Role of Honey Bees (Hymenoptera: Apidae) in the Pollination of Buckwheat in Eastern North America

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ABSTRACT Seed production in buckwheat, *Fagopyrum esculentum* Moench, can be lower than expected from the plant biomass. Low seed production is often blamed on inadequate pollination. Honey bees, *Apis mellifera* L., were at least 95% of the insect visitors to buckwheat flowers in fields of central New York State. The number of times each flower was visited by a honey bee ranged from zero to >40, but the number of honey bee visits did not increase daily seed initiation if each flower was visited at least twice. Pollen delivery sometimes limited seed set, but limitation was not associated with low honey bee visitation frequency. The yield and genetic quality of buckwheat is best with pollen deliveries of at least 10 grains, but honey bees delivered less pollen. The time between delivery of the 1st and 10th pollen grain was ≈1 h, which is more than enough for fertilization to occur. Buckwheat in New York is pollinated primarily by honey bees, but bee behavior is not well adapted to the crop, and the effectiveness of bees as pollinators was not improved at higher bee populations.

KEY WORDS *Apis mellifera, Fagopyrum esculentum,* pollination

CULTIVATED BUCKWHEAT, *Fagopyrum esculentum* Moench, is an insect-pollinated plant that exhibits great variability in seed set (Marshall 1969). Buckwheat has dimorphic, heterostylous self incompatibility requiring insect pollination to ensure cross-fertilization (Marshall 1969). European honey bees, *Apis mellifera* L., are frequently the most abundant pollinators of buckwheat, and are often assumed to be the most effective pollinators. Honey bees account for nearly all the insect visits to buckwheat flowers in many places: 90% in Germany (Müller 1883), 95% in western Poland (Banaszak 1983, Jablonski et al. 1986), 97% in Belorus (Kushnir 1976). Elsewhere, other insects dominate and honey bees account for few visits: 5% in Japan (Namai 1986), 37% in Orel, Russia (Naumkin 1992). The pollinators of buckwheat in its native range in Yunnan have not been identified (Ohnishi 1990). Buckwheat has been cultivated extensively in the northeastern United States since European settlement, but there have been no reports of which insects pollinate the crop in this region or whether these pollinators transfer enough pollen to assure sufficient pollen deposition.

Data on the rate of pollen deposition are needed to determine the effective flower pollen load because the total daily pollen deposition may include pollen that arrived after fertilization. Field measurements on buckwheat have been made only in a location where syrphid flies, *Eristalis cerealis,* were the predominant pollinators (Namai 1990). In that study, 4–5 insect visits were necessary for maximal seed set.

If pollen deposition limits seed production, and honey bees are effective pollinators of buckwheat, then buckwheat growers should be able to improve seed set and yield by having additional hives near the fields. Comparisons of yields between fields having many honey bees and those with few have shown differing results. Where honey bees were nearly absent, in Ukraine and Russia, yields were only 50–75% (Baga 1976) and 60% (Melnichenko 1976) of yields with hives. However, where honey bees were already present, in United States and Poland, Hartley (1964) and Jablonski and Szklanowska (1990) found no effect of adding hives. The importance of bees has also been tested by growing the crop in cages to exclude honey bees, with different results. The yield was either reduced by half (Ren and Liu 1986) or by 100% (Namai 1986), suggesting that pollination without flying pollinators is highly variable. These results have been incorporated as recommendations to farmers to add from 2 (Free 1970) to 5 (Smirnov 1985) hives per hectare, which represent a substantial production cost. Thus it is important to know when adding beehives is effective.

This article reports on investigations of whether honey bees are responsible for the characteristic yield variation in buckwheat, describing the effect of honey bee activity on seed set in buckwheat, and on the occurrence of pollen limitation. It also describes the timing of pollen removal from the anther sacs and deposition on the stigmas.

