

The Cost of Compensation

Andrew M. Simons* and Mark O. Johnston

Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

Submitted August 17, 1998; Accepted December 30, 1998

Keywords: bet hedging, compensation, fitness, life-history trade-off, *Lobelia inflata*, overcompensation.

Much recent attention has focused on the apparent benefit accrued by a plant through its partial destruction by grazing (Owen 1980; Belsky 1986; McNaughton 1986; Crawley 1987; Paige and Whitham 1987; Vail 1992; Belsky et al. 1993; Mathews 1994; Tuomi et al. 1994; Järemo et al. 1996; Nilsson et al. 1996; Lennartsson et al. 1997). The subject has been characterized by heated debate on two related issues: the empirical question of whether fitness is, in fact, increased by the partial destruction of plant tissue (overcompensation; Paige and Whitham 1987; Bergelson and Crawley 1992; Crawley 1993; Bergelson et al. 1996) and, if overcompensation exists, whether claims that grazing is thus beneficial to a plant are justified (Crawley 1987; Belsky et al. 1993; Vail 1993, 1994; Mathews 1994).

Empirical studies have concentrated on testing a plant's capacity for compensation by comparing the performance of grazed plants to ungrazed controls (Paige and Whitham 1987; Maschinski and Whitham 1989; Bergelson and Crawley 1992; Paige 1992; Wegener and Odasz 1997) and the claim that plants benefit from herbivore damage has been made (Owen 1980; Paige and Whitham 1987; Paige 1992). As a result of differing interpretations of what constitutes a "benefit" (Crawley 1987), this claim is viewed by some as a paradox. A benefit of being partially destroyed might be observed in a population for two different reasons. First, grazing of aboveground tissue might alter the plant's architecture such that fitness is increased by the removal of constraints. If partial destruction is truly beneficial to the plant through the removal of such obstacles as architectural constraints, the plant-herbivore association might be regarded as mutualistic (mutualism hypothesis).

Second, compensation could be the expression of an adaptive strategy that has evolved during a history of grazing (van der Meijden 1990; Lennartsson et al. 1997) or competition for light (Aarssen 1995; Järemo et al. 1996), in which case plants "cope" (Mathews 1994) with herbivores but any benefit is only proximal (Belsky et al. 1993) because it is attained at an evolutionary cost (trade-off hypothesis).

Bet-hedging models have been proposed that suggest that the capacity for compensation should evolve under size-selective herbivory (Vail 1992) and as a bet-hedging strategy under year-to-year variation in the risk of destruction (Nilsson et al. 1996). This note has three purposes: first, to present a model of compensation as a bet-hedging strategy that is simpler than, yet generalizes, the formulation of Nilsson et al. (1996); second, to suggest that empirical studies might be more constructive if directed toward measuring the costs of compensation; and third, to present empirical evidence for the existence of a phenotypic trade-off between reproductive success without destruction and reproductive success following destruction in Indian tobacco, *Lobelia inflata*, a monocarpic plant capable of compensatory regrowth.

A Model of Compensation as Bet Hedging under Constant Risk

Partial dedication of total resources to regrowth following destruction is expected to evolve as a bet-hedging strategy under among-season variation in the risk of herbivory (Nilsson et al. 1996). In the model of Nilsson et al. (1996), the intensity of herbivory is either low (good years) or high (bad years) and, in this respect, is reminiscent of Cohen's (1966) model of population-level optimal seed dormancy under environmental unpredictability. From the viewpoint of an individual plant, though, partial destruction is unpredictable even when the risk at the population level is predictable. Whereas Nilsson et al. (1996) restrict their results to year-to-year variation in herbivore pressure, the simple model developed below demonstrates that their results are, in fact, more general. In particular, the results apply also to individuals evolving in populations experiencing a constant risk of destruction.

* To whom correspondence should be addressed; e-mail: simons@is2.dal.ca.
Am. Nat. 1999. Vol. 153, pp. 683-687. © 1999 by The University of Chicago. 0003-0147/99/5306-0009\$03.00. All rights reserved.

