchberry, dogwood, plant motion, pollination

Introduction

Rapid movements to disperse spores and seeds have evolved multiple times in different plant and fungal groups (Ingold 1965; Simons 1992; Pringle *et al.* 2005; Skotheim & Mahadevan 2005). Within the angiosperms, flowers from a diverse array of plant families have developed fast motions for dispersing pollen. Some remarkable examples include pollen placement by *Catasetum* orchids (Orchidaceae) (Romero & Nelson 1986) and trigger plants *Stylidium* spp. (Stylidiaceae) (Armbruster, Edwards & Debevec 1994), the exploding flowers of New Zealand mistletoe (Loranthaceae) (Kelly *et al.* 1996), the extraordinarily rapid stamens of the white mulberry (Moraceae) (Taylor *et al.* 2006), and rapid pollen propulsion by the

flowers of bunchberry (*Cornus canadensis*) L. (Cornaceae) (Edwards *et al.* 2005). Although these rapid motions have been reported, the effectiveness of each type of movement is rarely, if ever, evaluated. Here we use a biomechanical model to determine the equations of motion of the stamens of *C. canadensis* during pollen launch. The model depends on floral morphology and is based solely on measurements of the floral organs. A detailed analysis of the model's results is used to determine how effectively the stamens propel their pollen.

The explosive opening of bunchberry flowers is an example of a movement based on a fracture-dominated mechanism, a mechanical process characterized by the sudden release of stored elastic energy that is triggered by the tearing of tissue. The most rapid motions executed are of the fracture-dominated variety (Skotheim & Mahadevan 2005), and as they do not rely on chemical processes or hydrodynamics, they can be described
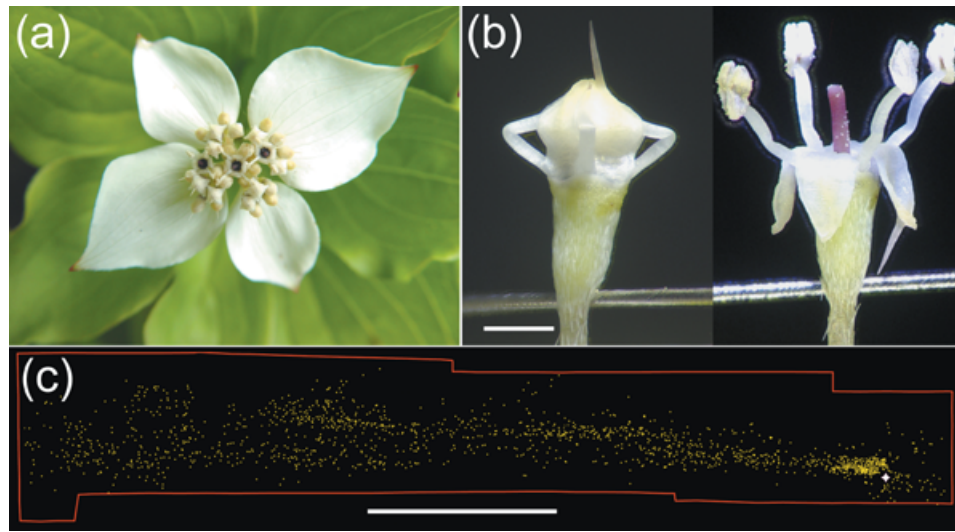
†Author to whom correspondence should be addressed. E-mail: dwight.l.whitaker@williams.edu

Fig. 1. Images of *Cornus canadensis* flowers and pollen distribution. (a) An inflorescence of 30 flowers in different stages of development. Three flowers are open and the four filaments protruding from between the petals are visible in mature buds. (b) Close-up of a single mature flower before and after opening. Elastic energy is stored in the bent filaments, which protrude from between the petals in a closed bud. Scale bar = 1 mm. (c) Pollen distribution from one flower triggered in a closed room showing that even minor air currents can carry pollen. White star shows location of flower; each yellow dot represents a pollen grain or clump of grains. Scale bar = 5 cm.

using straightforward physical models based on easily measured plant properties. The model is used to analyse the effectiveness of stamen motion for launching pollen vertically at high speeds. This behaviour enables the light pollen to be propelled rapidly upwards. Although *C. canadensis* has long been considered to be insect-pollinated (Lovell 1898; Barrett & Helenurm 1987), the facility with which pollen is carried in the air suggests that wind can also effect pollination. Here we tested for wind pollination by enclosing inflorescences in pollinator-exclosure cages. Flowers in the exclosure cages set seed, confirming wind pollination. Thus pollen launched vertically at high speed may enhance insect pollination by helping to make the light, dry pollen stick on visiting insects and by also allowing for successful wind pollination, making *C. canadensis* an ambophilous species.