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Materials and Methods

Field Sites. Seed set and honey bee effectiveness were measured in 5 fields in 1991, 3 in 1992, and 2 in 1993. These fields were at the New York State Agricultural Experiment Station in Geneva, NY, and on commercial farms within 50 km of Geneva. Each year, different fields were used as a consequence of crop rotation. In 1991, 2 locations had a pair of bee-exclusion cages (3 by 4 by 2 m), with the control cage in each pair open at the sides to account for shading. 'Manor' buckwheat was sown between 29 June and 6 July each year. The annual bloom period was from ≈5 August through 3 September each year, with most seeds initiated in ≈1 wk centered on 16 August (Björkman et al. 1995).

Honey Bee Visitation Frequency. Seven inflorescences were used to determine the visitation frequency. Every hour from 0830 to 1130 hours, the number and type of insects visiting each inflorescence was recorded for 15 min. From these counts, an estimate was made of the total number of honey bee visits to each flower during the period that pollen was available. Pollen was usually available for 90 min, and honey bees visited every open flower in each inflorescence. Therefore, the estimate was 6 times the mean number of honey bee visits to each inflorescence during the two 15-min counting intervals immediately after anther dehiscence. The time of anther dehiscence varied with the site and the weather.

Honey bees followed a fairly consistent pattern when visiting buckwheat plants. While pollen was available, honey bees stopped briefly in flight to inspect inflorescences from a distance of 5–10 cm. If the inflorescence was rejected, the honey bee inspected several additional inflorescences on the same plant or adjacent plants. If the honey bee landed, it visited all the open flowers on the inflorescence and then flew at least ½ m before inspecting another inflorescence. They rarely visited inflorescences on the same plant consecutively. This method of inspecting inflorescences may have been to determine the amount of nectar available. Visits to the marked flowers occurred at regular time intervals as would be expected with a constant rate of nectar flow. Preliminary counting showed that inflorescences with between 2 and 7 open flowers received the same number of visits.

Pollen Transfer. Seventy to 100 flowers on the plants used to measure honey bee visitation frequency were hand pollinated by brushing a compatible anther against the stigma while observing the pollen transfer under magnification. This method typically resulted in a load of >50 compatible pollen grains, ensuring that seed set was not limited by low pollen acquisition.

Seed Set. The fate of each flower was determined after 10 d. The 3 fates were dead flower, aborted seed, and normal seed; each fruit contains a single seed. At 10 d, normal seeds have elongated and swelled, having begun to accumulate starch in the endosperm and to reach nearly their final volume; aborted seeds accumulate little or no starch (Adachi and Kajita 1989, Horobowicz and Obendorf 1992). In aborted seeds, the ovule only elongated after being arrested at ≈3 d of normal development. All aborted seeds contained embryos, indicating that fertilization had been successful.

Flowers were scored as dead if the sepals had senesced and the ovary was shorter than the sepals, and as an aborted seed if the sepals had not senesced and the ovary was longer than the sepals but there was no swelling of the ovule. Seeds were scored as normal if the ovule had swelled to at least 5 times the initial volume with starchy endosperm. Intermediate fates were very rare, so the score of each flower generally fell easily into one of these categories.

The relationship between potential seed set and actual seed set was compared by linear regression, with the intercept set at the origin and potential seed set as the independent variable. The hypothesis that the seed set was equal under both pollination regimes was rejected if the slope was significantly <1, using Student's *t*-test. The relationship between visitation frequency and seed set was analyzed by testing for a significant positive correlation.

Pollen Availability. To determine when pollen was available on the anthers, 40 flowers were collected from 5 plants every half hour from flower opening (0830 hours) until all pollen was gone (1130 hours) and observed under a dissecting microscope. The 8 anthers of a flower collectively make ≈1,000 pollen grains (Ganders 1979). Each flower was scored using 4 categories: anthers unopened, abundant pollen (>15 pollen grains remaining per flower), traces of pollen (0–15 pollen), and no pollen.

