RESEARCH ARTICLE

Optimal resource allocation and prolonged dormancy strategies in herbaceous plants

J. Colton Watts [iD] | Brigitte Tenhumberg

School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE, USA

Correspondence
J. Colton Watts
Email: j.colton.watts@gmail.com

Abstract

1. Understanding the fitness consequences of different life histories is critical for explaining their diversity and for predicting effects of changing environmental conditions. However, current theory on plant life histories relies on phenomenological, rather than mechanistic, models of resource production.

2. We combined a well-supported mechanistic model of ontogenetic growth that incorporates differences in the size-dependent scaling of gross resource production and maintenance costs with a dynamic optimization model to predict schedules of reproduction and prolonged dormancy (plants staying below ground for ≥1 growing season) that maximize lifetime offspring production.

3. Our model makes three novel predictions: First, maintenance costs strongly influence the conditions under which a monocarpic or polycarpic life history evolves and how resources should be allocated to reproduction by polycarpic plants. Second, in contrast to previous theory, our model allows plants to compensate for low survival conditions by allocating a larger proportion of resources to storage and thereby improving overwinter survival. Incorporating this ecological mechanism in the model is critically important because without it our model never predicts significant investment into storage, which is inconsistent with empirical observations. Third, our model predicts that prolonged dormancy may evolve solely in response to resource allocation trade-offs.

4. *Significance*. Our findings reveal that maintenance costs and the effects of resource allocation on survival are primary determinants of the fitness consequences of different life history strategies, yet previous theory on plant life history evolution has largely ignored these factors. Our findings also validate recent arguments that prolonged dormancy may be an optimal response to costs of sprouting. These findings have broad implications for understanding patterns of plant life history variation and predicting plant responses to changing environments.

KEYWORDS
dormancy, life history, maintenance, monocarpic, polycarpic, resource allocation

1 | INTRODUCTION

A long-standing issue for plant ecologists is understanding the conditions under which different life histories evolve. Herbaceous plants (plants with above-ground structures that die back between growing seasons) show a wide variety of life histories; some use all resources for reproduction in a single growing season and die (i.e. semelparous or monocarpic plants), while others reproduce

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in several growing seasons (i.e. iteroparous or polycarpic plants). Among those that use all resources for a single, suicidal reproductive event, some reproduce and die in their first growing season (i.e. annuals) while some forego reproduction for several seasons before reproducing (i.e. monocarpic perennials). Polycarpic herbaceous plants also vary in the extent and duration of periods of prolonged dormancy in which no above-ground parts are produced, and therefore no reproduction or photosynthesis can occur (e.g. Lesica & Crone, 2007; Lesica & Steele, 1994; Shefferson et al., 2018). Classic life history theory provides some insight into the general demographic trade-offs that might favour the evolution of such life histories (e.g. Charnov & Schaffer, 1973; Hart, 1977; Stearns, 1976) but does not elucidate how these conditions arise from the resource allocation trade-offs individuals face. A mechanistic understanding of the role of natural selection in generating these diverse life histories requires understanding the factors that shape the relationship between individuals' resource allocation and their expected lifetime reproductive success.

If resources are limited, plants face a trade-off between allocating resources to reproduction in the current growing season and to storage for the next growing season. Allocating more resources to reproduction increases current reproductive output, but if all resources are used for reproduction the plant must die. Allocating resources to storage, on the other hand, may increase future resource accumulation by increasing survival (Boyce & Volenec, 1992) and facilitating growth in subsequent growing seasons (Wyka, 1999; Zimmerman & Whigham, 1992). This creates a trade-off between current and future reproductive success. The consequences of this trade-off for a plant's expected lifetime reproductive success can be illustrated by a curve relating current reproduction and expected future reproduction over the range of available allocation options, ranging from completely foregoing current reproduction to using all resources to reproduce and dying (Figure 1) (Gadgil & Bossert, 1970; Pianka, 1976; Pianka & Parker, 1975; Schaffer, 1974). If plants have evolved resource allocation strategies that maximize lifetime reproduction, then a plant's resource allocation should optimally balance this trade-off by maximizing the sum of current and future expected reproduction (Figure 1; Gadgil & Bossert, 1970; Pianka, 1976; Pianka & Parker, 1975; Schaffer, 1974).