Materials and methods

STUDY SITES AND PLANTS

Cornus canadensis uses a sophisticated, trebuchet-like mechanism to launch pollen straight upwards simultaneously from all four stamens, at speeds reaching 6 m s^{-1} in <0·5 ms (Edwards *et al.* 2005). In young flower buds, the filaments are short and the petals are completely fused along their edges, enclosing the stamens entirely. As the flower matures, the stamens lengthen more quickly than the petals and a bend forms in each filament, which eventually emerges from between the petals. Elastic energy builds up in the filament as it grows and bends. The explosive opening of the flower is entirely mechanical, and the elastic energy that drives the explosion depends on turgor pressure. The biological processes necessary to build up stored elastic energy are already complete in

mature flower buds, and the release of the stored energy does not require additional physiological processes (Edwards *et al.* 2005).

Flowering shoots of *C. canadensis* produce single inflorescences of small, self-incompatible (Barrett & Helenurm 1987) flowers subtended by four showy white bracts (Fig. 1a). Mature flowers (Fig. 1b) have four valvate petals fused only at the tip. The petals restrain the filaments, which store elastic energy used to launch the pollen. Typically, one of the four petals has a trigger that can be used to initiate floral opening when pressured. However, mature flowers eventually open without external contact. *Cornus canadensis* and its sister species *Cornus suecica* are common, growing circumboreally in the taiga of North America and Eurasia (Hultén 1968). Both are sub-shrubs and grow in dense patches carpeting the forest floor.

We studied *C. canadensis* collected in the relatively undisturbed forest at the north-eastern end of Isle Royale National Park, Lake Superior, MI, USA in June and July 2003 and 2004. All flowers were collected with permit from Edwards Island or on the main island of Isle Royale near Monument Rock. Flowers were transported by plane, and videos of exploding flowers were recorded within 48 h of the samples being collected. Samples used to estimate the masses of the anthers were shipped overnight and weighed and measured immediately after being opened.

Still images of closed and open flowers were recorded digitally at different focal planes and merged into a single image (HELICONFOCUS ver. 3·20·2, Kharkov, Ukraine) to improve depth of field.

HIGH-SPEED VIDEO ANALYSIS

To determine movement by the flowers, we recorded their opening with a charge-coupled device (CCD) camera
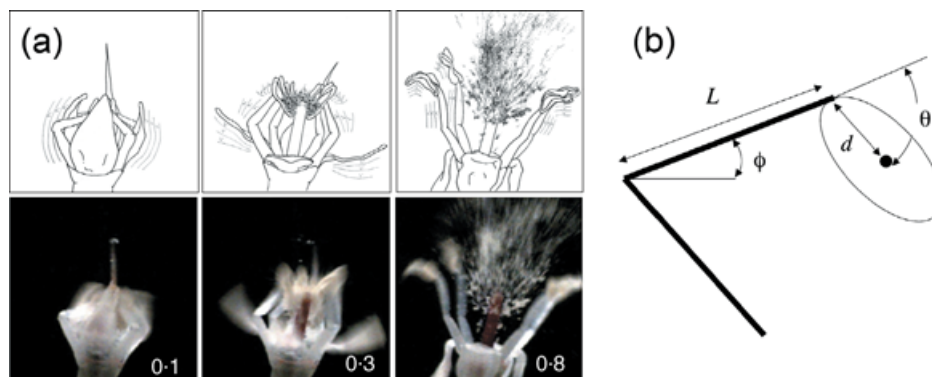
Fig. 2 Pollen launch by *Cornus canadensis*. (a) Line drawings and associated still frames from video of flower opening recorded at 10 000 fps. Time (ms) after opening is indicated in each frame. (b) Schematic diagram of the stamen model. The signs of angles θ and φ are both positive as drawn. The origin of our co-ordinate system is located at the vertex of angle φ in the drawing.