Pollen Deposition. Flowers were scored for deposition of pollen on the stigma every half hour in the morning and hourly in the afternoon. Twenty flowers of each flower type were collected in 70% alcohol at each time point. Honey bee visits were counted hourly through the day using the method described above. The pollen grains were later counted under a dissecting microscope. The alcohol caused the pollen to turn black, making further staining unnecessary. The pollen grains germinate within 2 min, and are then firmly attached to the stigma. Pollen from the same (incompatible) and the opposite flower type (compatible) were scored separately. The 2 types are easily distinguishable by size: the thrum pollen diameter is 50 μm, and pin pollen is 40 μm (Schoch-Bodmer 1934). The deposition of the 2 types of pollen on stigmas is described in detail by Björkman (1995).

Statistical Analyses. The relationship between visitation frequency and pollen limitation was tested by linear regression of the pollen limitation on the predictor, visitation frequency. Pollen limitation was taken as the difference between the po-

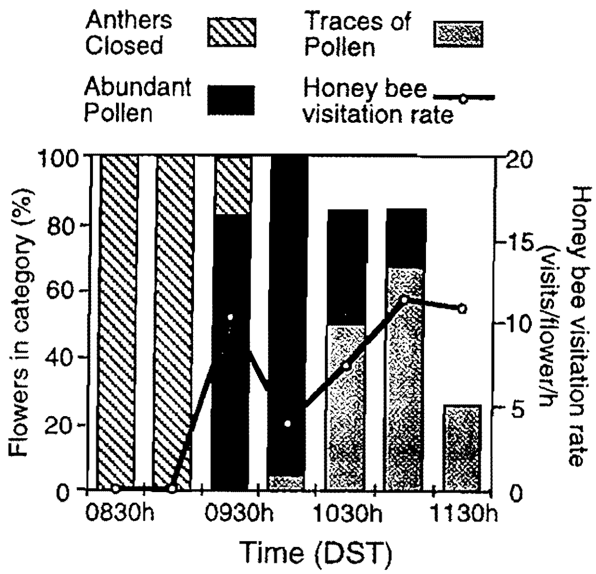


Fig. 1. Representative time course of honey bee visitation frequency and pollen removal from anther sacs. Honey bees appeared soon after the anthers dehisced and rapidly removed pollen. Bees could not collect pollen from closed anther sacs or from empty ones. Anthers with available pollen were scored in 2 classes, abundant pollen (15–1,000 grains) and traces of pollen (1–15 grains). Pierson Farm, 8 August 1991.

tential and actual seed set. The expected model would be a negative-exponential relationship with limitation approaching zero as pollinator activity increases. However, the data were not distributed appropriately for making such a fit. The simpler model was chosen, testing simply whether pollen limitation declined as visitation frequency increased.

The kinetics of pollen deposition were fitted with logistic regression using 3 parameters: the midpoint time, the rate of delivery, and the final value, in the model:

proportion of flowers with $\geq n$ pollen =

$$\text{final proportion} \times e^{[1+e^{-(\text{rate}\times[\text{time-of-day}-\text{midpoint}])}]}.$$

This model is used to fit proportional data that change from an initial value to a final value as a function of the predictor variable (Hosmer 1989). For these data, the initial value was known to be zero. The time between the delivery of the 1st pollen grain until there were 10 or more pollen grains was estimated as the difference in the time parameter, and tested as a linear contrast with a t-distribution. The proportion of flowers ultimately receiving $\geq$10 pollen grains was estimated as the asymptote parameter.

Results

On clear days the anthers opened between 0830 and 0930 hours; and by 1130 hours pollen was scarce. In cool or rainy weather the anthers opened 1 or 2 h later. A few scout bees appeared when the flowers first opened, but substantial numbers of honey bees appeared only when the anther sacs opened. After all the pollen had been removed, the number of honey bee visits decreased (Fig. 1). Honey bees constituted 95% of the insect visits to the flowers during the time that pollen was available. Other insects included flower flies, *Syrphus* spp. F.; houseflies, *Musca domestica* L.; ladybird beetles, *Cocinella novemnotata* Herbst; Eastern yellowjackets, *Vespula maculifrons* (Buysson); and bumblebees, *Bombus* spp. On most days, all the insect visitors were honey bees. No more than 5 visits by other insects were observed on any day, and these usually occurred when little pollen was left on the anthers. Therefore, honey bees appear to be the only important pollinator of buckwheat at these sites because they are the primary insect visiting the flowers while pollen is present.