The way in which the trade-off between current and future reproduction changes over a plant's lifetime determines the schedule of allocation decisions that should evolve by natural selection (Pianka, 1976; Pianka & Parker, 1975). Determining the factors that underlie changes in the trade-off between current and future reproduction over a plant's lifetime is therefore critical for determining the conditions under which different life history strategies should evolve. In general, current reproductive success depends on the resources available for reproduction and the efficiency with which resources allocated to reproduction can be converted into offspring. Future reproductive success, on the other hand, depends on the relationship between the resources retained as storage and the resources available in the next growing season, as well as the probability of survival.
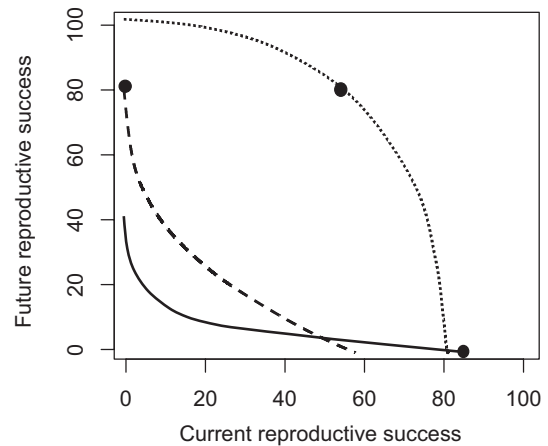

FIGURE 1 Examples of potential trade-offs between current and future reproductive success. Points represent the allocation of resources to current reproduction that maximizes the sum of current and future reproductive success. If small allocations to current reproduction strongly decrease future reproductive success (solid line and dashed line), then individuals should allocate either all (solid line) or none (dashed line) of their resources to reproduction. If small allocations to current reproduction only weakly decrease future reproductive success, individuals should allocate an intermediate proportion of available resources to current reproduction (dotted line)

Previous models of plant life history strategies have primarily focused on the effect of storage on future resources (Iwasa & Cohen, 1989; Klinkhamer, Kubo, & Iwasa, 1997; but see Pugliese, 1988). These models assume that net photosynthate production increases monotonically with the size of the plant's photosynthetic structures and that plants with greater storage at the beginning of the growing season are capable of producing a larger initial photosynthetic biomass. This results in a positive relationship between storage and future resource availability. However, this implicitly assumes that the allometric scaling of gross resource production and maintenance is similar. More recent theory suggests that resource production may generally increase less quickly with biomass than the costs of maintaining existing tissues (West, Brown, & Enquist, 2001). Thus, net resource production initially increases with biomass due to the increase in gross resource production, but decreases to zero as the costs of maintaining existing tissues approach the total quantity of resources produced (West et al., 2001). Net resource production may therefore be greatest at an intermediate biomass (i.e. a unimodal function of biomass, West et al., 2001). As a result, the benefit of increasing storage to begin the growing season with greater biomass may be fundamentally limited by the costs of maintaining existing tissues. This would contrast previous models in which the benefit of beginning the season with greater biomass depends only on the net photosynthetic rate and the length of the growing season (Iwasa & Cohen, 1989). How this difference in the relationship between storage and future resource availability affects the optimal life history strategy of herbaceous plants is currently unexplored.

Instead of sprouting in a given growing season, herbaceous plants may stay below ground in what has been referred

