

Adaptive and Selective Seed Abortion Reveals Complex Conditional Decision Making in Plants

Katrin M. Meyer,^{1,*} Leo L. Soldaat,² Harald Auge,³ and Hans-Hermann Thulke¹

1. UFZ–Helmholtz Centre for Environmental Research, Department of Ecological Modelling, Leipzig, Germany; 2. Statistics Netherlands, Den Haag/Heerlen, the Netherlands; 3. UFZ–Helmholtz Centre for Environmental Research, Department of Community Ecology, Halle, Germany

Submitted April 23, 2013; Accepted September 23, 2013; Electronically published January 29, 2014

Dryad data: <http://dx.doi.org/10.5061/dryad.k8m7b>.

ABSTRACT: Behavior is traditionally attributed to animals only. Recently, evidence for plant behavior is accumulating, mostly from plant physiological studies. Here, we provide ecological evidence for complex plant behavior in the form of seed abortion decisions conditional on internal and external cues. We analyzed seed abortion patterns of barberry plants exposed to seed parasitism and different environmental conditions. Without abortion, parasite infestation of seeds can lead to loss of all seeds in a fruit. We statistically tested a series of null models with Monte Carlo simulations to establish selectivity and adaptiveness of the observed seed abortion patterns. Seed abortion was more frequent in parasitized fruits and fruits from dry habitats. Surprisingly, seed abortion occurred with significantly greater probability if there was a second intact seed in the fruit. This strategy provides a fitness benefit if abortion can prevent a sibling seed from coinfection and if nonabortion of an infested but surviving single seed saves resources invested in the fruit coat. Ecological evidence for complex decision making in plants thus includes a structural memory (the second seed), simple reasoning (integration of inner and outer conditions), conditional behavior (abortion), and anticipation of future risks (seed predation).

Keywords: plant behavior, selective abortion, seed predation, parasite, Monte Carlo simulations, *Rhagoletis meigenii*, *Berberis vulgaris*.

Introduction

Behavior can be defined as the response of an organism to internal and external signals (Silvertown and Gordon 1989). Traditionally, however, animal and plant behavior have been considered to be fundamentally different (Trewavas 2005b). In animals, behavioral response is mostly dependent on movement. The majority of plants are sessile. Behavior, therefore, can be expressed only in growth and development phenomena (Trewavas 2003) such as

phenotypic plasticity (Borges 2005). A growing body of evidence supports the existence of plant behavior (e.g., Stenhouse 1974; Van Volkenburgh 1999; Gersani et al. 2001; Trewavas 2002, 2003, 2004, 2005a, 2005b; Balusca et al. 2004; Firn 2004; Hutchings and John 2004; Sack et al. 2006; Schurr et al. 2006; Sandras 2007), but the majority of these studies address physiological phenomena. Ecological evidence including interactions with other trophic levels is rare (Karban 2008).

Selective seed or fruit abortion may offer potential to corroborate behavior in plants but to our knowledge has not been studied in this context. Selective abortion of seeds or fruits has been considered both a passive reaction and an active defense mechanism against herbivorous insects (Stephenson 1981; Fernandes and Whitham 1989; Marquis 1992; Phillips and Walker 1997; Soldaat and Auge 1998). Selective abortion of lower-quality offspring is used as explanation for the surplus production of seeds in many species (Melser and Klinkhamer 2001) and can increase average progeny fitness (Vaughton and Carthew 1993). Passive selective abortion has been explained by differential resource allocation. If resources are limited, survivors gain fitness after removal of subquality offspring. The direct physiological response of seeds or fruits to physical damage or introduction of pathogens may also result in patterns of passive selective abortion. Active selective abortion of fruits or seeds has been shown to eliminate risks by outer circumstances to particular offspring caused for instance by seed predation after infestation by parasites (Janzen 1971; Soldaat and Auge 1998; Gazoul and Satake 2009).

To satisfy the definitions of adaptive behavior (Poulin 1995), that is, an adaptive change of a response to complex stimuli, the plant must coordinate internal conditions and external cues and extrapolate their joint potential effect into the future to make the decision on selective abortion. In this study, we evaluate the capability of barberry *Berberis vulgaris* L. to coordinate the information on the number

* Corresponding author. Present address: University of Göttingen, Department of Forest Sciences and Forest Ecology, Ecosystem Modelling, Büsgenweg 4, 37077 Göttingen, Germany; e-mail: kmeyer5@uni-goettingen.de.