Vail (1992), before showing that overcompensation should evolve when the probability of herbivore damage is size dependent, first models optimal allocation strategies under different constant levels of herbivory without size selection. Because of its clarity, we use Vail's (1992) base model as a point of departure to examine the relative fitnesses of different compensation strategies under constant risk of destruction. If a is the probability of destruction of initial effort, and b is the fraction of total available resources dedicated to initial reproductive effort, then

$$S = (1 - a)b + a(1 - b), \tag{1}$$

where S is expected fitness (Vail 1992). For monocarpic plants, expected fitness under this model is maximized either with complete dedication to initial reproduction, if the probability of destruction is <0.5 , or with complete dedication to secondary fruit production, if the probability of destruction is >0.5 (see Vail 1992, fig. 2).

Selection, however, acts to maximize the geometric mean fitness (Seger and Brockmann 1987; Philippi and Seger 1989). The geometric mean principle, despite its perception as a "special case" is the more general fitness measure and applies also to environmental constancy (Roff 1992, pp. 41–42), although the geometric and arithmetic mean fitnesses are identical under the special case of no variation in the optimal trait value among generations. The optimal allocation to initial reproduction, b , then, under unpredictability of destruction, is given by the geometric mean fitness (S_{GM}) over n generations such that

$$S_{GM} = \left[\prod_{1,n} [(1 - a')b + a'(1 - b)] \right]^{1/n}, \tag{2}$$

where a' represents destruction of initial reproductive effort, and is either 1, with probability a , or 0. Because a plant's initial effort is either destroyed or not destroyed each generation, the geometric mean fitness simplifies to

$$S_{GM} = \{ [b^{n(1-a)}] [(1 - b)^{na}] \}^{1/n}. \tag{3}$$

This model reveals intermediate optimal values of initial reproductive effort (b) for different values of the probability of destruction of initial reproductive effort (a ; fig. 1). The greater the probability of destruction, the greater the optimal allocation to potential regrowth: optimal initial reproductive effort (b ; corresponding to fitness maxima of fig. 1) is simply equal to the probability of the initial reproductive effort not being destroyed ($1 - a$). A constant risk of destruction, therefore, may select for any level of compensation, including an apparent benefit of destruc-

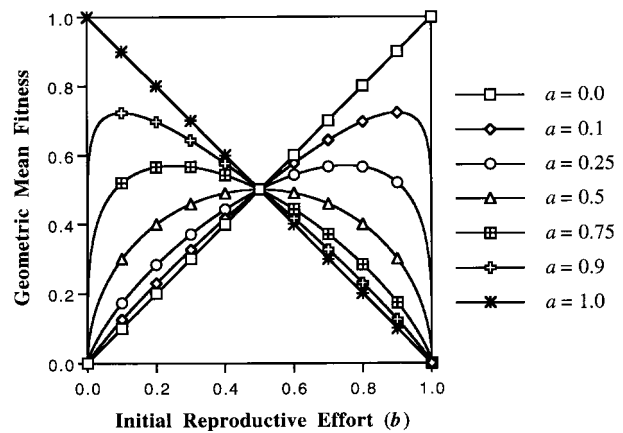


Figure 1: Geometric mean fitness as a function of initial reproductive effort, b , plotted for seven different constant probabilities of destruction, a . Maximum fitness values occur where the allocation to initial reproduction is 1 minus probability of destruction.

tion (overcompensation) when the risk of destruction is >0.5 .

