Variable offspring size as an adaptation to environmental heterogeneity in a clonal plant species: integrating experimental and modelling approaches

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Summary

1. The production of variably sized offspring has been hypothesized to be adaptive to temporal variability in environmental conditions.
2. This is difficult to verify empirically, and theoretical models are typically generic and not parameterized with data from real populations; studies integrating theoretical and empirical approaches to this problem are rare.
3. Here, we present experimental data on the growth of Scirpus maritimus, a clonal aquatic macrophyte that grows through vegetative extensions involving tubers.
4. The experiments show that offspring fitness (biomass productivity) is dependent on environmental conditions (water depth).
5. Experimental data indicate that variation in offspring (tuber) sizes can be approximated by a lognormal distribution.
6. We use these data to develop a different equation model of S. maritimus growth to test whether producing variably sized offspring is adaptive. The model compares fitness under the lognormal strategy to several hypothetical strategies with qualitatively different variance in offspring size.
7. The model results suggest that lognormal variation in S. maritimus tuber size may be adaptive to the temporal variation in water levels that characterize its natural Mediterranean environment.
8. We illustrate how the underlying principles that lend adaptive value to offspring size variation may apply to other species experiencing similar environmental conditions.

Key-words: bet-hedging, environmental variability, lognormal distribution, mathematical model, Plant population and community dynamics, Scirpus maritimus, size-number trade-off, theoretical model

Introduction

One of the central issues that have informed life-history theory is the trade-off between size and number of offspring (Stearns 1992; Moles & Westoby 2006). For a given level of resource investment, a parent may choose to produce a few large-sized offspring (with higher individual probabilities of survival to reproductive maturity) or many small-sized offspring (with lower probabilities of survival). A standard mathematical model predicts the evolution of a single optimal offspring size that maximizes maternal fitness, in situations where offspring fitness increases with size according to a certain functional form (Smith & Fretwell 1974). Subsequent work has extended this model and related it to ecologically important phenomena including competition, dispersal, predation and host–parasite relationships (Parker & Begon 1986; Venable 1992; Fox, Thakkar & Mousseau 1997; Marshall, Cook & Emlet 2006).

One such extension investigates whether the single-sized offspring strategy is still optimal when the environment varies unpredictably in time or in space. In this case, an alternative to a single-size strategy is for an individual to produce variably sized offspring. This may provide a buffer against environmental variability and constitutes a form of bet-hedging (Philippi & Seger 1989; Marshall, Bonduriansky & Bussière 2008; Olofsson, Ripa & Jonzen 2009). Since the 1970s, various authors...
have described offspring size variability in a large range of taxa, including plants, insects, fishes and birds, and suggested its possible adaptive value in variable habitats (for references, see the studies by McGinley, Temme & Geber 1987; Geritz 1995; Geritz, van der Meijden & Metz 1999; Westoby, Leishman & Lord 1996; Moles & Westoby 2006). However, variable offspring size within a species can arise from a number of genetic and environmental sources and can be partitioned in numerous ways: among populations, among individuals in the same population, within individuals, within a year or a clutch, or between years (Hangelbroek & Santamaria 2004). As a consequence, it is often difficult to determine whether the observed offspring size variation simply reflects developmental or resource constraints or whether it might also have adaptive value (Sakai 1995; Wolfe 1995; Simons & Johnston 1997, 2000; Vinuela 1997; Vaughton & Ramsey 1998; Forbes 1999; Einum & Fleming 2004). A second obstacle to establishing the adaptive value of offspring size variation is that the stipulation of specific functional forms relating fitness to offspring size and number is often difficult to establish (Einum & Fleming 2000; Torres-Vila & Rodríguez-Molina 2002; Moles, Warton & Westoby 2003; Gómez 2004; Moles & Westoby 2006). For example, it is generally admitted that the survival of seedlings increases with seed size; however, large seeds can also have higher risks of predation or reduced dispersal, resulting in a co-evolution of traits (Venable & Brown 1988; Moles, Warton & Westoby 2003). The relationship between offspring size and fitness may also vary between different stages of development or depend on parental behaviour (Hendry, Day & Cooper 2001). Hence, although there have been several empirical studies indicating that variation in offspring size can indeed be an adaptive response to unpredictable environmental variation (Crump 1981; Fox, Thakar & Mousseau 1997; Kudo 2001; Lips 2001; Koops, Hutchings & Adams 2003), empirical support for the hypothesis remains rare. Such obstacles also prevent the forging of more intimate links between theoretical and empirical approaches to the problem.

There have been a number of theoretical modelling studies of strategies for offspring size distribution and/or offspring numbers in the presence of temporally or spatially varying environments (Kaplan & Cooper 1984; Schultz 1991; Geritz 1995; Sasaki & Ellner 1995; Geritz, van der Meijden & Metz 1999; Kisdi 2007; Simons 2007; Olofsson, Ripa & Jonzen 2009). The process generally followed by mathematical models is to compare the fitness of a single-size strategy to a strategy of producing variably sized offspring under different conditions of habitat variability in space and/or time. Most of these theoretical approaches conclude that under certain assumptions, the optimal solution to the trade-off between size and number of offspring in a spatially and/or temporally variable environment is the production of variably sized offspring (Kaplan & Cooper 1984; Schultz 1991; Geritz 1995; Geritz, van der Meijden & Metz 1999). However, one modelling study concluded that variability in offspring size does not necessarily provide a fitness advantage over single-size strategies in a temporarily varying environment that can be either “good” or “bad” (McGinley, Temme & Geber 1987). These studies have generally not parameterized their models with empirical data, aiming for generality instead.