Am. Nat. 2014. Vol. 183, pp. 376–383. © 2014 by The University of Chicago. 0003-0147/2014/18303-5463\$15.00. All rights reserved.
DOI: 10.1086/675063

of seeds in a fruit (internal) and the risk of seed mortality due to future predation or water constraints (external). Our results establish sound ecological evidence for complex decision-making behavior in plants expressed as adaptively changing selective seed abortion.

Methods

Parasite-Host-System

Berberis vulgaris L. (barberry, Berberidaceae) is a deciduous shrub inhabiting dry scrub and open forests in Europe. The ovaries of *B. vulgaris* generally contain two ovules (Ahrendt 1961), hence the ripe fruits can bear up to two seeds (in rare cases, three seeds; L. Soldaat and H. Auge, personal observation). The specialist fruit fly *Rhagoletis meigenii* (Diptera, Tephritidae) is native to Europe where the larvae predate on seeds in the fruits of *B. vulgaris* (Hendel 1927; White 1988). The oviposition puncture of *R. meigenii* females can be determined on the fruit coat and on the seeds of the host. Usually, one larva develops per fruit that typically damages both seeds in the fruit, indicating that it needs more than one seed for optimal development. However, the larvae can also develop in one-seeded fruits. On average, larvae consume 1.75 seeds per fruit (Soldaat and Auge 1998). The abortion of an infested seed by *B. vulgaris* prevents the development of the insect and may save a second seed in the fruit from predation (Soldaat and Auge 1998). The probability of seed abortion and the probability of infestation by *R. meigenii* larvae increase with the number of oviposition punctures (Soldaat and Auge 1998) indicating that not all punctured seeds are aborted and not each puncture results in a larva.

Field Observations

We collected ripe fruits from seven *B. vulgaris* populations in central Germany among which four populations were located in the understory of mesic forests (P) dominated by Scots pine, *Pinus sylvestris*, and three in dry scrubs on rocky slopes (S). This provided us with fruits grown without and with water constraints (P and S, respectively). The mesic pine forests grew on deep sandy soils, while the dry scrubs grew on rocky slopes consisting of limestone or calcareous sandstone covered by a shallow dry rendzina. Mean indicator values (according to Ellenberg 1979) of the most frequent species of the herb layer: for light availability, 5.5 (partial shade) in pine forests and 7.3 (mostly full light) in dry scrubs (scale: from 1 = deep shade to 9 = full sunlight); for soil moisture, 4.8 (mesic soil) in pine forests and 2.9 (mostly dry soil) in dry scrub (scale: 1 = extremely dry soil to 9 = wet soil to 12 = permanently submerged); for nutrient availability, 4.9 (moderately nutrient rich) in

pine forest and 2.4 (nutrient poor) in dry scrub (scale: from 1 = very nutrient poor to 9 = excessively nutrient rich). Hence, the dry scrubs were characterized by higher light availability and lower nutrient availability but also by remarkably reduced water supply compared to the pine forests. Population size varied from 4 to 17 fruiting shrubs (on 489–12,000 m²) in pine forests and from 20 to 134 fruiting shrubs (on 3,750–44,000 m²) in dry scrubs. Average fruit production was 73 fruits m⁻³ shrub volume in the forest understory compared to 209 fruits m⁻³ in open scrubs. We collected the fruits in early October, when *B. vulgaris* fruits usually turn ripe and *R. meigenii* larvae have already left the fruits for pupation. Since oviposition in *R. meigenii* takes place in early summer (Soldaat and Auge 1998), this approach allowed us to quantify the whole amount of infestation by *R. meigenii* which is the only predispersal seed predator in *B. vulgaris* in our region. In each population, we selected four to six (depending on population size) individual shrubs at random. For each of these shrubs, we counted the total number of inflorescences and collected 40 to 50 inflorescences with ripe fruits from each plant, using random numbers. We inspected the fruits with a microscope for the presence of oviposition punctures, dissected them, and recorded the number of living seeds (solid consistency, white color), eaten seeds (similar to living seeds but only seed coat remaining), and aborted seeds (soft consistency, black color). Since there are mostly two ovules in each *B. vulgaris* fruit, one-seeded fruits usually contain one undeveloped ovule which is much smaller than aborted seeds. Oviposition by *R. meigenii* females takes place when seeds are close to their final size (Soldaat and Auge 1998), hence abortion of early-stage ovules cannot be caused by ovipositing flies. For our analysis, we therefore considered seeds aborted during later developmental stages only. We merged living seeds and eaten seeds into the category “nonaborted seeds.” According to the number of nonaborted seeds, each fruit has a unique state: for fruits with two seeds, F_0 : no nonaborted seeds (= two aborted seeds), F_1 : one nonaborted and one aborted seed, and F_2 : two nonaborted seeds; and for one-seeded fruits, f_0 : no nonaborted seed (= one aborted seed), and f_1 : one nonaborted seed. Observed frequencies of fruit states then form the fruit state distribution: $[\#F_0, \#F_1, \#F_2]$ for two-seeded fruits and $[\#f_0, \#f_1]$ for one-seeded fruits.

