A dynamic optimization model of the influence of allocation pattern and herbivore and pollinator environments on plant fitness

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Introduction

Fecundity and survival can be influenced by a plant's pattern of resource allocation, which trades off growth, reproduction, and defense functions[1]. **The phenology and abundance of herbivores and pollinators can affect growth[2], reproduction[3], and defense[4], and thus different allocation patterns may be optimal in different pollinator and herbivore environments.** Additionally, indirect herbivore-pollinator interactions mediated by plant traits[5-6] may feed back to alter influences on plant performance.

Dynamic optimization modeling has been used to predict patterns of optimal allocation to growth, sexual and vegetative reproduction, storage and defense for both annual and perennial plants, and some studies also consider herbivore pressure[7-8]. However, the concurrent influence of herbivores and pollinators on the fitness associated with plant allocation patterns has yet to be modeled.

Here we use an optimization model to consider how herbivore and pollinator phenologies influence the fitness of plant resource allocation patterns which may lead to insights into how allocation patterns are maintained in annual and perennial plants. This model complements a larger ongoing empirical project examining the interactions of herbivores, pollinators and plant resource allocation.

Model parameters

Fitness is defined by fruit set over a single 100 day season (annual plants) or a lifetime of 30 seasons (perennial plants). Fruit set is a function of open flowers, pollinator abundance, and herbivore abundance. Pollinator and herbivore abundance are described by Gaussian curves; flowers are a function of plant size and allocation to reproduction; plant size is a function of initial size and allocation to growth. Allocation pattern within a season is either an abrupt shift from growth to reproduction (Fig. 1a) or a gradual shift (Fig. 1b); either may occur at any point in the season Perennial and clonal plants have additional functions for allocation to storage and clonal growth.

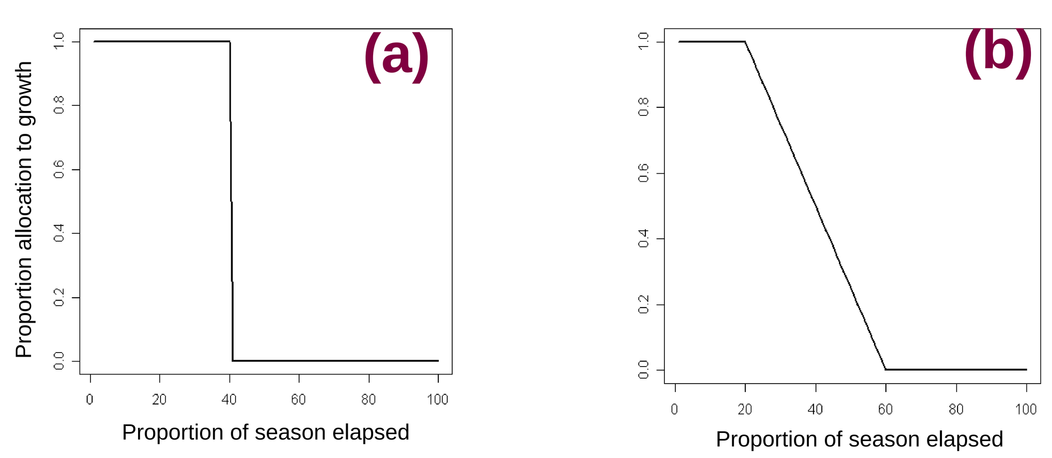

Fig. 1 (a-b). Allocation patterns for (a) abrupt and (b) gradual shift from growth to reproduction.

Results

Q1: How does allocation pattern affect fitness?

For both annual and perennial plants, average yearly fitness is highest for an abrupt late-season shift in allocation from growth to reproduction (Fig 2b,e). Annual life cycles are more likely to have two fitness peaks, a high peak when late pollination and late herbivory coincide, and a lower peak when mid-season pollination follows early-season herbivory.