Studies that parameterize theoretical models with empirical data to investigate the adaptive value of producing variably sized offspring in temporally varying environments remain relatively uncommon (see for example the study by Simons 2009). Here, we describe experiments carried out to investigate offspring size variation in a clonal plant species and use the experimental data to develop a species-specific mathematical model of growth. In particular, we experimentally determine the relationships between offspring size and fitness in the clonal plant *Scirpus maritimus* under different environmental conditions, and use these experiments to parameterize a mathematical (difference equation) model of biomass production over multiple seasons. We compare fitness under the observed offspring size distribution (i.e. lognormal) to fitness under two hypothetical alternatives: the single-size distribution, in which all offspring are of the same size, and the uniform distribution, in which the probability of producing tubers of a given size is a constant. The single-size distribution corresponds to the “optimal offspring size” theory and thus should be optimal in an environment without temporal variation. The uniform distribution represents an intermediate strategy between the single-size and lognormal strategies. These alternative strategies serve as theoretical controls for the lognormal strategy. We chose the route of “simulation as experiment” because of the difficulty in testing our hypothesis empirically (Peck 2004). We used longitudinal historical data on the temporally varying environment of *S. maritimus* to simulate continuous random temporal variability. To compare our predictions with previous models that predict a single optimal offspring size under a discrete number of possible states (good or bad) (Cohen 1966; Smith & Fretwell 1974; McGinley, Temme & Geber 1987), we investigate the impact of representing environmental variability through a continuous rather than a discrete distribution of possible states.

**Materials and methods**

**Study species**

We investigate the adaptive value of variable offspring size in the emergent macrophyte *Scirpus maritimus*. The species grows clonally by producing underground sympodial rhizomes. The initial above-ground shoot of a seedling produces from one to three rhizomes at its base which grow horizontally and turn upwards to form erect above-ground shoots. Each new above-ground shoot then produces from one to three new rhizomes. Branched systems composed of several tens of sympodial rhizomes can be produced from an initial shoot during a single growing season (Clevering 1995; Charpentier, Meslard & Thompson 1998). During the growing season, each shoot forms a tuber at its base. Among the tubers produced in a single growing season, tuber biomass increases from the early to the later-produced tubers along rhizome systems (Liefers & Shay 1982; Clevering 1995; Charpentier & Stuefer 1999). Clonal growth stops at the end of summer. Above-ground shoots dry out and die in the autumn, while tubers persist in the soil. In spring, new shoots are produced from
axillary buds situated on overwintering tubers, and these shoots then
start to produce between one and three rhizomes.

Several studies have described in detail the variation in tuber size in
this species (Lieffers & Shay 1982; Clevering 1995; Charpentier, Mes-
leard & Thompson 1998; Charpentier & Stuefer 1999). The variation
arises within individuals during a single season: tuber size increases
gradually from the first to the last produced tubers. This pattern is
observed in the field as well as in single plants grown in pots under sta-
ble conditions, suggesting that this variation can be attributed to a
developmentally programmed syndrome rather than environmental
stress or changes in environmental conditions during the season.

The ecology of this species allows us to expect a strong relationship
between size and fitness of offspring. In emergent macrophytes,
because of the low efficiency of underwater photosynthesis, it is gen-
erally assumed that the maximum water depth they can overcome in
spring depends on the amount of reserve stored in overwintering
organs (e.g. tubers, rhizomes) (Spence 1982; Grace 1989; Clevering,
Van Vierssen & Blom 1995). We can thus suppose that in S. maritimus,
the ability of shoots to emerge above the water surface in spring
is crucial for survival and depends on tuber size, i.e. the amount of
stored reserves. Therefore, (i) we can use offspring tuber biomass as
an analogue for vegetative offspring size in S. maritimus, (ii) we can
use water depth as an analogue for environmental quality and (iii) we
use total tuber biomass produced by an initially present tuber
during a growth season as an analogue for fitness of the initial tuber.
The water regime of wetlands that support S. maritimus world-wide
is variously described as irregularly exposed, temporary, irregular,
seasonally and permanently flooded, all characterized by a strong
variability in water levels (Kantrud 1996). Therefore, we can also sup-
pose that the variability and unpredictability of water regime repres-
ets a strong environmental pressure for the evolution and ecology of
this species.

EXPERIMENT

An experiment was performed at Utrecht University in 1999 to test
the hypothesis that biomass productivity of S. maritimus is dependent
on environmental quality and the size of the initial tuber. A total of
550 tubers were collected from a population in the wildlife reserve of
the Tour du Valat, Rhone delta, Southern France in autumn 1998.
Tubers were stored under moist dark conditions at 5 °C. In spring
1999, the fresh weight of all the tubers was measured. Three series of
30 tubers from the tubers collected from the field (see previous sec-
tion) with the following fresh weight (g) were selected for the experi-
ment: 0.5, 0.6, 0.9, 1.0, 1.1, 1.5, 1.6, 1.9, 2.0, 2.1, 2.5, 2.6, 2.9, 3.0, 3.1,
3.5, 3.6, 3.9, 4.0, 4.1, 4.9, 5.0, 5.1, 5.9, 6.0, 6.1, 7.0, 7.1, 8.0, 10.0. The
dry weight of the remaining 450 tubers was measured to establish the
fresh–dry weight relationship (freshweight = b × dryweight + a,
where b = 0.01 and a = 3.25 R2 = 0.88; P < 0.05).