(Motion HG-100K MotionXtra, Redlake Tucson, AZ, USA) at rates of 10 000 fps. Lighting was provided by a combination of two high-powered (300-W) incandescent lamps and a fibre-coupled 1000-W Xenon discharge lamp. Flowers were secured and triggered by gently touching the trigger with a 0·13-mm-diameter wire. In some cases, flowers exploded on their own.

Individual frames of video were analysed (IMAGEJ ver. 1·36b, National Institutes of Health, Bethesda, MD, USA) to determine the orientations of the filaments and stamens as a function of time. The data presented in this paper come from a video recording in which two stamens moved orthogonally to the line of sight. The time-scale of explosive opening in this recording matched those from other recordings. The orientation of both left and right stamens were recorded and averaged to produce the data shown. We defined $t = 0$ to correspond to the frame immediately after the petals begin to separate and the stamens are no longer restrained. To determine the orientation of the anthers and filaments, a line was drawn for each connecting two easily distinguished points. The angle of these lines with respect to the horizontal was measured for each frame and used to determine stamen position.

DETERMINING THE EQUATION OF MOTION

Because pollen is launched from the anthers through the release of elastic energy stored in the filaments (Edwards *et al*. 2005), we calculate the dynamics of the launch based on the masses and elastic properties of the parts of the stamens. We used a simplified model of the stamens (Fig. 2b), where the anther is a uniform beam of mass m that is free to rotate about the tip of the filament through an angle θ. The centre of mass of the anther is at distance d from the filament tip. The filament is a hinged beam with a restoring torque that acts to keep it straight. We assume that the lower portion of the filament, which connects to the base of the flower, does not move as the pollen is launched. This assumption agrees well with observations from high-speed video recordings (Fig. 2a). The moving part of the filament is considered to be a uniform rigid rod of length L and mass M. We assume a linear restoring torque proportional to the angle φ, which acts to keep the filament at an angle ϕ_0.

Based on these assumptions we can calculate the Lagrangian for the stamen's motion in terms of the variables φ and θ as well as their time derivatives $\dot{\phi}$ and $\dot{\theta}$. The kinetic energy, T, includes contributions from the anther's rotational and translational motion as well as the rotation of the filament about its pivot point. It is given by:

$$T = \frac{1}{2}m\left[\left(L^2 + \frac{4}{3}d^2 + 2Ld\cos\theta + \frac{M}{3m}L^2\right)\dot{\phi}^2 + \frac{4}{3}d^2\dot{\theta}^2 - 2\dot{\phi}\dot{\theta}\left(\frac{4}{3}d^2 + Ld\cos\theta\right)\right],$$

(eqn 1)

while the potential energy, U, is given by $U = \frac{1}{2}k(\phi_0 - \phi)^2$, where ϕ_0 is the equilibrium angle, which was measured in the video to be 126°; and k is a spring constant, which we have also measured. The equations of motion are determined from the Lagrangian ($\mathcal{L} = T - U$) by solving the Euler–Lagrange equations for θ and φ and their time derivatives (Fetter & Walecka 1980). These equations of motion are:

$$(L/d)\sin\theta\,\dot{\phi}^2 + \frac{4}{3}\ddot{\theta} - \left[\frac{4}{3} + (L/d)\cos\theta\right]\ddot{\phi} = 0 \quad \text{(eqn 2)}$$

and

$$k(\phi_0 - \phi) - m\left(L^2 + \frac{4}{3}d^2 + 2Ld\cos\theta + \frac{1}{3}\frac{M}{m}L^2\right)\ddot{\phi}$$
$$+ 2mLd\dot{\phi}\dot{\theta}\sin\theta + m\left(\frac{4}{3}d^2 - Ld\cos\theta\right)\ddot{\theta}$$
$$- mLd\dot{\theta}^2\cos\theta = 0.$$

(eqn 3)

Solutions to the coupled equations of motion (equations 2 and 3) were determined numerically (MATHEMATICA ver. 5·1, Wolfram Research, Champaign, IL, USA) using the function NDSolve. The initial orientations of

the anther and filament were determined from the video, and both were taken to start at rest.