Data Preparation

The collected seed data (available in the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.k8m7b>; Meyer et al. 2014) provided fruit state distributions for one-seeded and two-seeded fruits in four subsets of the data: fruits collected in dry scrub habitat with oviposition punctures (S+), in dry scrub habitat without punctures (S-), in

pine habitat with punctures (P+), and in pine habitat without punctures (P-). The fruit state distributions for two-seeded fruits were linked to an individual-based seed mortality model reflecting the hypotheses of nonselective (null hypothesis) versus selective (alternative hypothesis) abortion:

Model M_{uniform} (uniform seed abortion with probability m) reflecting the null hypothesis:

$$\begin{aligned} E_2: & (1 - m) \times (1 - m), \\ E_1: & (1 - m) \times m + m \times (1 - m), \\ E_0: & m \times m. \end{aligned} \quad (1)$$

Model $M_{\text{selective}}$ (abortion probability of one seed m_c exceeding the abortion probability of the other seed m_a) reflecting the alternative hypothesis:

$$\begin{aligned} E_2: & (1 - m_a) \times (1 - m_c), \\ E_1: & (1 - m_a) \times m_c + m_a \times (1 - m_c), \\ E_0: & m_a \times m_c. \end{aligned} \quad (2)$$

For the one-seeded fruits, only the uniform mortality model M_{uniform} was suitable. Mortalities were fitted to maximize the log likelihood ratio against the observed fruit state distributions (Zar 1999). Seed mortality of single-seeded fruits was estimated according to a standard binomial model.

Statistical Analysis

As a prerequisite for the test of differential abortion mortalities, we established nonhomogeneity over all observed fruit state distributions using a χ^2 test. Subsequently, we applied a χ^2 test with Bonferroni correction for multiple comparisons to find differences between the fruit state distributions of subsets P-, P+, S-, and S+. To test the null hypothesis of uniform seed mortality for two-seeded fruits, we determined the goodness of fit of the mortality model M_{uniform} . Hence, for each subset, we compared the fruit state distribution predicted by M_{uniform} to the observed fruit state distribution, using χ^2 statistics. To investigate the effect of the type of exposure (puncture or drought), we conducted a χ^2 test under exclusion of the data from the nonpunctured and non-drought-exposed fruits (P-).

Monte Carlo randomization was applied to evaluate the uncertainty of the mortality models accounting for stochastic variation (Manly 1997). For the given mortality parameters m , m_c and m_a of the models M_{uniform} or $M_{\text{selective}}$, we generated the possibility spectrum of fruit state distributions by simulations: For each individual seed of a fruit, a random number from the interval $[0, 1]$ was compared with the respective mortality parameter to determine

abortion or survival of the seed. This procedure was repeated for the total number of fruits in the corresponding subset of the data resulting in one simulated fruit state distribution $[F_0, F_1, F_2]$ per subset P-, P+, S-, and S+. By iteration of this procedure, 1,000 fruit state distributions were generated for every mortality model. We plotted each fruit state distribution as a point in a three-dimensional graph. Due to the random numbers involved in this procedure, the simulations formed a cloud of 1,000 points clustered around the point representing the expected fruit state distribution. This cluster reflects the possibility spectrum for each subset P-, P+, S-, and S+ (e.g., fig. 1). The expected fruit state distribution was calculated from the respective mortality model.

To derive the $(1 - \alpha)$ percentile envelope of a mortality model we used the fact that the expected $[F_0, F_1, F_2]$ state distribution represented the center of gravity of the simulated cluster of points. The length of the 1,000 lines between any point of the cluster and the center of gravity was determined, and the $1,000 \times \alpha$ most distant points were removed to obtain the $(1 - \alpha)$ envelope. Before the most distant points were identified, a standardization was