On 17 May 1999, the three series of tubers were randomly allocated
to one permanent water level treatment: shallow (15 cm), medium
(45 cm) or deep (85 cm). Single tubers were planted at a depth of
2 cm in pots of 21 cm in diameter, filled with a 1 : 2 compost–sand
mixture. The pots were put outside into containers under the three
permanent water levels above the soil surface. In Amsterdam from
May to September 1999, key weather indices determining the growth
environment of the tubers were: mean air temperature 16.5 °C, mean
humidity 76.2%, total precipitation 41.1 cm and mean wind speed
16.2 km h⁻¹. In September 1999, the dry weight of every tuber pro-
duced by each planted tuber was recorded. For each planted tuber,
the mean and standard deviation in offspring tuber weights were.

For each of the three water treatment levels, we selected the
three planted tubers that produced the largest number of offspring
 quickest tubers as an analogue for fitness of the initial tuber.
(Smith & Fretwell 1974): offspring fitness Fw is in a given water level w is related to the size s of the off-
spring via

\[ F_w(s) = \begin{cases} 1 - \left(\frac{s}{w}\right)^b & s > m_w \\ 0 & s \leq m_w \end{cases} \quad \text{eqn 1} \]

where \( m_w \) is the minimum viable offspring size in water level w and \( s_w \)
is a constant determining how quickly the fitness curve approaches its
asymptotic value as s increases. Here, \( F_w \) is the total biomass pro-
duced by a tuber of initial biomass s in the course of the growing
season. In the special case, where the environmental quality is constant
over time, the optimal offspring size \( s^* \) can be obtained from eqn 1
(Smith & Fretwell 1974):

\[ s^* = m(1 + q/\alpha)^{1/\alpha} \quad \text{eqn 2} \]

We computed the best fit of the experimental results to eqn 1 for
each of the three environmental conditions using the nonlinear-fitting
algorithm in \( \text{R} \), and setting maximum observed biomass produced
as the maximum fitness level. Hence, we obtained three sets of \( m_w \) and \( s_w \) values for each of the three experimental water levels.

MATHEMATICAL MODEL

We derived a discrete-time difference equation model of the temporal
dynamics of total biomass production under the three strategies for
some given temporal variation in water level. The model was simu-
lated in the C Programming Language. The total biomass produced
in the current year depends in a simple way upon how many tubers
were present at the beginning of the growing season (produced the year
previous), their size distribution and how much biomass a tuber of
some given size can produce as dependent on this year’s average water level.
Mathematically, the total biomass \( b_t \) produced by an individual in
year \( t \) is related to the biomass \( b_{t-1} \) produced in the previous year by
the individual and the water levels \( w(t) \) and \( w(t-1) \) in years \( t \) and \( t-1 \), by the equation

\[ b_t = b_{t-1} \int_{0}^{\phi_w(s_{t-1},w(t))} \frac{F_w(s_{t-1},w(t))}{\delta_{t-1}} ds \quad \text{eqn 3} \]

where \( s_{t-1} \) is the mean tuber size produced in year \( t-1, \phi_w(s_{t-1}) \) is the
offspring size distribution of an individual tuber, i.e., the probability a tuber produces an offspring of size s when
the average water level in year \( t \) is \( w(t) \), and \( F_w(s_{t-1},w(t)) \) is the fitness
function, eqn 1 (see Supporting Information for derivation).

S. maritimus individuals may die through excessive water depth.

This source of mortality is represented in eqn 1 because no biomass is produced in year $t$ if all tubers produced in year $t-1$ are smaller than the minimal offspring size $m_{min}$ for year $t$. This happens if there is a string of years with sufficiently high water levels. To account for other causes of mortality (such as herbivory, disease), we assumed a 1% probability of individual death each year from other causes.

The varying water level from year to year, $w(t)$, was modelled after field conditions. The population from which the tubers were taken was located in a temporary marsh in a region that experiences strong between-year variation in water level because of the unpredictable rainfall patterns characteristic of a Mediterranean climate. Rainfall data for 1932–2003 were obtained from a meteorological station a few kilometres from the marsh. The water depth in the marsh was monitored from 1995 to 2003. The relationship between the total rainfall from September to March (start of the growing season) was determined for 1995–2003 (Fig. S1). Using this relationship, the yearly water level was then derived for the period 1932–2003 based on the historical rainfall data for 1932–2003. The frequency distribution of water levels was fit by several distributions using the statistical software program jmp version 5.1 for Macintosh and MATLAB (version 7.6 for Macintosh; MathWorks, Natick, MA, USA). Accordingly, the frequency distribution of the water level $w$ from 1932 to 2003 (Fig. 1a) was best described by a function of the form

$$f(w) = aw \cdot \exp(-bw) \quad \text{eqn 4}$$

The best-fit ($r^2 = 0.937, P < 0.001$) parameters were found to be $a = 2.323, b = 0.080$. This function provided a better fit than common distributions such as gamma and lognormal.

Let $R_t = h_t/h_{t-1}$ denote the ratio of biomass produced in year $t$ to biomass produced in year $t-1$. This quantity is analogous to fecundity, in the sense that it must remain above one for the individual to experience net growth over multiple seasons. From eqn 3, $R_t$ is given by

$$R_t = \int_0^\infty \frac{\phi_{s(t)}F_{w(t)}(s)}{s_{t-1}} \, ds \quad \text{eqn 5}$$

Then, we define fitness as the geometric mean of the values of $R_t$ for $t = 1 \ldots T$, where $T$ is the longevity of the individual in years. Thus,

$$K = \sqrt[R_t]{R_1R_2 \cdots R_T} = \sqrt{bh_T} \quad \text{eqn 6}$$

The geometric mean is a good measure of fitness in situations where environmental conditions vary from year to year (McGinley, Temme & Geber 1987), because the geometric mean would indicate zero fitness for an individual that died before time $T$, whereas the arithmetic mean would indicate positive fitness in the same situation. We note that $T$ is not a parameter but rather the simulated output longevity of the individual, obtained by identifying in what year the biomass goes to zero because of individual death (computing fitness from fecundity for $t > T$ is trivial because it would yield $K = 0$ always). The units of $K$ are $e^{1/T}$.