MORPHOMETRIC DATA

To compare the results of our model with the observed motion of the stamens, we measured the physical parameters L, d, m, M and k. To determine the mass of the anther (m), we weighed 48 anthers with their pollen from 21 mature flowers (2·0 mg), with an average mass of 0·024 mg. We estimated the uncertainty for this mass by looking at the size variation within a sample. Assuming that the mass of the anthers scales as their length cubed, the fractional uncertainty in mass will be three times the uncertainty in length. Length measurements taken on nine anthers had a standard error of 2%, which corresponds to a statistical uncertainty in mass of ±6%. A still frame from the high-speed video recording was used to determine the sizes of the anther (d) and filament (L) as well as the filament's mass, M. The length of the anther was 0·070 mm, which corresponds to $d = 0·035$ mm. The length of the upper part of the filament, L, was 0·80 mm with an average diameter of 0·16 mm. The mass of the upper portion of the filament was estimated by assuming that it had the density of water. Assuming cylindrical symmetry, we obtain a mass of 0·016 mg. The filament diameter varies by about ±10% along its length. As the volume of the cylinder depends on this value squared, we assume an uncertainty of ±20% in its mass. Finally, to determine the spring constant k, we measured the force required to re-bend a filament through a known angle. We measured forces (typically $\approx 10^{-4}$ N) by bending a filament against the pan of an electronic balance (model AB104, Mettler Toledo, Greifensee, Switzerland). The restoring torque was determined by measuring the magnitude and position of the force required to hold the filament at a number of known angles. Measurements on three samples gave a restoring torque, Γ, which varied linearly with ϕ from its equilibrium condition, $\Gamma = -k(\phi_0 - \phi)$. We found that $k = (1·5 \pm 0·9) \times 10^{-7}$ J. The error is based on uncertainties in measuring the contact point of the digital balance and the statistical error of a linear fit to the data. We also measured the force required to keep a filament bent in a flower that had not yet opened, by restraining a single filament with the pan of the electronic balance as a flower was triggered open. This method measured only the force for a single angle, but data taken on two samples gave an average spring constant of $k = 1·1 \times 10^{-7}$ J, which lies within the range of values for already opened flowers. From this we conclude that the elastic properties of the stamens are not significantly affected by the opening process.

ANTHER ARRANGEMENT

To determine the arrangement of anthers in mature flower buds, we carefully removed one petal from an unexploded flower to view the interior of the bud. We also made thin cross-sections of fixed mature flower buds. Unexploded mature buds fixed in 3% glutaraldehyde in 0·1 M Hepes buffer (pH 7·1) were rinsed three times in Hepes buffer and placed in 1% osmium tetroxide in deionized water for 1 h. Buds were then dehydrated in an ethanol series [70, 80, 90, 95, 100% (3×) each for 5–10 min] and propylene oxide (twice at 5 min). Buds were then placed in 50% propylene oxide and 50% Embed-812 resin overnight on a rotator followed by 4 h in 100% Embed-812, and polymerized at 70 °C overnight. Sections of 1 µm (made with a diamond knife on a Reichert–Jung Ultracut E ultramicrotome) were stained with toluidine blue and azure II, and viewed with a compound light microscope.

TESTING FOR WIND POLLINATION

To test for wind pollination we quantified seed set for inflorescences, which were caged to exclude insect pollinators. We chose 10 matching pairs of inflorescences based on proximity, number of flower buds and their stage of development. One was randomly selected to be caged and the other to be left in the open. Cages were made of 45 cm (l) × 20 cm (w) × 26 cm (h) wire frames covered with fine nylon bridal netting (mesh size = 1·8 mm) with a taller wire placed in the centre to keep the netting off the flowers.