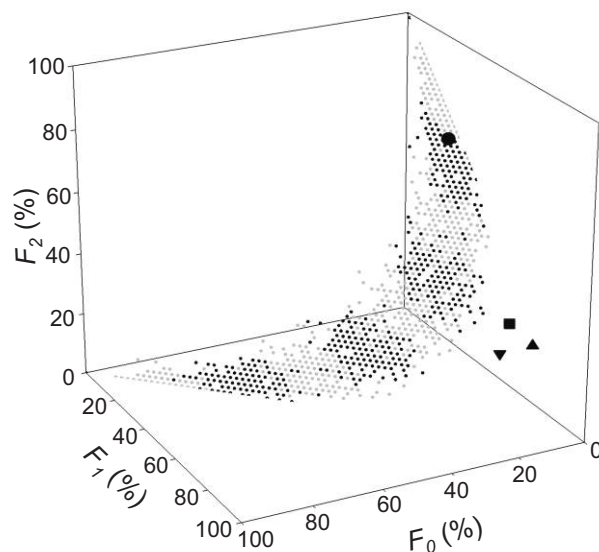


Figure 1: Simulated and observed fruit state distributions for the uniform mortality model. Observed fruit state distributions refer to fruits without punctures or water constraints (P-, large circle), with punctures and without water constraints (P+, upward triangle), without punctures and with water constraints (S-, square), and with punctures and water constraints (S+, downward triangle). Small circles represent 95% possibility spectra $[F_0, F_1, F_2]$ for uniform mortalities m from 0.0 to 0.9 in 0.1 steps from top to bottom with the change between gray and black circles symbolizing a new step. For clarity, we present possibility spectra generated from only 100 simulations.

Table 1: Observed number of fruits per fruit state and drought/infestation combination

Fruit state distribution	P−	P+	S−	S+
One seed per fruit:				
f_1	402	37	116	167
f_0	16	1	4	27
Total	418	38	120	194
Significance assessment				
	a	ab	a	b
Two seeds per fruit:				
F_2	321	17	24	91
F_1	131	61	64	356
F_0	11	2	5	49
Total	463	80	93	496
Significance assessment				
	A	B	B	B

Note: P−: pine habitat without water constraints and without parasite infestation, P+: pine habitat without water constraints and with parasite infestation, S−: scrub habitat with water constraints and without parasite infestation, and S+: scrub habitat with water constraints and with parasite infestation. For one-seeded fruits: f_0 , no living seed; f_1 , one living seed. For two-seeded-fruits: F_0 , no living seeds; F_1 , one living seed; F_2 , two living seeds. Different letters in the significance assessments indicate significantly different fruit state distributions based on pairwise χ^2 tests.

performed to compensate the nonspherical distortion of the point cloud. For standardization, each of the three coordinates of a point was divided by the maximum difference found in that coordinate for any one point and the center point. If an $(1 - \alpha)$ envelope of a proposed mortality model did not overlap with the point specified by an observed fruit state distribution or if two simulated models did not intersect by their $(1 - \alpha)$ envelopes, the hypothesis of homogeneity was rejected at the level of α . In all tests the significance level α was set to .05.

Results

The observed fruit state distributions (table 1) were not homogeneous for presence and absence of water constraints and parasite oviposition punctures ($\chi^2 = 290.6$, $P < .001$). The pairwise comparison of fruit state distributions of two-seeded fruits revealed a significant difference between nonpunctured and punctured fruits without water constraints (P− vs. P+, $\chi^2 = 69.7$, $P < .0001$). For nonpunctured fruits, the fruit state distributions with and without water constraints were also significantly different (P− vs. S−, $\chi^2 = 62.3$, $P < .0001$). Additionally, we found significant differences between nonpunctured fruits without water constraints and punctured fruits under water constraints (P− vs. S+, $\chi^2 = 255.6$, $P < .0001$). Punctured fruits without water constraints and nonpunctured fruits

with water constraints were not significantly different in their fruit state distributions (P+ vs. S−, $\chi^2 = 1.6$, $P > .45$). Excluding the data from the nonpunctured and non-drought-exposed fruits (P−), we did not find any significant differences in the remaining data (3×3 table, $\chi^2 = 8.3$, $P > .08$).

In order to demonstrate that abortion was selective on outer conditions, we tested the null hypothesis of uniform mortality. When the uniform mortality model M_{uniform} was fitted to the empirical fruit state distribution for two-seeded fruits, only the model for fruits without water constraints or punctures (P− in table 2) produced an acceptable fit. If any outer risk was considered, the fitted model resulted in significant deviation from the observed data (P+, S−, and S+ in table 2). We simulated the full range of uniform mortalities between 0 and 1 by way of Monte Carlo simulations (fig. 1). Only the observed fruit state distribution of the fruits without water constraints or punctures (P−) fell within the range of simulated possibility spectra. The null hypothesis of uniform mortality was not able to reproduce the complete data and, therefore, was rejected.