to as 'prolonged dormancy' or 'vegetative dormancy' (Lesica & Steele, 1994; Shefferson et al., 2018). Prolonged dormancy has been widely proposed to represent a bet-hedging strategy that reduces variation in fitness caused by temporal variation in environmental conditions (Gremer, Crone, & Lesica, 2012; Gremer & Sala, 2013; Hawryzki, Allen, & Antos, 2011; Jäkäläniemi, Crone, Närhi, & Tuomi, 2011; Shefferson, 2009). However, the evolution of prolonged dormancy may also be favoured by costs associated with the seasonal re-growth of above-ground structures per se (e.g. reduced potential for future growth and reproduction due to expenditure of resources stored in perennating organs, or greater mortality due to increased herbivory or water stress; Lesica & Crone, 2007; Shefferson, 2009; Shefferson et al., 2018; Shefferson, Warren, & Pulliam, 2014). Entering prolonged dormancy may allow plants to circumvent these costs while also potentially accumulating resources that increase survival or reproduction in subsequent growing seasons. Shefferson et al. (2014) found that observed frequencies of prolonged dormancy in yellow lady's slipper orchid *Cypripedium parviflorum* and common hepatica *Anemone americana* were better predicted by demographic models that incorporated relationships between prolonged dormancy and survival in subsequent growing seasons than those that accounted for stochastic environmental variation. Similarly, in Spalding's silene *Silene spaldingii*, prolonged dormancy was associated with increased flowering probabilities in subsequent growing seasons (Lesica & Crone, 2007). In bitterroot milkvetch *Astragalus scaphoides*, plants that prolonged dormancy had lower concentrations of stored non-structural carbohydrates (NSC) at the beginning of the growing season but accumulated as much NSC by the end of the growing season as plants that sprouted (Gremer, Sala, & Crone, 2010). More generally, prolonged dormancy appears to be more common among herbaceous plants that accumulate resources through mycorrhizal associations and may therefore be less dependent upon photosynthesis for resource production (Shefferson et al., 2018). While these empirical data suggest a role of prolonged dormancy in balancing life history trade-offs caused by costs of sprouting, to our knowledge no theoretical study has assessed the plausibility of costs of sprouting as a general explanation for the evolution of prolonged dormancy in herbaceous plants.

In this study, we use a stochastic dynamic programming (SDP) model that explicitly links individuals' allocation decisions with their current and future reproductive success to predict the schedules of reproduction and prolonged dormancy that maximize lifetime reproductive success. The trade-off between current and future reproduction in the model emerges from mechanistic descriptions of the consequences of a plant's resource allocation, including allocating resources to sprouting. Similar models have been used previously to predict optimal life history strategies in plants (e.g. Iwasa & Cohen, 1989; Klinkhamer et al., 1997; Pugliese, 1988) and we expand on this foundation in four key directions. First, we derive the relationship between a plant's storage and its future resource production using a mechanistic model of resource production that accounts for differences in the scaling of resource production and maintenance costs with mass (West et al., 2001). Second, the relationship

between storage and future resource production in our model accounts for the effect of mass on survival during the growing season (Cain, 1990; Cook, 1980; Roach & Gampe, 2004; Schmitt, Eccleston, & Ehrhardt, 1987; Shefferson, 2006; Solbrig, 1981; Tenhumberg, Suwa, Tyre, Russell, & Louda, 2015). Third, we account for the effect of a plant's storage on the probability that it survives to the next growing season (Boyce & Volenec, 1992). Fourth, we incorporate the potential for plants to enter prolonged dormancy to explore the conditions under which periods of prolonged dormancy represent an adaptive solution to resource allocation trade-offs associated with sprouting.

2 | MATERIALS AND METHODS

2.1 | Model overview

The model considers exclusively sexually reproducing, herbaceous plants that are either hermaphroditic or female, are not pollen limited and which grow in seasonal environments and must therefore spend the non-growing season below ground. We are concerned with predicting the between-season resource allocation strategies that maximize plant fitness; thus, we divide a plant's life into discrete growing seasons $y = (1, 2, 3, ..., Y)$, beginning with the first growing season in which a seed germinates. We used SDP to determine the life history decisions at the end of each growing season that maximize a plant's lifetime reproductive success. An SDP model has three components: the state variables and their dynamics, the set of decisions and the pay-off function (Bellman, 1957; Clark & Mangel, 2000). The optimal set of decisions for a given state maximizes the total fitness (i.e. the sum of current and future fitness) from the current time point to the end of the individual's lifetime (Bellman, 1957; Clark & Mangel, 2000). Current fitness depends on the consequences of a given set of decisions for immediate reproductive output, whereas future fitness depends on how the consequences of those decisions for an individual's state affect the total fitness gained from the next season onward. To avoid searching all possible sequences of future decisions forward in time to calculate the future fitness associated with the state in the next season, we work backward in time from the end of an individual's life (Y), taking advantage of the fact that the optimal decision for each state maximizes fitness from that season onward. Thus, the future fitness payoffs for the different states that an individual could possess in the next season as a result of their decisions are already known—they are the total fitness payoffs already calculated for the next season. The optimal state-dependent decisions predicted by the model can then be used to predict the optimal life history (i.e. the among-season schedule of reproduction and dormancy) given an individual's initial state.