All cages were anchored around the base with cloth tubes filled with sand. To allow for wind pollination, the caged inflorescence and a minimum of four other inflorescences were included inside the cage, making pollen flow through the mesh unnecessary. The genetic diversity of the inflorescences was not known, but studies of other clonal boreal herbs show that clones often interdigitate (Edwards 1984), making it likely that cages contained shoots from separate plants. All inflorescences were checked daily from 27 June to 14 July 2003. We recorded the number of flowers open, and also noted if any insects had accessed the cages. During the first week of August, all 20 inflorescences were collected and pressed. Seed counts were made in the laboratory and data were analysed using a two-tailed paired *t*-test. To measure how far launched pollen could be carried in air, we triggered individual flowers fixed to a black cardboard base indoors, where air currents were minimal. We photographed the distribution of pollen and recorded the location of each pollen grain or clump of grains.

Results

COMPARISON OF PREDICTED AND ACTUAL FLORAL MOVEMENTS

The calculated time evolution of the angles θ and ϕ from our model is plotted in Fig. 3. The curves are obtained using only the measured morphological data presented above, and do not rely on any free parameters. The calculated equation of motion from our model matches the observed motion of the stamens for the
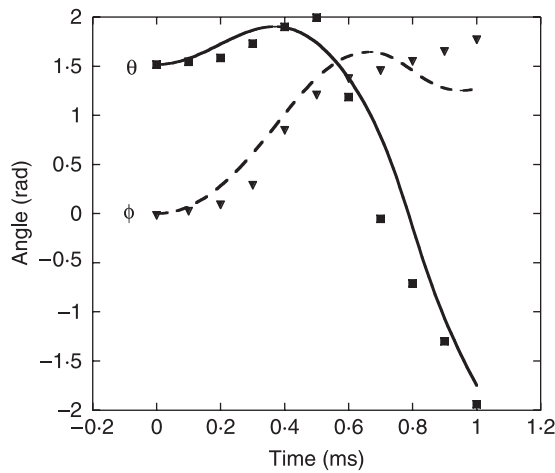
Fig. 3 Angles ϕ and θ (Fig. 2b) as a function of time. Measured angles from the high-speed video are represented by triangles (ϕ) and squares (θ); values based on the model are represented by dashed (ϕ) and solid (θ) lines. The results of our model agree well with the observed flower motion for the first 0·8 ms of the launching process.

first 0·8 ms of the launch process (Fig. 3). Because the pollen is launched in <0·5 ms, an analysis of the results from the calculated equation of motion can be used to understand how effectively the stamens launch pollen with this catapult mechanism. After 0·8 ms, the observed motion of the filament starts to deviate from the motion predicted by the model. This is probably because we have not considered the forces that act to damp the motion of the filaments, and because the anther is not free to rotate through an angle.

ANTHER ARRANGEMENT

Pollen is held by the anthers so that it is released only when the vertical speed is at its maximum. In mature buds, thecae dehisce longitudinally prior to flower opening (Fig. 4a). The thecae are angled inwards so that the stomia from adjacent stamens face each other, and pollen is held between adjacent anthers (Fig. 4b,c). As long as the movement of the anthers is purely vertical, the neighbouring anther sacs do not move apart and the pollen is not released. The co-ordinated motion of all

four anthers efficiently launches pollen straight upwards, as pollen is released only when the anthers move away from the centre and the stomia separate. To achieve maximum height, the anthers first accelerate upwards to a maximum speed before moving horizontally and separating.

OPTIMALITY OF LAUNCHING SPEED

The rotation of the anthers about the filament tip during the launch process delays the release of pollen from between the anthers until the vertical speed is maximized. While the filament moves in a circular arc, the anther tip accelerates straight up before moving sideways (Fig. 5a). Our model shows that the onset of lateral motion occurs only after the tip of the anther sac has accelerated to near its maximum vertical speed (Fig. 5b). The tips of the anthers reach a maximum vertical speed of 7·5 m s^{-1} approximately 0·5 ms after the petals open. With anthers that rotate, the onset of lateral motion is delayed until the filament is almost at its equilibrium position (2·2 rad), meaning nearly all the elastic energy available to the stamens has been transferred into vertical motion of the anthers before the pollen is released. Furthermore, the pollen is released only after the filament has reached its maximum vertical displacement and no longer provides an upward acceleration of the anthers. The relative time-scales for the anthers to rotate about the filament tips, and for the filaments to straighten, depend on the sizes, masses and stiffness of constituent parts of the stamen. The stamens of *C. canadensis* have a morphology in which the rates of anther movement and filament motion combine to release pollen immediately after it has been fully accelerated vertically. The coupled motion of the anthers and filaments results in a pollen launcher that passively releases its payload after it has been fully accelerated in the desired direction, much like an ancient trebuchet, which held its projectiles with a flexible strap.