SIMULATION EXPERIMENTS

We carried out three sets of simulation experiments:

Simulation experiment #1: fitness at empirical parameter values under continuous water level variation

We compared the fitness of the three strategies when the model parameters are set to match the empirically observed values and where the water level varies from year to year according to patterns observed in the field.

Simulation experiment #2: fitness landscape under continuous water level variation.

We examined fitness of the three strategies across a range of parameter values (mean and standard deviation) to determine whether the empirical values fall near the global maximum of the fitness landscape.

Simulation experiment #3: fitness at empirical parameter values under a “good or bad” environment

McGinley, Temme & Geber (1987) model fitness using eqn 1 but only allow for two possible environmental states – “good” and “bad” – each with corresponding values for $m$ in the fitness function – together with three possible offspring sizes: “small”, “medium” and “large”. To compare our results to those obtained by McGinley, Temme & Geber (1987), we performed a simulation experiment that allows only two possible water levels – “good” and “bad” – that occur with probabilities $p_G$ and $p_B = 1 - p_G$, respectively. McGinley, Temme & Geber (1987) computed the geometric fitness of strategies for various values of $p_G$, and various possible differences in quality between good and bad environments ($k$ in their notation) and found that a variable size

![Fig. 1. (a) Frequency distribution of water level at the end of March over the period 1932–2003 ($n = 71$) and fitted water level distribution function, eqn (4); (b) relationship between the total biomass of produced tubers and the size of planted tubers, with fitted fitness functions, eqn 1, for the three experimental water levels: shallow (15 cm), medium (45 cm) and deep (85 cm).](image)
strategy was favoured only for sufficiently large $k$ (large difference in environment quality) and sufficiently large $p_C$. In our model, we choose the “good” and “bad” environments based on results from the experiments.

Results

EXPERIMENT

Water level had a significant effect on tuber survival. In the shallow treatment, all planted tubers survived and produced new tubers, while in medium and deep conditions, all planted tubers smaller than 0.33 g and 0.79 g, respectively, produced a shoot that never reached the water surface and died during the summer (Fig. 1b). The water level also affected the total biomass of newly produced tubers. Productivity was highest in shallow water and decreased successively under medium and deep water levels (Fig. 1b).

After fitting eqn 1 to the experimental data from individual tubers, the following parameter values for shallow, medium and deep, respectively, were obtained: $m_{15} = 0.05$ g, $m_{45} = 0.31$ g, $m_{85} = 0.77$ g, $x_{15} = 0.22$, $x_{45} = 0.17$, $x_{85} = 0.07$, where $m_w$ is the minimum viable offspring size in water level $w$ and $x_w$ is a constant determining how quickly the fitness curve approaches its asymptotic value as $s$ increases ($P < 0.01$). The indexing indicates water level. For instance, $m_{15}$ is the average tuber size produced when the water level is 15 cm. A least squares regression between the three values of $m_w$ and water level $w$ fits the data very well ($r^2 = 0.99$, $P < 0.01$),

$$m_w = 0.010w - 0.124$$  \hspace{1cm} \text{eqn 7}$$

and the fit between the three values of $x_w$ and $w$ is also significant ($r^2 = 0.98$, $P < 0.05$),

$$x_w = -0.002w + 0.258$$  \hspace{1cm} \text{eqn 8}$$

These fits are based on the three data points emerging from the three experimental treatments. Using the parameterized fitness functions, we can estimate the optimal offspring tuber size $s^*$ from eqn 2 for a clonal plant species in a hypothetical environment with unchanging water level: $s^* = 0.08$ g for shallow, $s^* = 0.85$ g for medium and $s^* = 1.97$ g for deep water levels. For an unchanging water level of 25.5 cm, which is the average water level in the field as computed from eqn 4, the optimal tuber size would be $s^* = 0.332$ g. In absolute terms, this is somewhat below the observed mean (0.533 g) and median (0.505 g) tuber size in the field, although it is not clear what relationship should be expected between offspring tuber sizes observed in field populations experiencing temporally varying environmental quality and tuber sizes predicted from a model that assumes a constant environmental quality.

The offspring sizes of individual planted tubers were highly variable under all water level treatments (Table S1). The lognormal distribution provided the best fit for the individual offspring size distribution in almost all of the planted tubers that were tested (Table 1).

The mean size of the produced tubers was significantly affected by water level. The produced tubers were significantly larger in shallow ($\bar{w}_w = 0.62$ g, $SE = 0.02$) than in medium ($\bar{w}_w = 0.46$ g, $SE = 0.03$) or deep water ($\bar{w}_w = 0.30$ g, $SE = 0.03$) (one-way ANOVA on log-transformed data; $F = 28.8$, d.f. = 2, $P < 0.001$). The three data points relating mean tuber size produced ($\bar{w}_w$) to water level ($w$) are well-fit by a linear regression ($r^2 = 0.99$, $P < 0.01$):

$$\bar{w}_w = -0.005w + 0.680$$  \hspace{1cm} \text{eqn 9}$$

MATHEMATICAL MODEL

We used the individual-level results from Table 1 to parameterize the mathematical model. We compared biomass production under the observed lognormal strategy to two hypothetical alternative strategies: the single-size distribution, in which all offspring are of the same size, and the uniform distribution, in which the probability of producing tubers of a given size $x$ is a constant, nonzero value over a given interval of sizes $[s_{lower}, s_{upper}]$, and is zero outside the interval (Fig. S2 and equation A1).