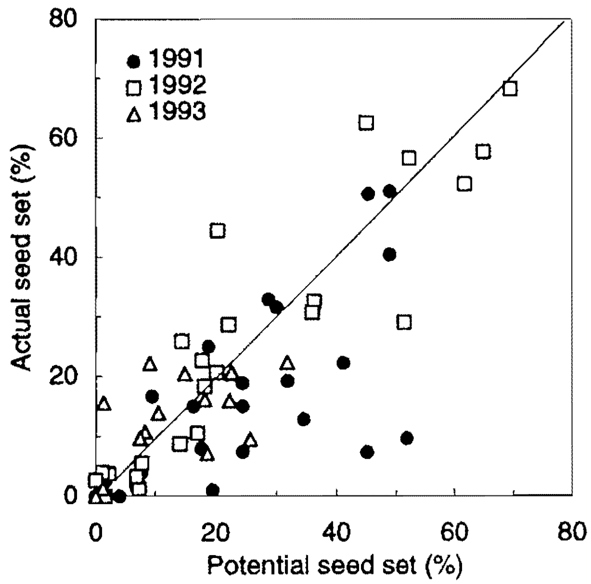


Fig. 2. Efficiency of natural pollinators in obtaining the potential seed set. The potential seed set is the proportion of flowers setting seed with hand pollination. The actual seed set is the proportion of flowers making seeds following pollination by natural pollinators. Each point is the results for 1 field on 1 d. For 1991, actual seed set averaged 66% of potential seed set, in the other 2 yr it was not significantly less than the potential set. The ideal, where natural pollination produces the full potential seed set, is indicated by the line.

Limitation of seed set by pollination was determined by examining whether hand pollination resulted in better seed set than natural pollination. Insufficient pollination limited seed set in 1991, but not in 1992 and 1993 (Fig. 2). In 1991, the seed set was only 66% of potential seed set (t = 4.42, $P < 0.01$ that it is <100%), in 1992 and 1993 the slopes were not significantly different from 100% (t = 0.78 and t = 0.13 respectively). Cold, rainy weather in 1992 was expected to inhibit honey bee activity, and exceptionally warm, dry weather in 1991 was expected to favor honey bee activity.