WIND POLLINATION

Seeds were produced by three of the nine caged inflorescences, suggesting that, even with limited pollen donors, wind pollination is possible. One pair was excluded from
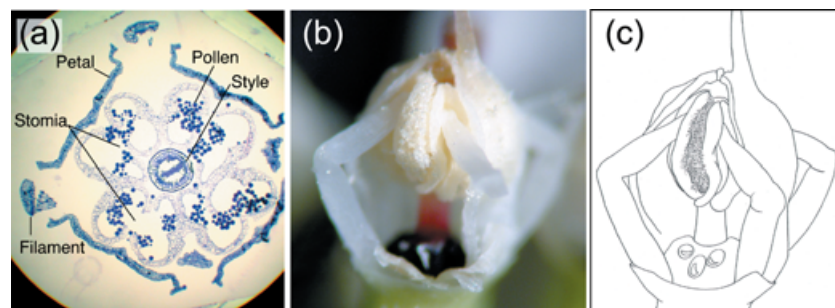

Fig. 4 Anthers and pollen position in bud. (a) Cross-section of a mature bud. The filament and stomia from a single stamen are labelled. Stomia from adjacent anthers meet, and pollen is held between them. (b) Photograph; (c) corresponding line drawing of a closed flower with one petal removed, showing that the pollen from dehisced thecae is held between adjacent anthers.
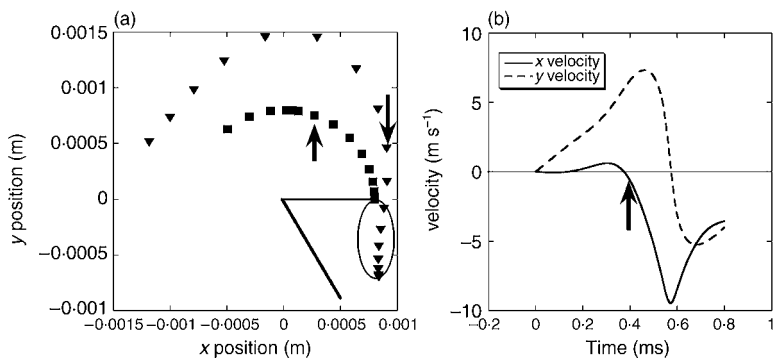
Fig. 5 Movement of filament and anther during pollen launch. (a) Parametric plot of the position of points on the tips of anther (triangles) and filament (squares) in 0·05-ms intervals. The schematic drawing of the stamen represents the orientation at $t = 0$. After the flower opens, the anther and filament move up and to the left. The average velocity of each time interval is proportional to the vector, which connects sequential positions. (b) The x (solid line) and y (dashed line) velocity components of the tip of the anther sac. The co-ordinate system is as in (a) such that movement along $-\hat{x}$ is away from the style. Arrows indicate the times when the anther tips begin to separate and release pollen.

the analysis because insect pollinators were found in the cage; the other nine cages remained pollinator-free. Seed set for *C. canadensis* is low in general, with only five of the nine uncaged inflorescences setting seed; of those, only 11–36% of the flowers in each inflorescence set seed. The caged inflorescences that set seed did so in 3–33% of flowers. Although sample size is low, seed set was not significantly different between the uncaged flowers (mean = 4, $n = 9$) and caged inflorescences (mean = 2, $n = 9$) (paired *t*-test, $t = -2·121$, $P = 0·0667$). Because overall seed set is highly variable and low, a larger sample size would be needed to distinguish between the relative importance of wind and insect pollination. The pattern of pollen deposition (Fig. 1c) shows that pollen is light enough to be carried over 22 cm, even in a room with only minor air currents. The ease with which pollen is carried by even the smallest air currents is also supported by its low terminal velocity (0·12 ± 0·03 m s^{-1}; Edwards *et al*. 2005), which indicates that any wind speed >0·12 m s^{-1} is sufficient to carry the pollen. As the mean density of bunchberry inflorescences in 10 randomly sampled 20-cm-radius plots was 26·8 ± 3·3 (mean ± SEM), pollen is likely to be carried to another inflorescence by wind, even with minimal air currents.