Turning to the alternative hypothesis of selective abortion, seed mortality was expected to be different between the two seeds in a two-seeded fruit (i.e., $M_{\text{selective}}$). Fitting the mortality models $M_{\text{selective}}$ to the observation necessarily gave a perfect fit (table 3). We found the possibility spectrum of $M_{\text{selective}}$ for fruits without any outer constraint (P−) to be clearly separated from the possibility spectra of the other three drought/infestation status combinations (P+, S−, S+; fig. 2). The three mortality models of stressor-subjected fruits produced possibility spectra that overlapped by their $(1 - \alpha)$ envelopes (P+, S−, S+; fig. 2). Thus, the form of outer constraint—that is, drought or parasite infestation—did not affect the outcome, while multiple stressors had the tendency to promote abortive response.

Table 2: Results of fitting the uniform mortality model to the observed data

Drought and infestation status	Estimated m (%)	P value	Minimal χ^2
P−	16.5	.86	.3
P+	40.6	<.0001	27.0
S−	39.8	<.0002	17.7
S+	45.8	<.0001	98.6

Note: The uniform model (M_{uniform}) assumes random abortion of individual seeds in two-seeded fruits. Only in the control group P− was the model fit acceptable. P−: pine habitat without water constraints and without parasite infestation, P+: pine habitat without water constraints and with parasite infestation, S−: scrub habitat with water constraints and without parasite infestation, and S+: scrub habitat with water constraints and with parasite infestation.

Table 3: Results of calibrating the selective mortality model to the observed data

Drought and infestation status	m_e (%)	m_a (%)
P−	22.5	10.6
P+	78.0	3.2
S−	72.1	7.5
S+	79.0	12.5

Note: The selective model ($M_{\text{selective}}$) assumes more likely abortion of one selected seed m_e compared to the mortality m_a of the other seed in two-seeded fruits. For all water constraints and infestation status combinations, the respective model fitted the data perfectly as expected for 2 degrees of freedom. P−: pine habitat without water constraints and without parasite infestation, P+: pine habitat without water constraints and with parasite infestation, S−: scrub habitat with water constraints and without parasite infestation, and S+: scrub habitat with water constraints and with parasite infestation.

The final step was to confirm that abortion response was adapted to the number of seeds left in a fruit. The mean probability of abortion for the single seed in one-seeded fruits ranged from 2.6% to 13.9% (table 4). For neither of the drought/infestation status combinations, the confidence interval of the abortion mortality exceeded 20% (table 4). For two-seeded fruits, all calibrated abortion mortalities of first seeds were greater than 20% (m_e in table 3), while the probability of abortion for the second, the sibling seed, was found between 3.2% and 12.5%. Hence, the presence of a second seed led to an increase of seed mortality due to abortion.

Discussion

Our results showed that seed mortalities were greatly increased if the fruit was subject to outer constraints (selective abortion) but only if another intact seed existed in the fruit (adaptive abortion). More specifically, we showed that seed abortion probability in barberry fruits was not uniform (null hypothesis of uniform mortality), that the exceeding mortality of the selected seed in an exposed two-seeded fruit did exceed the mortality of the other seed by 6 to 20 times (alternative hypothesis of selective mortality), and that the seed abortion probability in exposed one-seeded fruits never reached the level of excess mortality determined for exposed two-seeded fruits. Moreover, mortalities tended to be higher when water constraints and

infestations occurred together. Note that higher infestation levels in dry scrubs may be due to greater fruit production in dry scrubs and a positive correlation of fruit number and infestation levels (Soldaat and Auge 1998).

Exposing the fruits of a plant to a stressor almost certainly reduces the fitness of the plant. Selective seed abortion is the method of choice for the plant to minimize its fitness loss by protecting a single remaining seed in the fruit. Here we consider drought and parasite infestation as stressors, but other abortions may have been the result of factors that were not considered in our study, such as genetics, methods of fertilization, or other environmental factors. In case of environmental stress such as drought, aborting a seed may avoid allocation of scarce resources to all seeds in the fruit and prevent subsequent loss of all seeds if resources cannot sustain all seeds. Niesenbaum (1996) showed that fruit abortion rates increased with increasing intensity of competition among seeds in an experiment where resources were reduced by defoliation. In case of parasite infestation, the plant should selectively