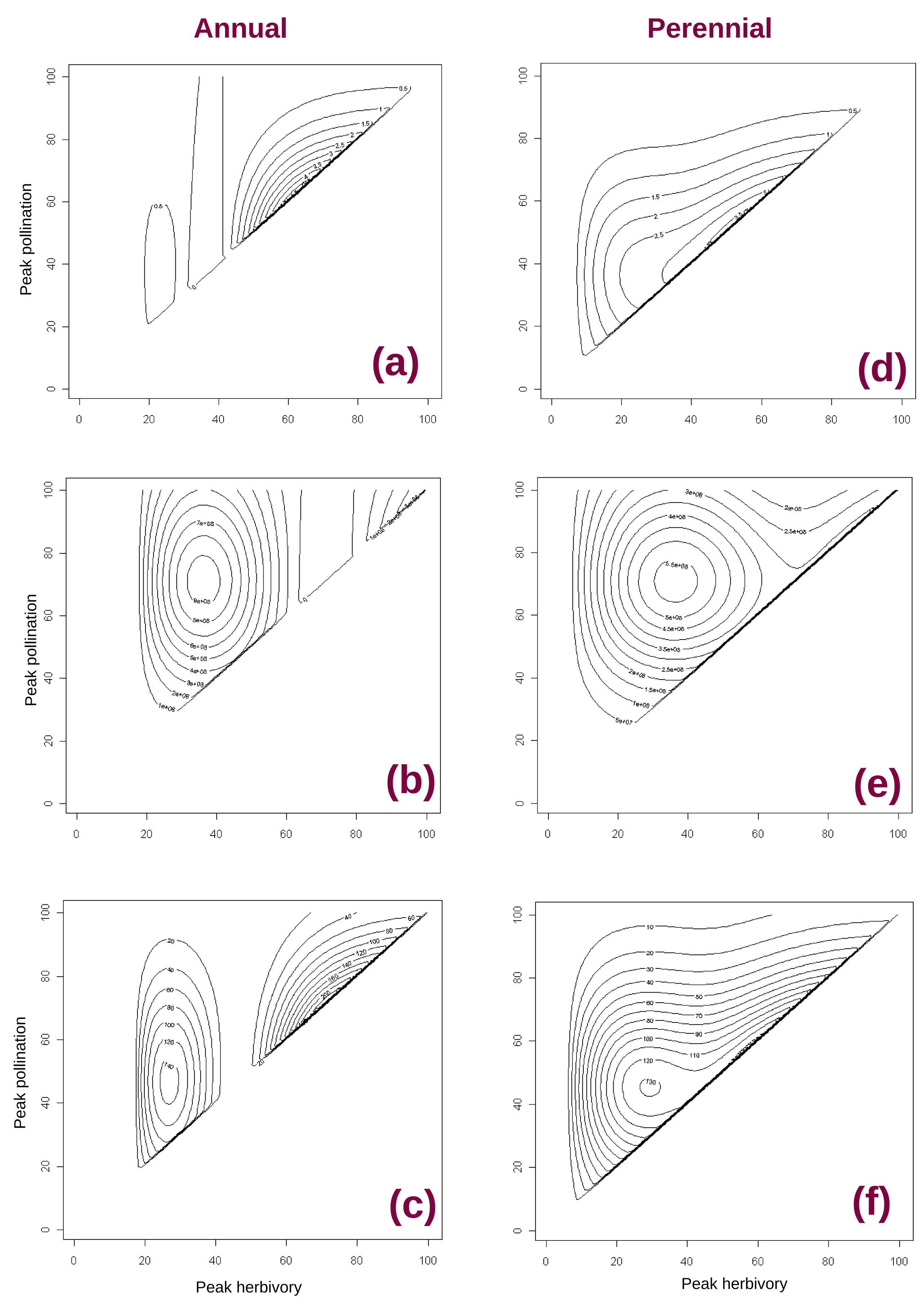

Fig. 2 (a-f). Fitness surfaces under changing peak herbivory and pollination levels with (a,d) early abrupt, (b,e) late abrupt and (c,e) gradual shift from growth to reproductive allocation, for annual (a-c) and perennial (d-f) life cycles. Peak herbivory and peak pollination coincide at the 1:1 line.

Results

Q2: How do herbivory and pollination affect fitness?

For annual plants, early-season herbivory reduces fitness more than late-season herbivory (Fig. 3), while in general changes in herbivory have a sharper effect on fitness than do changes in pollination (seen in the steepness of the decrease from the fitness peak as herbivore phenology changes in Fig. 2b and 2c, in contrast to the shallower slope as peak pollination changes). Regardless of allocation pattern, fitness is highest with late-season pollination; fitness is very low when peak pollination occurs earlier than peak herbivory (Fig 2).

