Exploring Alternate Conceptions of Flowering Phenology with an Interactive Systems Model

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A systems model of alfalfa pollination [1, 2] can be used to compare two alternative conceptions of flowering phenology. In this context, phenology refers to the pattern of change in the number of open flowers over time. For example, many plants show a right-skewed flowering distribution: flowering begins rapidly and tails off slowly [3]. Although the model was designed for alfalfa pollination, it is relevant to other flowering plants with indeterminate growth as well.

In the first conception, the pattern of bloom is intrinsic to the plant, interacting with abiotic factors such as temperature and day length. In the second conception, bloom shuts down as a result of the accumulation of fruit or seeds; therefore, phenology is dependent on the rate of pollination. Feedback from maturing fruits/seeds on flowering is well known for many angiosperms with indeterminate growth [4]. Yet, the implications of this feedback are not well explored, and much of the literature on flowering phenology suggests that genetic and abiotic factors are the most important proximate cause of patterns of bloom over time.

Alfalfa is grown for seed production in the Pacific Northwest (USA) where the alfalfa leafcutting bee, *Megachile rotundata* F. is managed for pollination. Up to 100,000 bees may be released per hectare. Bloom in alfalfa fields typically follows a right-skewed curve, reaching an early peak, followed by a slower decline in bloom [5, 6]. In two studies of commercial alfalfa seed fields [5, 6], peak nesting activity of the bees was delayed by two or three weeks relative to peak bloom, so that most bee nesting occurred under conditions of intense competition for flower resources. Bosch and Kemp [6] conclude that "pollination could have been accomplished on younger flowers, with smaller bee populations whose nesting was better timed with peak bloom"; i.e, if bees were released earlier, peak nesting activity would correspond with peak flower resources, and fewer bees would be necessary to provide pollination.

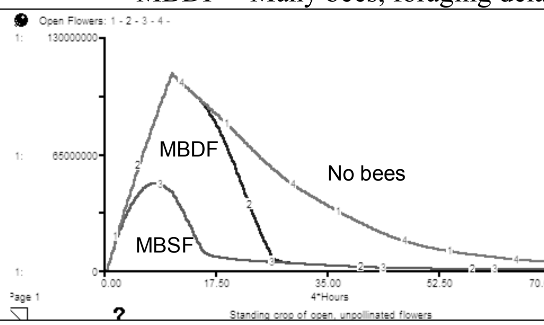
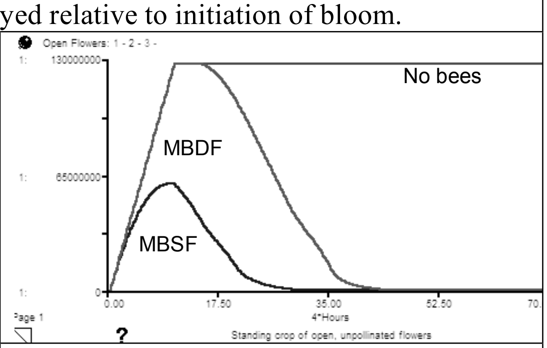
I used the model of alfalfa pollination to determine how the timing of foraging by leafcutting bees relative to initiation of bloom impacts seed yield over a range of bee population sizes. In the first version of the model, the rate of bud opening is rapid initially and declines exponentially over time. In the second version of the model, rate of bud opening is rapid initially, but it declines exponentially in response to the accumulation of seed pods. A sample of the results are summarized in Figure 1.

If pollination is delayed relative to the start of bloom, seed set is reduced when flowering phenology is internal. However, if flowering phenology is mediated by the pollinators, then seed set is delayed but not reduced (everything else being equal) by delayed pollination. To determine the impact of pollinator population and timing on seed yield, it is not enough to monitor bloom and pollinator population size over a season. Rather, it is important to determine how the rate of bloom varies in the absence of pollination. More generally, the faster the rate of bloom when pollination begins, the higher the seed yield.

Conference participants will be able to examine the underlying structure of the model, to run a baseline version, to examine how the model parameters change over time, and to vary the model parameters to determine the impact on pollination.

References

[1] Strickler, K. (1996) *J. Kansas Entomol. Soc.* 69:201–215.
[2] Strickler, K. (1997) In: K.W. Richards, ed. *Proc. Int'l. Symp. on Pollination Acta Horticulturae* 437, ISHS pp. 109–113.
[3] Thomson, J.D. (1980) *Ecology* 61:572–579.
[4] Rathcke, B., and E.P. Lacey (1985) *Ann. Rev. Ecol. Syst.* 16:179–214.
[5] Strickler, K., and S. Freitas (1999) *Environ. Entomol.* 28:178–187.
[6] Bosch, J., and W. Kemp (2005) *J. Econ. Entomol.* 98:1077–1086.

<table>
<tr><td></td><td>Internal control of bloom: the rate of bud opening starts out high and declines exponentially over time.</td><td>Bloom depends on feedback from pods: the rate of bud opening starts out high and declines exponentially as seed pods accumulate.</td></tr>
<tr><td></td><td colspan="2">MBSF = Many bees, foraging synchronized with initiation of bloom.
MBDF = Many bees, foraging delayed relative to initiation of bloom.</td></tr>
<tr><td>Phenology: Number of open flowers over time</td><td>
</td><td>
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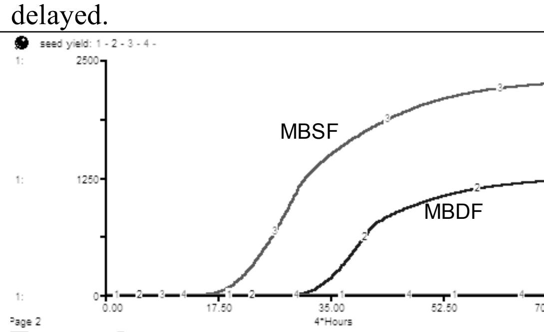
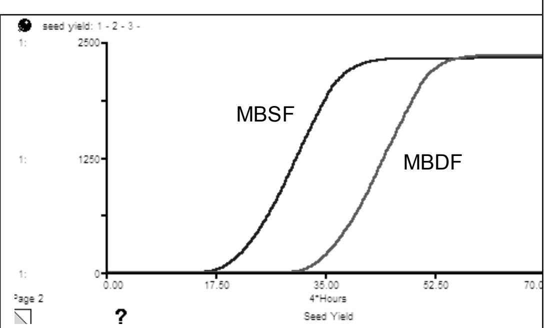
<tr><td></td><td>Bloom declines even in the absence of bees.</td><td>Bloom remains high in the absence of bees</td></tr>
<tr><td></td><td colspan="2">In both cases: Right-skewed bloom curve; peak bloom is lower and pollination is completed sooner when bee foraging is synchronized with bloom than when foraging is delayed.</td></tr>
<tr><td>Cumulative seed yield over time</td><td>
</td><td>
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<tr><td></td><td>Seed yield by the end of the season is greater when bee foraging is synchronized with initiation of bloom compared with delayed foraging.</td><td>Seed yield by the end of the season is the same whether foraging is synchronized with initiation of bloom or delayed.</td></tr>
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Figure 1. Comparison of two conceptions of bloom.