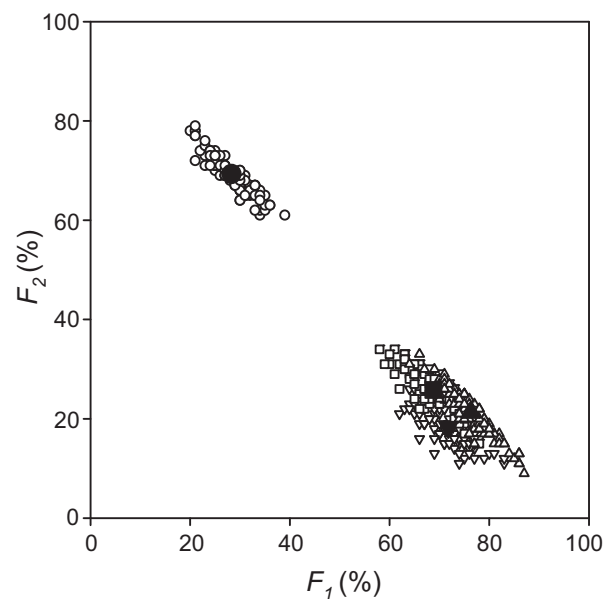


Figure 2: Simulated and observed fruit state distributions for the selective mortality model. Observed fruit state distributions (large solid symbols) refer to fruits without punctures or water constraints (P−, circles), with punctures and without water constraints (P+, upward triangles), without punctures and with water constraints (S−, squares), and with punctures and water constraints (S+, downward triangles). Small open symbols represent 95% possibility spectra [F_0 , F_1 , F_2] for the selective mortality $M_{\text{selective}}$ model. The mortality parameters m_e and m_a have the values given in table 3. We do not present the third dimension (F_0) of the simulated fruit state distributions which always overlap with the observed distributions. For clarity, we present possibility spectra generated from only 100 simulations.

Table 4: Number of fruits and seed abortion probability for one-seeded fruits

Drought and infestation status	<i>N</i>	<i>m</i> (%)	CI (%)
P−	418	3.8	2.2–6.1
P+	38	2.6	.1–13.8
S−	120	3.3	.9–8.3
S+	194	13.9	9.4–19.6

Note: The number of one-seeded fruits *N*, the estimated mean probability of abortion for individual seeds *m*, and the 95% confidence interval (CI) of the estimate for the different combinations of water constraints and infestation status. Even if statistical uncertainty of estimates (CI) was taken into account, the probability of abortion did never exceed 20%. P−: pine habitat without water constraints and without parasite infestation, P+: pine habitat without water constraints and with parasite infestation, S−: scrub habitat with water constraints and without parasite infestation, and S+: scrub habitat with water constraints and with parasite infestation.

abort the seed that possibly contains a future seed predator. It has been shown that seed abortion in *Berberis vulgaris* kills the eggs and thus potential larvae of its predator *Rhagoletis meigenii* which otherwise would destroy all seeds of a fruit (Soldaat and Auge 1998). Hence, selective seed abortion as response to outer constraints provides a fitness advantage to the host plant. However, in fruits with only one seed, nonabortion of a punctured seed can result in a fitness benefit, since not every oviposition puncture leads to larval development and seed predation (Soldaat and Auge 1998). The invested resources used to build the fruit pulp and coat are contained completely in the last (or single) seed of a fruit making it valuable for the plant and—in two-seeded fruits—more valuable than the first seed. Note that in the case of high seed predator pressures it could be valuable for the plant to offer fruits as a feeding sink for predator larvae even if they contain aborted seeds.

High probability to abort one of two seeds in punctured fruits could be explained by seed damage due to oviposition and subsequent introduction of pathogens. In *B. vulgaris*, the probability of fungal infection increases from 3% to 33% when fruits are parasitized by *R. meigenii* larvae (Soldaat and Auge 1998). Under this hypothesis, however, one would expect that affected seeds are aborted equally likely regardless of their origin from one- or two-seeded fruits. This is contradicted by our data: even the upper confidence limit of the seed mortality estimate in punctured one-seeded fruits (2.6%; CI: 0.1%–13.8%; table 4) did not reach the level of abortion probability fitted for the first seed in two-seeded punctured fruits (78%; table 3). The difference in abortion probabilities is more likely

an expression of adaptive plant behavior. This conclusion is underlined by the abortion probability calculated for any second seed of an exposed two-seeded fruit which lay comfortably inside the confidence interval of the respectively exposed one-seeded fruits (cf. tables 3 and 4). Thus, abortion of a single remaining seed is similarly low in one- and two-seeded fruits, which indicates adaptation of abortion behavior to the changed cost-benefit ratio of killing the last seed.

Selective seed or fruit abortion may be considered as an induced plant defense (Jolivet and Bernasconi 2006; Karban et al. 1999). Incompatible selfing can promote seed abortion during later developmental stages and has been suggested as an adaptive means of plants to counter the effects of predispersal seed predation (Gazoul and Satake 2009). In contrast to other reported defence mechanisms, however, we show that seed defence in barberry plants is modulated by coordinating the future risks with the inner conditions. Moreover, the observation that oviposition attempts increase the probability of seed abortion (Soldaat and Auge 1998) but do not ensure abortion demonstrates the complex response pattern involved in the abortion decision that go beyond simple stimulus-response schemes.