Simulation experiment #1: fitness at empirical parameter values under continuous water level variation.

The water level $w(t)$ in a given year $t$ was a random variate sampled from eqn 4 at best-fit parameter values, normalized to yield a probability density function. Then, $x_w$, $m_w$ and $\bar{w}_w$ for the sampled water level $w(t)$ were determined from eqns 7–9. For $w < 12.01$ cm in eqn 7, we set $m_w = 0$ because otherwise $m_w$ is negative; likewise for $w > 114.91$ cm in eqn 8, we set $x_w = 0$ because otherwise $x_w$ is negative. Thence, fitness $F_w(s)$ was determined from eqn 1 and $\phi_w(s)$ from equation A1 (Supporting Information). Finally, total biomass $b_t$ produced during the season was determined from eqn 3.

For a given water level $w$, the three strategies produce the same mean tuber size $\bar{s}_w$ given by eqn 9. Thus, the strategies differ only in the way that tuber offspring size is distributed about the mean, and any difference in strategy fitness arises from the standard deviation $\sigma$ of the offspring size distribution. For the single-size strategy, $\sigma = 0$ by definition. To parameterize the lognormal strategy, it is crucial to use the best-fit standard deviation from individual-level data (Table 1) rather than aggregated data from field populations. The best-fit standard deviation from the 8 individuals in Table 1 is roughly the same across all treatments, ranging from about 0.7 to about 0.9. Therefore, we used the median value of $\sigma = 0.82$ as the parameter governing variance of the lognormal strategy. For the uniform strategy, $\sigma$ is determined by $s_{half}$; we used $s_{half} = 0.1$ and considered only $s > s_{half}$. The value $s_{half} = 0.1$ was chosen because it produces a distribution broad enough to be meaningfully different from the single-size distribution, yet narrow enough to allow a large range of mean

Table 1. Fit of test distributions to individual data in shallow, medium and deep water levels. N refers to the sample size (number of produced tubers by a planted tuber) used to fit the distributions. We used the three largest sample sizes for shallow and medium treatments and the two largest for the deep treatment (see Table S1). Lognormal fitting used two different methods (Kolmogorov–Smirnov–Lilliefors (KSL) with test statistic D and Shapiro–Wilks with test statistic W) to be able to compare P-values directly with the method commonly used for fitting the normal distribution. In most cases (marked in bold type), the lognormal fit the data tested best. In the few cases where the data were fit by the normal distribution, the lognormal fit was better. None of the data were fit by the gamma distribution. Note that the null hypothesis tested in each case is different; however, for ease of presentation Accept/Reject refers to the null hypothesis that the data belong to the distribution labelled in the respective column.

<table>
<thead>
<tr>
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<th>Distribution fitted</th>
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<td>Shallow (15 cm)</td>
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<td></td>
<td>D = 0.179</td>
<td>W = 0.908</td>
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<td></td>
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<td>σ = 0.805</td>
<td>σ = 0.831</td>
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<tr>
<td></td>
<td>D = 0.102</td>
<td>W = 0.914</td>
</tr>
<tr>
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<td>P &gt; D = 0.15</td>
<td>P &lt; W = 0.206</td>
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<tr>
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<tr>
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<tr>
<td></td>
<td>D = 0.73</td>
<td>W = 0.924</td>
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<tr>
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<tr>
<td>N = 10</td>
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<td>Accept</td>
</tr>
<tr>
<td></td>
<td>D = 0.128</td>
<td>W = 0.936</td>
</tr>
<tr>
<td></td>
<td>P &gt; D = 0.15</td>
<td>P &lt; W = 0.51</td>
</tr>
<tr>
<td></td>
<td>µ = -1.44</td>
<td>µ = -1.44</td>
</tr>
<tr>
<td></td>
<td>σ = 0.775</td>
<td>σ = 0.817</td>
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tuber sizes to be tested (everything up to $\bar{s}_w = 0.1$). All baseline parameter values for this and subsequent simulation experiments are summarized in Table 2.

At the empirical parameter values, the lognormal strategy had the highest average fitness across all realizations (mean 663.6, SD 222.9), followed by the uniform strategy (mean 327.9, SD 362.7) and the single-size strategy (mean 229.6, SD 240.6). The lognormal strategy had the highest fitness in 56% of realizations, followed by the uniform strategy (24%) and the single-size strategy (18%). The distribution of mean geometric fitness $K$ over all realizations appears to be approximately exponential (Fig. 2a), which is why the mean approximately equals the standard deviation. Accordingly, longevity tends to be distributed exponentially as well (Fig. 2b). Exponentiality arises from the assumption of a constant probability of death because of causes other than excessive water depth. Under the lognormal strategy, individuals also had the longest mean longevity (mean 89.6 years, SD 84.0), followed by the uniform (mean 36.6, SD 37.3) and single-size strategies (mean 23.6, SD 24.4).