Our model considers three states V, D and y. V specifies the amount of resources at the beginning of the growing season (hereafter 'spring storage' for brevity, although the model also applies to plants growing in non-temperate seasonal environments), D specifies whether a plant sprouted ($D = 0$) or entered prolonged dormancy ($D = 1$), and y indicates plant age in growing seasons. Thus, for

a plant of a given spring storage V and dormancy status D having experienced y previous growing seasons, the expected fitness accrued between season y and the end of the plant's lifetime Y is $F[V, D, y]$. For an exclusively sexually reproducing plant, the expected fitness can be approximated by the sum of seed production in the current season and the expected seed production in all future seasons of life, assuming the plant expresses the optimal life history strategy in future seasons. We do not attempt to model the optimal allocation of resources used in reproduction among offspring (i.e. the model does not consider trade-offs between quantity vs. quality of offspring) and, for simplicity, we assume that any reproduction takes place in a single reproductive bout at the end of the growing season. We set the terminal fitness function (i.e. the future fitness expectation for a plant in the final season Y of its life, $F[V, D, Y + 1]$) to 0 because no fitness can be accrued after death. A plant's expected lifespan depends on how resources are allocated (described below). Thus, to ensure that our model predictions are not affected by the assumption of a fixed lifespan (Houston & McNamara, 1985; Real, 1990) we set Y to 1,000 growing seasons, which is much larger than the maximum possible lifespan given our model parameters (Table 1). We consider values of $V = (0, 1, 2, 3, ..., 150)$, as this well exceeds the amount of spring storage that plants accumulate over their lifetime for the parameter values we explore. Thus, the state space for our model consisted of $V = (0, 1, 2, 3, ..., 150)$, $D = (1, 2)$ and $y = (1, 2, 3, ..., 1,000)$, for a total of 300,000 combinations of state variables.

The life history decisions we focus on are (a) the dormancy status in the next growing season (sprouting [$D = 0$] or prolonged dormancy [$D = 1$]) and (b) the proportion r of resources allocated to reproduction in the current growing season versus storage kept over the non-growing season (hereafter 'overwinter storage'). Note that we do not model seed dormancy, but rather prolonged dormancy sensu Lesica and Steele (1994), in which plants remain underground during one or more growing seasons following germination. The initiation and maintenance of prolonged dormancy is poorly understood; however, at least some of the physiological changes that determine the conditions under which plants resume growth appear to occur at the onset of seasonal dormancy (Tylewicz et al., 2018). We therefore assume that both decisions occur at the end of each growing season. Because the optimal allocation to reproduction r may depend on whether the plant decides to enter dormancy or sprout in the next season, we assume that these decisions are made simultaneously. In other words, fitness is maximized over the possible combinations of r and D; a plant's reproductive allocation is not constrained by a prior choice of dormancy status in the next season, nor vice versa.

Importantly, the options available to the plant at the end of a growing season depend on its current dormancy state. For sprouted plants (current dormancy $D = 0$), the plant may allocate a proportion r of the resources expected to be available at the end of the season, $S(y)$, to reproduction, with the remainder $(1 − r) \times S(y)$ retained as overwinter storage, and decide whether to sprout again in the next season (D stays 0) or enter prolonged dormancy (D changes to 1). Because resources are typically lost between growing seasons

TABLE 1 Default parameter values used for the stochastic dynamic programming model

Symbol	Definition	Value
Y	Number of growing seasons	1,000
α	Efficiency of converting storage to initial above-ground biomass	0.5
a	Maximum rate of photosynthate production per unit above-ground biomass	0.35
b	Metabolic costs of maintenance per unit above-ground biomass	0.10
c	Increase in metabolic maintenance cost per unit storage	0.01
T	Growing season length	150
μ_0	Minimum log odds of surviving the season	−1.35
μ_1	Effect of m_s on the odds of surviving the season	0.09
μ_2	Effect of growth g on the odds of surviving the season	2.17
μ_3	Effect of T on the odds of surviving the season	−0.005
μ_4	Interaction between growth g and T on the odds of surviving the season	0.007
ξ_0	Minimum log odds of surviving over winter	−3.75
ξ_1	Effect of overwinter storage $(1 − r) \times S(y)$ on the odds of overwinter survival	0.20
γ	Proportion of storage remaining after overwintering period	0
i	Maximum rate of storage increase per unit storage during prolonged dormancy	1
ν_0	Minimum log odds of survival during prolonged dormancy	0.5
ν_1	Effect of V on the odds of surviving the season	0.012