There is further evidence that selective adaptively changing seed abortion in *B. vulgaris* is a complex behavioral response that integrates different information qualities: The specialist fruit fly *R. meigenii* extended its host range to *Mahonia aquifolium*, a plant species closely related to *B. vulgaris* but introduced to Europe fewer than 200 years ago. This plant does not show the same behavior that we found for *B. vulgaris* in response to *R. meigenii* attack: while infestation rate by *R. meigenii* is even higher in *M. aquifolium* than in *B. vulgaris*, puncturing by ovipositing fruit flies leads to a much weaker response in terms of seed abortion compared to the original host plant (Soldaat and Auge 1998). This indicates that a coevolutionary arms race between the insect and its original host plant produced the complex response behavior of adaptive selective seed abortion in *B. vulgaris*.

Our results showed that seed mortalities were greatly increased if the fruit was subject to outer constraints (selective abortion), but only if another intact seed existed in the fruit (adaptive abortion). The existence of a second seed is part of the internal structure of the plant which has been suggested to represent the memory of the plant (Trewavas 2003). Moreover, the plant integrates this information generated by internal assessment of its structural memory with environmental information outside the sphere of influence of the plant, that is, presence of a stressor. Such a combination of internal and external information resulting in an integrated response has been described as simple reasoning and decision making (Seeley

and Levien 1987). Moreover, the plant extrapolates current stress to future fitness loss in a way that requires opposite abortion decisions depending on the presence of a second seed in the fruit.

In conclusion, we provided strong ecological evidence for the existence of complex decision making through adaptive selective abortion in plants. The idea that plants exhibit complex behaviors in response to environmental stimuli is not new (Karban 2008). Here, we show how environmental and internal cues can be integrated during plant decision making. This adds a new dimension to the phenotypic plasticity of plants, to plant defense against herbivores and pathogens but also to the many trade-offs between plant traits that possibly are more strongly interrelated and mutually limiting than previously thought. The existence of complex plant behavior makes new ecological interactions possible that are mediated by interplant communication and sheds new light on coevolutionary relationships.

Our findings raise new questions such as how these coordinative capabilities of plants evolved, what the underlying physiological mechanisms are, and what their relative importance for plant performance in an ecological community is. By demonstrating adaptive, selective seed abortion as a form of complex plant behavior, an important step expanding this field in ecology is made.

Acknowledgments

We thank D. Eisinger and F. Hansen for their support during the implementation of the model. We also thank R. Mager and A. Thondorf for their assistance in inspecting and dissecting some thousands of *Berberis* fruits and counting the seeds.