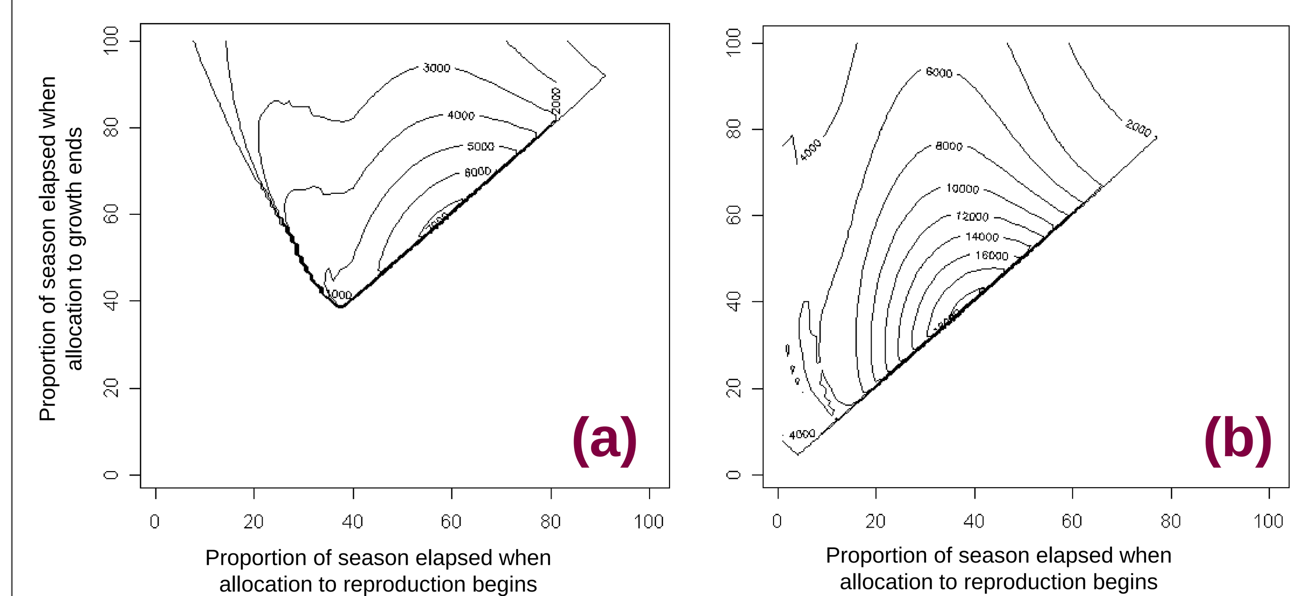

Fig. 3 (a-b). Fitness surfaces for an annual plant under (a) early-season and (b) late-season herbivory. Abrupt shifts in allocation to reproduction occur for points near the 1:1 line, and gradual shifts occur for points in the upper left region.

For both annuals and perennials, changing the strength of herbivory (the height of the distribution in Fig. 1) changes the shape of the fitness surfaces (Fig. 4 a-b), with lesser changes in fitness occurring when pollination is strong. Increasing the strength of pollination causes a direct increase in fitness values, regardless of the strength of herbivory. Fitness contours are similar for annual and perennial plants, except that average yearly fitness for annuals is higher than for perennials, which divert some resources from reproduction to storage.

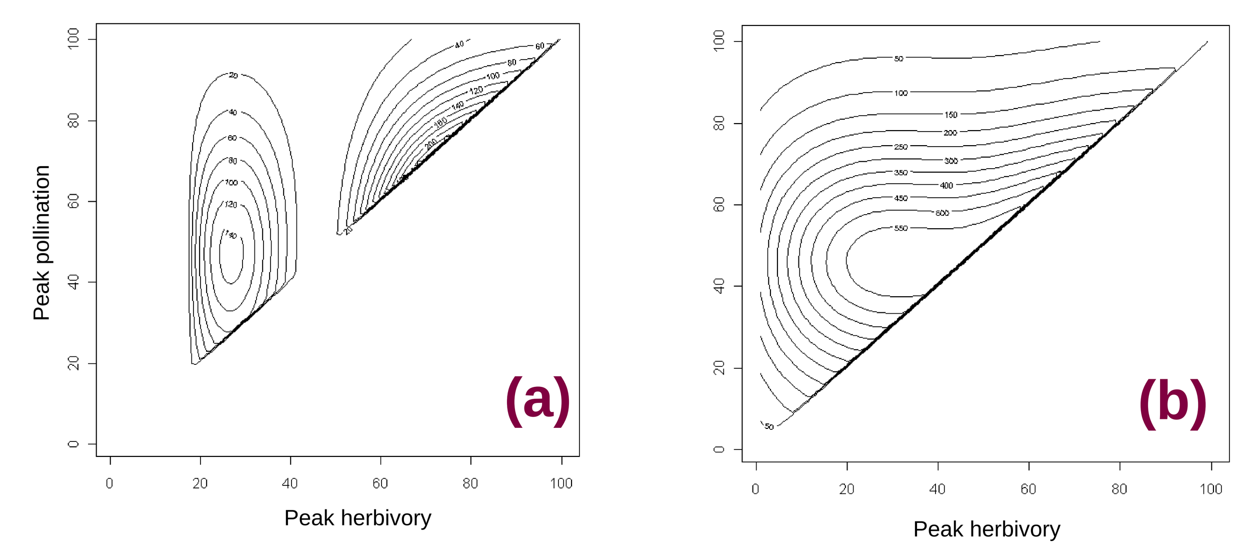

Fig. 4 (a-b). Fitness surfaces for an annual plant under (a) strong herbivory and strong pollination and (b) weak herbivory and strong pollination. This pattern holds for perennial plants, with marked changes to the surface with changing herbivory but not with pollination.

Conclusions

For the parameter values we use, an abrupt shift in allocation from growth to other functions yields higher fitness than a gradual shift, but only when the shift occurs late in the season. Fitness is always low under late peaking herbivory, unless pollination is likewise late.

Changes in herbivore phenology markedly change the shape of the fitness surface, while increases in pollination strength ameliorate deleterious herbivory effects. Changes in herbivore phenology have a stronger effect of optimal allocation patterns than changes in pollinator phenology.

The influence of herbivory on both fitness values and the shape of the fitness contour agree with previous theoretical work. If natural plant populations reflect results of this model, wide ranges of herbivory and pollination environments will favor late shifts to reproduction. However if herbivore and pollinator phenologies are similar and pollination success can compensate for effects of herbivory, a greater diversity of allocation patterns may persist, particularly for perennials.

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Acknowledgments

Thanks to N. Underwood,D. McNutt, and the Inouye and Underwood labs for comments and assistance.

For further information

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