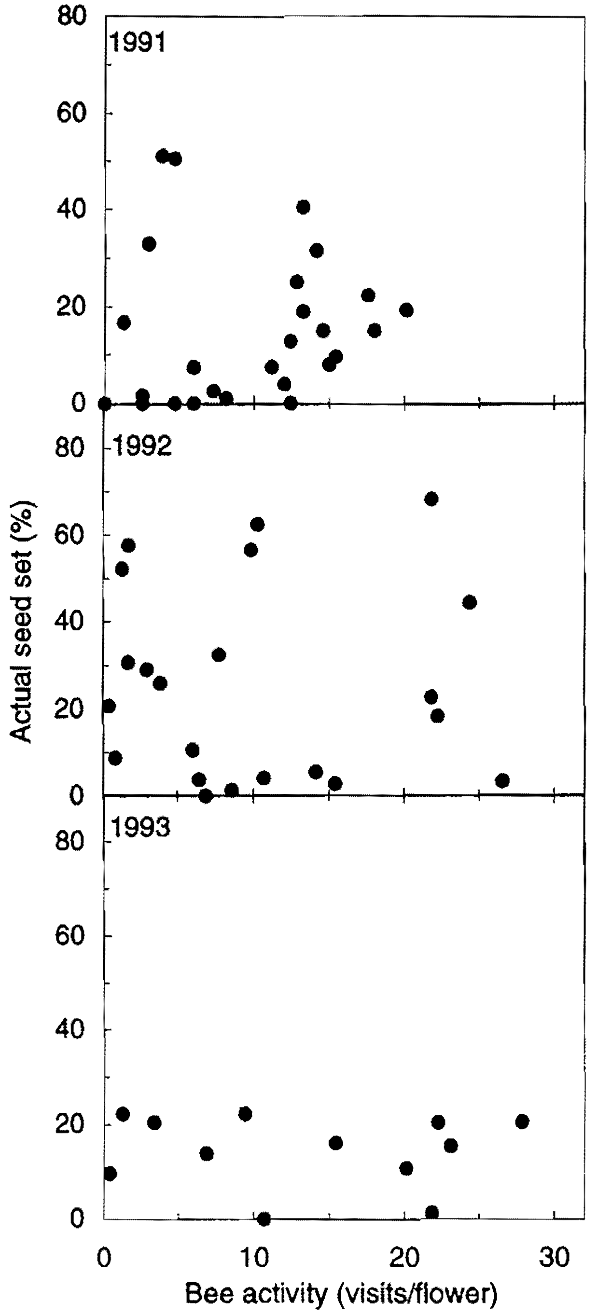


Fig. 3. Effect of honey bee visitation frequency on seed set. The visitation frequency is the mean number of times each flower was visited by a bee during the period that pollen was available on anthers. The seed set is the proportion of flowers open on that day that later made a seed. Each point is the measurement in 1 field on 1 d.

Interestingly, visitation frequency was similar in these years (Fig. 3) and pollination was inadequate only under the conditions expected to favor honey bee activity.

To determine the visitation frequency necessary for full seed set, the number of honey bee visits to each flower was related to the seed set for each day. High seed set could be obtained with as few as 2 honey bee visits (Fig. 3). In bee-exclusion cages in 1 field, hand pollination produced seed set

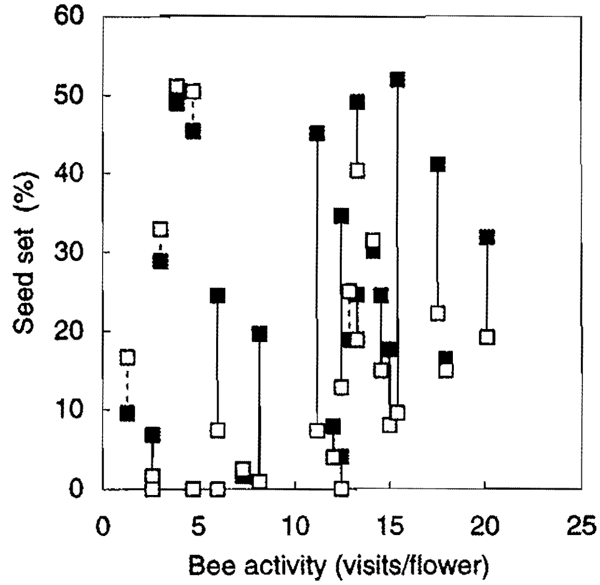
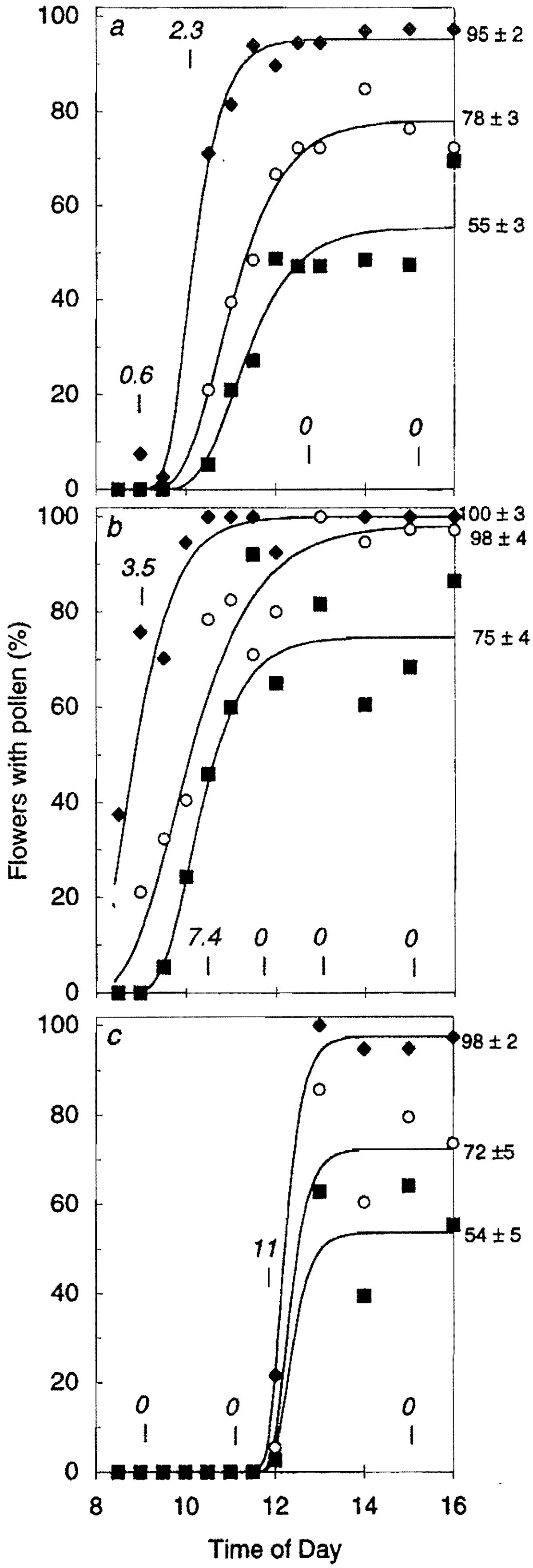