Simulation experiment #2: fitness landscape under continuous water level variation

In simulation experiment #2, we examined fitness of the three strategies across a range of parameter values to determine whether the empirical values fall near the global maximum of the fitness landscape. Water level varied according to eqn 4, which is a continuous function describing year-to-year variation in rainfall in the field site. The lower bound for $r_w$ was 0. The upper bound for $r_w$ was chosen as the value above which discrete effects invalidate the use of the model (see Supporting Information). Accordingly, $r_w$ varied in the range [0, 1.5] in increments of 0.1 to explore the fitness landscape. We also

Table 2. Parameter values used in simulations for simulation experiment #1 (fitness at empirical parameter values under continuous water level variation), #2 (fitness under continuous water level variation), #3 (fitness at empirical parameter values under a “good or bad” environment) and #4 (fitness in an unchanging environment)

<table>
<thead>
<tr>
<th>Parameter/Function</th>
<th>Definition</th>
<th>Values</th>
</tr>
</thead>
</table>
| $f(w) = aw \cdot \exp(-bw)$ | Probability distribution function for fluctuations in water level $w$ from year to year | Simulation set #1: $a = 4.646, b = -0.080$  
Simulation set #2: $a = 4.646, b = -0.080$  
Simulation set #3: $a/n$ (used only two possible water levels)  
Simulation set #4: $a/n$ (used a constant water level of 25 cm)  
Sets #1, 3: 0.821  
Sets #2, 4: varies on [0,1.5] |
| $\sigma$ | Variance of $\log(S)$ for a lognormally distributed tuber size $S$ | Sets #1, 3: 0.821  
Sets #2, 4: varies on [0,1.5] |
| $m_w = c_w + d$ | Minimum viable offspring size as a function of water level $w$ | $c = 0.010, d = -0.124$ g for all sets  
eq 0.022, f = 0.258 for all sets |
| $\alpha_w = \gamma_w + \beta$ | Shape parameter for fitness function as a function of water level $w$ | Sets #1, 3, 4: $\gamma_w = 0.680$ g  
Set #2: $\gamma_w$ varies on [0 g, 2 g]  
0.1 g for all sets except in Figure 3 where it is varied |
| $\tilde{s}_w = \frac{1}{327} w + y_{int}$ | Mean tuber size produced as a function of water level $w$ | Sets #1, 3, 4: $y_{int} = 0.680$ g  
Set #2: $y_{int}$ varies on [0 g, 2 g] |
| $s_{half}$ | Width parameter for uniform distribution | 0.1 g for all sets except in Figure 3 where it is varied |
| $T_{MAX}$ | Duration of simulation runs | 350 years per simulation run for all sets  
Sets #1, 2, 4: 8,000  
Set #3: 5,000 |
| $R$ | Number of realizations per set | |
varied the slope of the linear relationship between mean tuber size produced and water level, eqn 9. This corresponds to a trade-off between producing many small tubers or a few large tubers. The water level at which no tubers are produced (the x-intercept of eqn 9) was fixed at 137.7 cm. We assumed the inability to produce tubers beyond this depth to be an absolute constraint on the organism. Hence, we varied the slope of eqn 9 by changing the y-intercept (y_int). High y_int means that fewer, but larger, tubers are produced. For all three strategies, y_int was varied in the range [0, 2] in increments of 0.05. Beyond y_int = 2, fitness approaches zero monotonically and discrete effects may become important (see Supporting Information).

As in simulation experiment #1, the water level was sampled from eqn 4 and we used eqns 3, 7–9 to model biomass dynamics. Together, the parameters σ and y_int control the most important degrees of freedom in an organism’s offspring size strategy: σ controls the amount of variability in offspring size and y_int controls whether few large tubers or many small tubers are produced. Therefore, a fitness landscape with σ and y_int on two axes should indicate whether selection is expected to occur with respect to those parameters.

Figure 3 shows the fitness landscape of the lognormal distribution and the uniform distribution for the range of y_int and σ values described above. For the lognormal distribution, the fitness landscape has a single peak at y_int = 0.5, σ = 0.8, corresponding to a maximal fitness of 724 g^1/2 (Fig. 3a). This peak is close to the empirical parameter values (y_int = 0.671, σ = 0.821). This maximal fitness is higher than that obtained for the single-size and uniform strategies. For the uniform distribution, the fitness peak occurs at unrealistic parameter values and the maximal fitness is only 613 g^1/2 (Fig. 3b). This comparison between lognormal and uniform distributions for a range of values of the standard deviation and slope allows us to correct for potential confounding between distribution type and variance effects per se and the results appear to support the adaptive value of the lognormal distribution. The proximity of the empirical parameter values to the hypothetical values where fitness is maximized is consistent with an adaptive response to temporal variation in water level, according to a classic optimality perspective. However, we emphasize that this is not conclusive proof that the lognormal strategy is adaptive in S. maritimus because the location of the fitness peak could—in principle—shift away from the empirical values if model assumptions or parameterization are changed. The fitness changes more dramatically with changes in y_int than with changes in σ; this suggests that selection upon the size-number strategy is stronger than selection on the degree of variability in offspring size, although it is difficult to know how absolute changes in fitness for changing σ maps to absolute strength of selection on variance in natural populations.

Simulation experiment #3: fitness at empirical parameter values under a “good or bad” environment

To compare our model results to those of McGinley, Temme and Geber (1987), we adopted their approach of simplifying environmental variability down to either “good” or “bad” environments. We chose the “good” environment to be w = 16.9 cm, yielding m = 0.60 and σ = 0.22 (equivalent to k = 1 in the notation of McGinley, Temme and Geber 1987). For “bad” environments, we looked at w = 21.8, 31.5, 41.2, 50.9, 60.6, and 70.4 cm (equivalent to k = 2, 4, 6, 8, 10, 12 in the notation of McGinley, Temme and Geber 1987) with corresponding values for m and σ from eqns 7 and 8.

When we allow environmental quality to be either “good” or “bad” in this way, the single-size strategy wins more often (Table 3), which is consistent with what McGinley, Temme and Geber (1987) found. This suggests that the success of the lognormal strategy derives from the fact that real-world environmental conditions are continuously distributed such that there is a nonzero probability of a year with arbitrarily poor conditions. When environmental conditions are distributed as a continuous random variate with nonzero probability for all
possible environmental conditions, then for any given tuber size, there must eventually occur a year in which water levels are too deep for the organism to survive. Hence, an individual adopting a single-size strategy would eventually die because of a rare but unfavourable year in which water levels were excessive. By comparison, for an individual adopting a lognormal strategy, there is a greater probability of a few large tubers being produced that can survive arbitrarily deep water levels.