Discussion

We developed a biomechanical model, which reproduces the observed motion of the stamens of bunchberry flowers launching pollen. The model is based solely on morphometric data taken from living samples and has no free parameters, which allows an independent way to pinpoint when pollen release should occur if vertical launch speed is being maximized. Analyses from the results of our calculation confirm that the flowers of *C. canadensis* have a morphology that is optimal for

catapulting light pollen upwards at high speeds. The rates at which the filament straightens and the anthers rotate about the filament tip depend on the stiffness of the filaments, and the masses and sizes of stamen parts. A longer or more massive filament would straighten more slowly than a short one, and a smaller or less massive anther would rotate about the filament tip more quickly than a larger one. To launch pollen vertically at high speeds, the morphology of bunchberry flowers is such that the rotation rate of the anthers and the time to extend the filaments combine so that anthers separate and release pollen immediately after it reaches its maximum vertical speed. The optimization of movement to effect a large initial vertical velocity is important because the pollen is light and decelerates quickly due to drag forces from the air. The vertical propulsion of pollen is consistent with wind dispersal of the pollen, as the higher the pollen gets the further it can be carried by the wind. The pollen grains are sufficiently light and dry to be carried easily by wind currents. In a windless laboratory we observed that pollen was launched to heights exceeding 2·5 cm; in the field, with a slight wind, pollen was carried >1 m at ground level (Edwards *et al*. 2005). Because the flowers of the bunchberry grow so close to the ground, even a small increase in elevation above the forest floor places pollen into areas with higher wind speeds. Pollen launched sideways would not be carried up into wind currents. The pollen print (Fig. 1c), which was done in a closed room, shows that pollen is carried even by weak air currents and blankets a wide area between the flower and the pollen carried furthest, making contact with another flower likely in these densely growing populations. Furthermore, the stigmatic papillae of flowers elongate after the flower explodes open, increasing the surface area for capturing pollen. Finally, because *C. canadensis* is self-incompatible (Barrett & Helenurm 1987), seed set by flowers in pollinator-exclosure plots supports pollination by wind.

When pollen is launched at sufficiently high speeds, it can also become embedded in the hairs of visiting insects. This is significant because, in order to be successful at wind pollination, the pollen grains of *C. canadensis* are smooth, unlike typical sticky pollen grains in exclusively entomophilous flowers (Proctor & Yeo 1973). Consequently, large impact speeds are required to make pollen stick to visiting insects. In the field, we observed that visitors that triggered flowers to open were blasted with pollen, which coated the undersides of their bodies, allowing it to be transported to another inflorescence. Insects too light to trigger flowers to open rarely carried pollen. Touching the style to an insect coated with pollen removed pollen from within the hairs of the insect. This higher affinity of the stigmatic papillae for pollen facilitates transfer of pollen between different flowers via biotic vectors.

A detailed analysis of the motion of the stamens of *C. canadensis* flowers using a biomechanical model reveals that they are ideal for catapulting their pollen vertically at high speeds. Field observations confirm

that this behaviour enables dual methods of pollination. Therefore the sophisticated launching mechanism of *C. canadensis* flowers may increase fitness by providing an alternative pollination method when insect populations are limiting. This behaviour supports recent hypotheses (Waser *et al.* 1996; Johnson & Steiner 2000) that dual pollination syndromes stabilize seed production, and adds to the list of plants that are successful at both wind and biotic pollination (Culley, Weller & Sakai 2002; Lázaro & Traveset 2005).

Acknowledgements

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Ecological Society,
Functional Ecology,
21, 219–225