Fig. 4. Effect of honey bee visitation frequency on pollen limitation. Pollen limitation was inferred if saturating hand pollination produced greater seed set than natural pollination. Open symbols, hand pollinated; closed symbols, naturally pollinated. Points for individual days are connected by vertical lines, with solid lines indicating pollen limitation.

comparable to the open cages (up to 43%), but there was no natural seed set; thus, flying insects were essential pollinators. The potential seed set varied substantially, decreasing as the season progressed, causing much unrelated variation in Fig. 3. That variation can be reduced by making a more direct comparison between varying visitation frequency and pollen limitation (Fig. 4). Visitation frequency was frequently high on days in 1991 when pollination was limiting. (Pollination was never limiting in 1992 and 1993, so the comparable comparison for these years is the same as Fig. 3.) This relationship was analyzed by testing whether pollen limitation declined as the visitation frequency increased. Limitation did not decline, the relationship being: pollen limitation = +0.417% × honey bee visits (±0.186%, $P = 0.035$). Pollen limitation was, if anything, greater with many honey bees than with few.

The kinetics of pollen deposition was similar to that of pollen removal from the anthers, occurring over 1–2 h (Fig. 5). The pattern of visitation frequency on 6 and 11 August was typical of that occurring when the data in the previous figures were collected. The flower load of compatible pollen per visit was small: it took nearly an hour between delivery of the 1st pollen grain and delivery of the 10th: the difference in the half-time parameter of the logistic fit was 63 ± 6 min on 6 August and 87 ± 7 min on 11 August. An exceptional situation was observed on 20 August, when rain delayed anther dehiscence until late morning. When the anthers did dehisce, the honey bees began working intensively, and transferred the pollen especially



quickly. On this date, the time between the 1st and 10th grain was only 10 ± 3 min.

The peak honey bee visitation frequency occurred at the time of peak pollen accumulation on each of the days (Fig. 5). High visitation frequency was also associated with a high pollen accumulation rate (the dimensionless logistic coefficient): 6 August, 2.3 visits per hour → 1.3 rate; 11 August, 7.4 visits per hour → 1.6 rate; 20 August, 11 visits per hour → 3.3 rate.

Discussion

Seed yield of insect-pollinated crops is reduced when pollinators are absent, but if indigenous pollinators are already sufficient, adding beehives will have no benefit. In buckwheat production, it is not known how abundant natural pollinators must be for added beehives to be worthwhile. The minimum number of honey bees for satisfactory pollination can be estimated by determining the relationship between visitation frequency and seed set. It is possible to determine whether seed set is pollen limited by comparing the natural seed set with that following saturating pollination.