As in the study by McGinley, Temme & Geber (1987), the single-size strategy wins when \( k \) is small, but the variable-size strategies win more often as \( k \) increases (Table 3). The main difference between our results and those obtained by McGinley, Temme & Geber (1987) is that the variable-size strategy does better when \( p_G \) is larger in their model but when \( p_G \) is smaller in our model. When \( k \) is small (such that the difference between “bad” and “good” years is small) or when \( p_G \) is large (such that “bad” years are rare), the lognormal strategy does worse than the single-size strategy because it needlessly invests resources in large tubers. Such a strategy would work well when \( k \) is large or when \( p_G \) is small, but when “bad” years are rare, it is more efficient to invest resources in producing large numbers of small tubers that are guaranteed to succeed. The lognormal distribution is more successful than the single-size distribution for larger \( k \) and smaller \( p_G \) because the water levels are too deep for any but the largest tubers to survive.

### Discussion

A model proposed by Smith & Fretwell (1974) predicted that in an unchanging environment, the optimal strategy is to produce propagules of a single size. Subsequently, modelling analyses (some using empirical data to parameterize model) have investigated whether strategies such as dormancy and the production of variably sized offspring might represent adaptive responses to temporally varying environments (see Introduction for references). Most modelling analyses of offspring size distribution strategies have found that producing variably sized offspring confers higher fitness than a single-size strategy in variable environments under many scenarios. Here, we presented and analysed experimental data from the clonal macrophyte species *Scirpus maritimus* showing that the distribution of offspring tuber sizes is highly variable and is best described by a lognormal distribution. The experiments also showed that the distribution was lognormal even under fixed water level conditions, suggesting that production of variably sized offspring is a developmentally programmed syndrome. We then used a mathematical model parameterized with experimental data to illustrate how production of variably sized offspring tubers can lead to higher fitness than a single-size strategy, by acting as a buffer against temporal environmental variability. This was illustrated using three simulation experiments. The first experiment showed that at the empirical parameter values controlling the investment strategy in offspring sizes, the fitness under the lognormal strategy was higher than the fitness under the single-size and the uniform strategy. The second experiment showed how the empirical parameter values lie near the global maximum in the fitness landscape of an individual adopting a lognormal strategy, whereas a uniform strategy generates a lower peak at values far from the empirical

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#### Table 3. Results for simulation experiment #3. Each cell shows the ratio of lognormal strategy fitness to single-size strategy fitness (top entry in each cell) and lognormal fitness to uniform strategy fitness (bottom entry in each cell) for various values of \( p_G \) and \( k \). Clear cells (resp. light grey and dark grey cells) denote cases where the single-size strategy (resp. uniform and lognormal) obtained the highest fitness.

<table>
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<tr>
<th>Probability of a Good Year ( (p_G) )</th>
<th>Difference in environmental quality ( (k) )</th>
<th></th>
<th></th>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( k = 1 )</td>
<td>( k = 2 )</td>
<td>( k = 4 )</td>
<td>( k = 6 )</td>
<td>( k = 8 )</td>
<td>( k = 10 )</td>
<td>( k = 12 )</td>
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occurs eventually with 100% probability, and hence a dormant are prone to extinction. However, this effect would be lessened becoming unviable or being removed through other processes. We speculate that dormancy will mitigate this effect but may not have a posteriori by considering the model equations. For a given tuber size $s$, there is a 100% probability that a water level sufficiently deep to preclude any biomass production eventually occurs, i.e. $s < m_w$ in eqn 1. This is because $f(w) > 0$ for all $w$ in eqn 4 and so any given water level $w$ will eventually occur if enough time passes. Hence, for any given offspring tuber size under a single-size strategy, there will eventually occur a water level sufficiently deep to kill the individual. By comparison, the lognormal strategy always has a nonzero probability of producing tubers of any given size, including sizes bigger than the single-size strategy for any given value of $s$. Hence, in this model system, single-size strategies are prone to extinction. However, this effect would be lessened in an individual-based model because the probability of producing arbitrarily large tubers under the lognormal strategy becomes very small; hence, very large tubers will not appear in all realizations of a stochastic individual-based model. We speculate that dormancy will mitigate this effect but may not remove it altogether: a string of sufficiently bad years also occurs eventually with 100% probability, and hence a dormant tuber may not be able to emerge in a favourable year before becoming unviable or being removed through other processes. By comparison, for a large individual adopting a lognormal strategy, for any given water level $w$, there is a nonzero probability of having offspring tubers large enough to survive a year of arbitrarily poor quality ($s > m_w$), because $f_{log}(s) > 0$ for all values of $w$ and $s$. This effect does not occur when environmental states are sampled from a small, discrete set (see Simulation Set #3 Results). Heterogeneity in water levels could also mitigate this effect because it is not likely water depth would be uniform across a given area; therefore, deep water habitats could be recolonised by individuals in shallower water habitats in following years.