Literature Cited

- Ahrendt, L. W. A. 1961. *Berberis* and *Mahonia*. A taxonomic revision. *Botanical Journal of the Linnean Society of London* 57:1–410.
- Balusca, F., S. Mancuso, D. Volkmann, and P. Barlow. 2004. Root apices as plant command centres: the unique “brain-like” status of the root apex transition zone. *Biologia* 59:7–19.
- Borges, R. M. 2005. Do plants and animals differ in phenotypic plasticity? *Journal of Biosciences* 30:41–50.
- Ellenberg, H. 1979. *Zeigerwerte der Gefäßpflanzen Mitteleuropas*. *Scripta Geobotanica* 9:1–122.
- Fernandes, G. W., and T. G. Whitham. 1989. Selective fruit abscission by *Juniperus monosperma* as an induced defense against predators. *American Midland Naturalist* 121:389–392.
- Firn, R. 2004. Plant intelligence: an alternative point of view. *Annals of Botany* 93:345–351.
- Gazoul, J., and A. Satake. 2009. Nonviable seed set enhances plant fitness: the sacrificial sibling hypothesis. *Ecology* 90:369–377.
- Gersani, M., J. S. Brown, E. E. O’Brien, G. M. Maina, and Z. Abramsky. 2001. Tragedy of the commons as a result of root competition. *Journal of Ecology* 89:660–669.
- Hendel, F. 1927. Trypetidae. Pages 1–231 in E. Linder, ed. *Die Fliegen der paläarktischen Region*. Vol. 49. Schweizerbart, Stuttgart.
- Hutchings, M. J., and E. A. John. 2004. The effects of environmental heterogeneity on root growth and root/shoot partitioning. *Annals of Botany* 94:1–8.
- Janzen, D. H. 1971. Escape of *Cassia grandis* L. beans from predators in time and space. *Ecology* 52:964–979.
- Jolivet, C., and G. Bernasconi. 2006. Experimental analysis of constitutive and induced defence in a plant-seed-predator system. *Functional Ecology* 20:966–972.
- Karban, R. 2008. Plant behavior and communication. *Ecology Letters* 11:272–279.
- Karban, R., A. A. Agrawal, J. S. Thaler, and L. S. Adler. 1999. Induced plant responses and information content about risk of herbivory. *Trends in Ecology and Evolution* 14:443–447.
- Manly, B. F. J. 1997. *Randomization, bootstrap and Monte Carlo methods in biology*. Chapman & Hall, London.
- Marquis, R. J. 1992. The selective impact of herbivores. Pages 301–325 in S. Fritz and E. Simms, eds. *Plant resistance to herbivores and pathogens: ecology, evolution and genetics*. University of Chicago Press, Chicago.
- Melser, C., and P. G. L. Klinkhamer. 2001. Selective seed abortion increases offspring survival in *Cynoglossum officinale* (Boraginaceae). *American Journal of Botany* 88:1033–1040.
- Meyer, K. M., L. L. Soldaat, H. Auge, and H.-H. Thulke. 2014. Data from: Adaptive and selective seed abortion reveals complex decision making in plants. *American Naturalist*. Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.k8m7b>.
- Niesenbaum, R. A. 1996. Linking herbivory and pollination: defoliation and selective fruit abortion in *Lindera benzoin*. *Ecology* 77:2324–2331.
- Phillips, P. A., and G. P. Walker. 1997. Increase in flower and young fruit abscission caused by citrus bud mite (Acari: Eriophyidae) feeding in the axillary buds of lemon. 90:1273–1282.
- Poulin, R. 1995. “Adaptive” changes in the behavior of parasitized animals: a critical review. *International Journal for Parasitology* 25:1371–1383. doi:10.1016/0020-7519(95)00100-X.
- Sack, L., P. J. Melcher, W. H. Liu, E. Middleton, and T. Pardee. 2006. How strong is intracanalopy leaf plasticity in temperate deciduous trees? *American Journal of Botany* 93:829–839.
- Sadras, V. O. 2007. Evolutionary aspects of the trade-off between seed size and number in crops. *Field Crops Research* 100:125–138.
- Schurr, U., A. Walter, and U. Rascher. 2006. Functional dynamics of plant growth and photosynthesis: from steady-state to dynamics—from homogeneity to heterogeneity. *Plant, Cell and Environment* 29:340–352.
- Seeley, T. D., and R. A. Levien. 1987. A colony of mind: the beehive as thinking machine. *Sciences* 27:38–43.
- Silvertown, J., and G. M. Gordon. 1989. A framework for plant behavior. *Annual Review of Ecology and Systematics* 20:349–366.
- Soldaat, L. L., and H. Auge. 1998. Interactions between an invasive plant, *Mahonia aquifolium*, and a native phytophagous insect, *Rhagoletis meigenii*. Pages 347–360 in U. Starfinger, K. Edwards, I. Kowarik, and M. Williamson, eds. *Plant invasions: ecological mechanisms and human responses*. Backhuys, Leiden.
- Stenhouse, D. 1974. *The evolution of intelligence: a general theory and some of its implications*. Allen & Unwin, London.

- Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology, Evolution, and Systematics* 12:253–279.
- Trewavas, A. 2002. Mindless mastery. *Nature* 415:841.
- . 2003. Aspects of plant intelligence. *Annals of Botany* 92:1–20.
- . 2004. Aspects of plant intelligence: an answer to Firn. *Annals of Botany* 93:353–357.
- . 2005a. Green plants as intelligent organisms. *Trends in Plant Science* 10:413–419.
- . 2005b. Plant intelligence. *Naturwissenschaften* 92:401–413.
- Van Volkenburgh, E. 1999. Leaf expansion: an integrating plant behavior. *Plant, Cell and Environment* 22:1463–1473.
- Vaughton, G., and S. M. Carthew. 1993. Evidence for selective fruit abortion in *Banksia spinulosa* (Proteaceae). *Biological Journal of the Linnean Society* 50:35–46.
- White, I. M. 1988. Tephritid flies. Diptera: Tephritidae. Pages 1–134 in C. Barnard, and R. R. Askew. *Handbook for the identification of British insects*. Vol. 10 (5a). Royal Entomological Society, London.
- Zar, J. H. 1999. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ.
- Associate Editor: Uta Berger
Editor: Troy Day



Detail of barberry plant (*Berberis vulgaris*) with fruits. Photo credit: Katrin Meyer.