Honey bees are the main pollinator of buckwheat in New York State, they accounted for >95% of insect visits. Being generalized pollinators, they are not necessarily effective pollinators of all the species they visit (Westerkamp 1991). In fact, they were poor at transferring buckwheat pollen, both in the total amount and in the rate of delivery. A related study found that they were also poor at cross-pollinating between the 2 flower types (Björkman 1995).

Pollen was available for transfer only for 1–2 h after anther sacs dehisce. Honey bees were especially active during this time, to the exclusion of other insects. To determine whether a sufficient honey bee population exists in a particular field, visitation frequency must be measured during this period.

The weak relationship between visitation frequency and seed set could be caused by abiotic pollination. However, no seed was set in the ab-

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Fig. 5. Kinetics of pollen accumulation. The 3 curves in each panel are proportion of flowers having any compatible pollen (◆), >5 compatible pollen grains (○) or >10 compatible pollen grains (■) at each time. Twenty flowers of each morph were inspected at each time through the day, and visitation intensity recorded several times. The solid lines are the fitted logistic equations. The italic numbers within the figure are the bee activity (visits per flower per h) at the time indicated by the vertical bar. The calculated proportion of flowers ultimately pollinated with each load is indicated on the right, with the standard error. The logistic fit r^2 = 0.982, 0.949, and 0.984, respectively, for the 3 panels. Data were collected during the main period of seed set in 1993, on 6 August (*a*), 11 August (*b*), and 20 August (*c*).

sence of insect pollinators. Although wind pollination is possible (Marshall 1969), airborne pollen is negligible, and the seed set caused by airborne pollen is the same (1%) as in pollen-free air (Namai 1986). Contributing to the poor relationship could be the common occurrence of low seed set with high visitation frequency caused by reduced maternal function late in the season (Björkman et al. 1995).

The genetic quality of progeny plants benefits from pollen competition (Mulcahy and Mulcahy 1975), for which simultaneous delivery of >10 pollen grains is needed in buckwheat (Björkman 1995). The pollen tubes grow so quickly that effective competition would only occur among pollen delivered within a few min of each other. The gradual delivery of pollen by honey bees precludes pollen competition. Even in a field with high visitation frequency, it took an hour between delivery of the 1st and the 10th compatible pollen grain, and as many as half the flowers never got 10 pollen grains. Because the progeny produced under conditions of pollen competition are more vigorous than those without pollen competition (Mulcahy and Mulcahy 1975, Björkman 1995), this potential mechanism for maintaining genetic quality in the germplasm is lost when honey bees are the main pollinator. The slow delivery of pollen may be explained by the morphology of the honey bee with respect to the flowers. The flowers are quite small (5 mm) compared with the honey bee. When the honey bee alights on the flower, only its legs and lower thorax touch the reproductive parts of the flower. It may be advantageous to identify a more effective pollinator of buckwheat for commercial buckwheat production in places where pollination is insufficient.

The measurements made here can be used to estimate the honey bee population required to pollinate a buckwheat crop. Honey bees visit about 20 flowers per minute (Hamakawa 1986), there are ≈1,000,000 plants per hectare, 40 open flowers per plant each day, and each flower needs to be visited twice during the 100 min that pollen is available. Therefore, to make the needed 80,000,000 visits in 100 min requires ≈40,000 actively working honey bees per hectare. If this many honey bees are already present, adding more bees cannot be expected to increase seed set. The number of hives needed to obtain enough active bees in nearby buckwheat fields depends too much on local conditions to accurately evaluate Free's (1970) recommendation of 2 hives per hectare.

In summary, honey bees are the most important pollinator of buckwheat in central New York. The maximum seed set was observed with as few as 2 bee visits per flower. Feral honey bee populations resulted in 2–40 visits in all the sites sampled, hence supplemental hives would not have increased the seed yield. Honey bees were not effective at delivering large pollen loads over a short time, yet large pollen loads are valuable for ensuring fertilization by superior pollen through pollen competition.

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