Compensation as Trade-Off

Previous models demonstrate that compensation is expected to evolve under size-selective herbivory (Vail 1992) and among-season variability in the risk of herbivory (Nilsson et al. 1996). An assumption of these models is that a proportion of the plant's resources, measured as the total number of potential buds or meristems (Tuomi et al. 1994) is allocated to initial growth, and the remaining resources are available for compensatory regrowth in the event of partial destruction of aboveground tissue. If individuals dedicate reserves to postdestruction fruit production, and these reserves are unavailable for initial reproduction, a trade-off is expected between initial and postdestruction reproductive potential. The benefit of partial destruction is thus achieved at a cost: if plants had evolved in the absence of destructive forces such as herbivory, all resources might be dedicated to initial fruit production, and total seed production would therefore be higher. The capacity for compensation is expected to evolve in proportion to the relative benefit of compensatory regrowth compared to primary growth and should be viewed as occurring on a continuum of potential compensatory responses from undercompensation to overcompensation (Maschinski and Whitham 1989; Belsky et al. 1993; Nilsson et al. 1996).

The significance of overcompensation from the viewpoint of the trade-off hypothesis is simply that it represents all values past the midpoint on the scale of 0%–100%

dedication of resources to postdestruction fruit production. The very existence of overcompensation has been extensively debated (Belsky 1986; Bergelson et al. 1996) but, because overcompensation is predicted by both the mutualism and the trade-off hypotheses, evidence of overcompensation cannot be used to distinguish between these hypotheses. Empirical evidence for a trade-off between the dedication of reserves to primary and postdestruction fecundity, though, would support the hypothesis that destruction bears a cost and would thus count against the mutualism hypothesis.

A Phenotypic Trade-Off in *Lobelia inflata*

Lobelia inflata (L.), an annual, biennial, or monocarpic perennial, typically inhabits disturbed areas (Baskin and Baskin 1992). This species exhibits compensatory regrowth following removal of aboveground tissue (A. M. Simons, personal observation) and because it reproduces only once in its lifetime and only by seed, it is ideally suited for studies on compensation. In plants capable of compensatory growth, resources are wasted if the plants are not damaged. The greater the allocation to regrowth, the smaller the proportional allotment to initial growth. If the proportion of unused resources allocated to regrowth could be measured for undamaged plants, then the trade-off between initial and secondary growth could be quantified. In this experiment, we assess allocation to regrowth in undamaged plants by damaging the stems only after having allowed plants to completely mature without destruction. The trade-off between initial and secondary growth is measured as the number of fruits produced initially compared to that produced secondarily but, because we are interested in allocation relative to total available resources, both initial and compensatory fruit numbers are corrected for rosette size immediately before bolting.

The expression of regrowth is known to be influenced by the timing of damage (Maschinski and Whitham 1989) or, more precisely, by the developmental stage at which damage occurs (Bergelson et al. 1996). The cutting treatment administered only following initial fruit maturation in the present experiment, however, does not represent herbivory late in the season. The plants were allowed ample time to regrow following partial destruction, and the late destruction is simply a means to reveal the trade-off between allocation to initial versus secondary fruit production.

Seeds of *L. inflata* were placed on moistened filter paper in petri plates and allowed to germinate in a growth chamber. Seedlings were transplanted, one per cell, into Kord cell packs and were grown under a continuously diminishing photoperiod regime designed to simulate conditions through the summer. Rosette size was measured weekly,

and size and date at bolting were noted. Plants bolted at various times throughout the "summer," and all plants were allowed to develop until no new flowers appeared and all fruits had ripened. Individuals that remained vegetative (rosettes) were not used in the experiment, and total fruit production was recorded for plants that had bolted.

Stems were cut to 2 cm, and the cell packs containing the remaining tissue were covered and placed at 5°C for 30 d before initiating regrowth. Plants that died up until this stage were discarded (see final paragraph, this section). The 58 remaining plants were transferred into a growth room under long day conditions (15L : 9D; 21°C, 14°C). Final secondary fruit number was recorded and ranged from one to 69 with a mean of 10.5.

Because of the possibility that environmental correlations between initial and secondary fruit production might obscure a genetic trade-off, fruit number was first corrected for rosette size, measured as the longest leaf, at the time of bolting. Rosette size at bolting is a significant predictor of total fruit number (A. M. Simons and M. O. Johnston, unpublished data), and we assume that it is an appropriate correlate of the total resources available to an individual. The trade-off was thus measured as the correlation between the residuals from the relationship between log (initial fruit number) versus rosette size at the time of bolting, and the residuals from the relationship between log (secondary fruit number) versus rosette size at the time of bolting.