Tuber production in *S. maritimus* appears to be a multiplicative process rather than an additive one, because the size of tubers produced in a given season along a rhizome greatly increases from the first to the later produced along that rhizome. This pattern suggests that resource translocation (especially carbohydrate) to younger tubers placed at the end of rhizome chains allows for the successive increase in tuber size. The young tubers constitute a resource sink and strongly benefit from resources supplied by all the shoots previously produced along the rhizome. Furthermore, if the change in a variate obeys the law of proportionate effect (the change at any step in the process is a random proportion of the previous value), then the variate will tend to be lognormally distributed. This is also true of *S. maritimus* tuber production. Tuber size distribution remains lognormal whatever the quality of the environment, whereas mean tuber size is highly plastic to water level, with a significant decrease under poor environment (i.e. deep water level). These factors may explain why *S. maritimus* tuber size is lognormally distributed rather than according to some other continuous probability distribution with nonzero variance. If a lognormal distribution may be the product of a complex set of processes not directly relating to fitness, a lognormal distribution per se cannot be called adaptive. However, it is adaptive in the sense that the species may exploit the fact that a lognormal distribution entails production of variably sized offspring. Moreover, it may be possible for a species to evolve with respect to some of the processes that determine the variance of the lognormal distribution. Hence, the variance of the distribution may evolve until the optimal value $\sigma \approx 0.8$ is reached.

Several additional factors suggest that the observed lognormal distribution may be the result of a bet-hedging strategy rather than a null expectation based on patterns of plant growth stemming from the law of proportionate effect. First, the fact that in *S. Maritimus*, the small tubers are produced before large ones is not really expected within a null pattern of plant growth. A null pattern would be the opposite, because resources become limiting at the end of the growing season. Simons & Johnston (2000) for example find that seed-size variation among fruits within individuals of *Lobelia inflata* (Campanulaceae) is substantial. They cite Wolfe (1992) in stating that “the size of plant reproductive structures, because of architectural and resource constraints, may diminish the later in the season they are produced”. Using a more theoretical approach, Halpern (2005) states that “an increase in trait variation under stress usually is interpreted as maladaptive developmental instability (reviewed by Simons & Johnston 1997).” If we compare the mean tuber size variance (coefficient of variation) at the individual level between the shallow (CV = 0.356) and the deep (= stressful; CV = 0.686) treatment, we indeed find that it is much lower ($F$-test; $P < 0.008$), suggesting an adaptive value of variability in this species.

As with any theoretical model, there are several limitations to the present model. For instance, our experiment simulates stable water levels within a growing season, whereas in wetlands, water level variations occur within the growing season as well as across space. As a result, our model does not assess the interactive effect of temporal and spatial variation on the evolution of offspring size distributions. As we only had three treatment levels in the experiments, we only had three points with which to make a regression model, which may have hid potential nonlinearities that should be present in eqn 7 and 8. Another limit of our model is that it does not take into account the possibility that tubers may remain dormant for several years before sprouting. Several studies have suggested that...
dormancy may be an adaptive response to temporal variability in plants as well as in animals (Hairston & Munns 1984; Kalisz & McPeek 1993; Simons & Johnston 2006; Evans et al. 2007; Venable 2007). Dormancy and density dependence were not incorporated because of lack of empirical data on those aspects of S. maritimus growth. Dormancy should mitigate the effects of temporal variability in the environment because a portion of tubers can remain dormant during bad years. This alone would not change the relative fitness of the strategies, because dormancy would benefit all strategies to a similar extent (just as the probability of an arbitrarily bad year eventually occurring is 100%, so is the probability of a string of arbitrarily bad years, and therefore, a single-size strategy remains more prone to failure than a variable-size strategy). Other model limitations include the lack of density dependence in growth dynamics (again, we speculate that this alone would probably not change relative fitness for similar reasons) and the use of a continuous model instead of an individual-based (agent-based) model. An individual-based model would allow us to account for discrete effects and/or plasticity. The combination of adding several factors such as dormancy, discreteness and density dependence could cause the qualitative predictions of the model to diverge from what we have predicted. Hence, an important priority for future work is developing a model that can account for all of these factors.

We have focused primarily on temporal heterogeneity in water level fluctuations as the source of diversifying selection in S. maritimus tubers. Nonetheless, in our experiment, other environmental parameters such as water temperature were less buffered in the containers that in wetlands and may also have influence plant growth. However, the widespread distribution of S. maritimus in the world suggests that this species tolerates a wide range of environmental conditions, especially water temperature (Kantrud 1996). Other different selective pressures could also interact to produce a diversity of tuber sizes in the population. For example, it is well known that S. maritimus tubers are consumed by geese, which selectively remove small tubers from the population, influencing the size distribution (Desnouhes et al. 2007). Our results obviously do not preclude the possibility that the observed tuber size distribution in S. maritimus could arise from other explanations and a multitude of mechanisms, and we agree that is “generally unwise to assume a particular model is correct” (Rees et al. 2010). However, it is striking that the lognormal distribution appears within an individual in one season (from the experiments), strongly suggesting a genetic component to this variation. Hangelbroek & Santamaría (2004) have studied Potamogeton pectinatus, another aquatic macrophyte that reproduces via tubers and displays considerable size variation (though they do not explicitly discuss the size distribution and nature of variability). They suggest that the size variation is maintained through the interaction of maternal and genetic effects. They find that maternal effects play a major role in determining the size of tubers produced and note that these effects can result in an amplification of within-clone variation in tuber size across generations. As explained previously, this amplification effect is a well-known mechanism for producing lognormally distributed offspring. Hangelbroek and Santamaria 2004 claim that this effect alone is sufficient to maintain variation in the population and reduce selection pressure towards an optimal tuber size; however, they do not discuss the link between these effects and the offspring size distribution.

In summary, this study supports the hypothesis that production of variably sized offspring in species like S. maritimus can increase fitness by acting as a buffer or bet-hedge against unpredictable temporal variation in an organism’s environmental quality and hence may be adaptive. This work illustrates the benefits of integrating mathematical modelling and empirical approaches in the same investigative framework.

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