Empirical data support the existence of compensatory plant regrowth following partial destruction, but no previous study has directly asked whether the potential for secondary regrowth incurs a cost to initial flower production. In this simple study we find that, for a given rosette size, a phenotypic trade-off exists between initial fruit production and secondary fruit production ($r = -0.262$; $P = .047$; $N = 58$) in *L. inflata*.

Secondary fruit number (2°) is predicted by the multiple regression equation that includes rosette size (ros) and initial fruit number (1°):

$$\log(2^\circ) = 2.16 + 0.041(\text{ros}) - 0.815 \log(1^\circ).$$

Fruit number was log transformed because the relationship between the absolute value of the residual secondary fruit number increases significantly with rosette size before (slope = 0.468; $P = .001$) but not after (slope = 0.013; $P = .175$) transformation (Zar 1984, p. 288). Although this residual relationship for initial fruit number is nonsignificant (slope = 0.421; $P = .161$), logs were taken before analysis for consistency and because this transformation aided in detrending the data

(slope = -0.002 ; $P = .699$). Furthermore, the use of untransformed initial fruit number and log transformed secondary fruit number does not qualitatively alter the finding of a phenotypic trade-off ($r = -0.282$; $P = .032$; $N = 58$).

The above results include only plants that were alive at the beginning of the regrowth period. Complete trays of plants desiccated during storage and were excluded because it is most reasonable to attribute their demise to environmental factors unrelated to allocation to primary fruit production. It is possible, however, that the few (13) dead plants on the remaining trays might have been those with zero allocation to regrowth. The data were reanalyzed to include the individuals with zero secondary fruit production. The analysis was performed by first adding 1 to all fruit numbers, primary and secondary, before log transforming, but was otherwise identical to the above correlation analysis. The correlation between initial and secondary fruit production is stronger ($r = -0.317$; $P = .007$; $N = 71$) with the inclusion of the dead individuals: these individuals had, given their rosette sizes, produced disproportionately many fruits during initial flowering.

Conclusions

Theoretical analyses (Vail 1992; Tuomi et al. 1994; Nilsson et al. 1996) have assumed the existence of a trade-off between initial and secondary growth. The trade-off between initial and secondary fruit production observed in *Lobelia inflata* supports these analyses and implies that there is a phenotypic cost associated with the potential for regrowth after partial destruction; individuals that dedicate a higher proportion of total resources to regrowth produce fewer fruits initially. Genetic correlations are a more appropriate measure of evolutionary costs (Reznick 1992) because positive phenotypic correlations may be driven by common environmental effects. In the present experiment, a negative phenotypic correlation is observed despite this possibility. Therefore, the idea that the increase in fitness following grazing has evolved as a mutualistic relationship between plants and herbivores (Owen 1980) is not supported.

Previous models suggest that compensation is expected under particular conditions (van der Meijden 1990; Vail 1992; Nilsson et al. 1996). Our model shows that compensation, and even overcompensation, may be expected under the more general conditions of a constant risk of destruction. As has been noted by Mathews (1994), evidence of overcompensation is not evidence that plants benefit from partial destruction. If they were immune to forces such as herbivory, drought, frost, and trampling, plants dedicating resources to regrowth would be at a selective disadvantage relative to plants able to allocate all

available resources to initial reproduction. Therefore, further empirical work to determine the genetic correlation between initial and secondary fruit production would greatly enhance our understanding of the evolutionary cost of compensation.

Acknowledgments

We thank P. Li, C. Paoletti, and A. P. Simons for discussion and J. Bergelson and two anonymous reviewers for helpful comments. This work was supported by Natural Sciences and Engineering Research Council of Canada grants to M.O.J.

Literature Cited

- Aarssen, L. W. 1995. Hypotheses for the evolution of apical dominance in plants: implications for the interpretation of overcompensation. *Oikos* 74:149–156.
- Baskin, J. M., and C. C. Baskin. 1992. Role of temperature and light in the germination ecology of buried seeds of weedy species of disturbed forests. I. *Lobelia inflata*. *Canadian Journal of Botany* 70:589–592.
- Belsky, A. J. 1986. Does herbivory benefit plants? a review of the evidence. *American Naturalist* 127:870–892.
- Belsky, A. J., W. P. Carson, C. L. Jensen, and G. A. Fox. 1993. Overcompensation by plants: herbivore optimization or red herring? *Evolutionary Ecology* 7:109–121.
- Bergelson, J., and M. J. Crawley. 1992. Herbivory and *Ipomopsis aggregata*: the disadvantages of being eaten. *American Naturalist* 139:870–882.
- Bergelson, J., T. Juenger, and M. J. Crawley. 1996. Regrowth following herbivory in *Ipomopsis aggregata*: compensation but not overcompensation. *American Naturalist* 148:744–755.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* 12:119–129.
- Crawley, M. J. 1987. Benevolent herbivores? *Trends in Ecology & Evolution* 2:167–168.
- . 1993. On the consequences of herbivory. *Evolutionary Ecology* 7:124–125.
- Järemo, J., P. Nilsson, and J. Tuomi. 1996. Plant compensatory growth: herbivory or competition? *Oikos* 77:238–247.
- Lennartsson, T., J. Tuomi, and P. Nilsson. 1997. Evidence for an evolutionary history of overcompensation in the grassland biennial *Gentianella campestris* (Gentianaceae). *American Naturalist* 149:1147–1155.
- Maschinski, J., and T. G. Whitham. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *American Naturalist* 134:1–19.
- Mathews, J. N. A. 1994. The benefits of overcompensation

- and herbivory: the difference between coping with herbivores and liking them. *American Naturalist* 144: 528–533.
- McNaughton, S. J. 1986. On plants and herbivores. *American Naturalist* 128:765–770.
- Nilsson, P., J. Tuomi, and M. Åström. 1996. Bud dormancy as a bet-hedging strategy. *American Naturalist* 147: 269–281.
- Owen, D. F. 1980. How plants may benefit from the animals that eat them. *Oikos* 35:230–235.
- Paige, K. N. 1992. Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. *Ecology* 73:2076–2085.
- Paige, K. N., and T. G. Whitham. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *American Naturalist* 129:407–416.
- Philippi, T., and J. Seger. 1989. Hedging one's evolutionary bets, revisited. *Trends in Ecology & Evolution* 4:41–44.
- Reznick, D. 1992. Measuring the costs of reproduction. *Trends in Ecology & Evolution* 7:42–45.
- Roff, D. A. 1992. *The evolution of life histories: theory and analysis*. Chapman & Hall, New York.
- Seger, J., and J. Brockmann. 1987. What is bet-hedging? *Oxford Surveys in Evolutionary Biology* 4:182–211.
- Tuomi, J., P. Nilsson, and M. Åström. 1994. Plant compensatory responses: bud dormancy as an adaptation to herbivory. *Ecology* 75:1429–1436.
- Vail, S. G. 1992. Selection for overcompensatory plant responses to herbivory: a mechanism for the evolution of plant-herbivore mutualism. *American Naturalist* 139: 1–8.
- . 1993. Overcompensation as a life-history phenomenon. *Evolutionary Ecology* 7:122–123.
- . 1994. Overcompensation, plant-herbivore mutualism, and mutualistic coevolution: a reply to Mathews. *American Naturalist* 144:534–536.
- van der Meijden, E. 1990. Herbivory as a trigger for growth. *Functional Ecology* 4:597–598.
- Wegener, C., and A. M. Odasz. 1997. Effects of laboratory simulated grazing on biomass of the perennial Arctic grass *Dupontia fisheri* from Svalbard: evidence of overcompensation. *Oikos* 79:496–502.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice Hall, Englewood Cliffs, N.J.

Associate Editor: Joy Bergelson