(Wyka, 1999), the spring storage in the next growing season is $V(1 − r, y + 1) = \gamma \times (1 − r) \times S(y)$, where γ represents the proportion of storage remaining after overwintering (e.g. due to losses from respiration, herbivory, or disease). Thus, for sprouted plants ($D = 0$), the fitness payoff associated with the optimal life history decisions is

$$F[V, 0, y] = \max_{D,r} \left\{ R(r) + \xi(1 − r) \times F[V(1 − r, y + 1), D, y + 1] \right\}, \quad (1)$$

where max indicates that the optimal plant life history decisions are the options that maximize the expected fitness, and the letters below the max indicates the decisions over which fitness is maximized. Thus, plants use the combination of dormancy decision D and allocation to reproduction r that maximizes the expected fitness. The $R(r)$ term specifies the number of offspring produced in the current growing season given r, which is either a linear or increasing exponential function of the quantity of resources allocated to reproduction, $R(r) = \beta[r \times S(y)]$ (Klinkhamer et al., 1997; Schaffer, 1974). An increasing exponential relationship between offspring number and resources allocated to reproduction might arise if successful reproduction requires a large quantity of reserves to produce a large bolting structure

(i.e. the 'reproductive effort model', Schaffer, 1974) or to saturate seed predators (Janzen, 1976; Klinkhamer et al., 1997). The term $\xi(1 - r)$ represents the probability of surviving between growing seasons (hereafter 'overwinter survival'), which depends on overwinter storage (Boyce & Volenec, 1992), $(1 - r) \times S(y)$, and is given by

$$\xi(1 - r) = 1/\{1 + \exp[-\xi_0 - \xi_1 \times (1 - r) \times S(y)]\}. \quad (2)$$

This implies that any increase in r which determines seed production (current fitness) is traded off with a reduction in overwinter survival (future fitness). The term $F[V(1 - r, y + 1), D, y + 1]$ represents the expected fitness from the next season onward, which depends on both the dormancy decision D and the allocation to reproduction r.

Dormant plants (current dormancy $D = 1$) cannot allocate any resources to reproduction in the current season ($r = 0$) because sexual reproduction cannot occur in the absence of above-ground structures. Thus, dormant plants only need to decide whether to remain dormant in the next growing season (D stays 1) or sprout (D changes to 0). The fitness payoff associated with the optimal life history decision for dormant plants ($D = 1$) is therefore.

$$F[V, 1, y] = \max_D(\xi(1) \times F[V(1, y + 1), D, y + 1]), \quad (3)$$

where fitness is maximized over the decision to sprout in season $y + 1$ ($D = 0$) or remain in prolonged dormancy instead ($D = 1$). Plants face the same overwintering conditions regardless of their decision to sprout or remain dormant in the next growing season, so overwinter survival ξ is independent of this decision and the spring storage in the following year is $V(1, y + 1) = 1 \times \gamma \times S(y)$. We assume that dormant plants have the potential to accumulate reserves during the growing season (i.e. $S(y) > 0$); these dynamics are described below (see Section 2.2).

2.2 | Within-season resource dynamics for sprouting plants

The resources available to a plant at the end of the season, $S(y)$, depend on the dormancy status of the plant. At the beginning of the first growing season and each subsequent season in which the plant sprouts (as opposed to entering or remaining in prolonged dormancy), the plant generates an above-ground photosynthetic structure of initial size $m_0(y)$ by converting stored resources (e.g. carbon, nitrogen) contained in the seed [$V(y = 1)$] or kept as overwinter storage from the previous growing season [$V(y > 1)$] with a conversion efficiency $0 \leq \alpha \leq 1$ (Chapin, Schulze, & Mooney, 1990) such that $m_0(y) = \alpha \times V(y)$. Greater quantities of spring storage $V(y)$ thus support the generation of larger m_0, consistent with empirical data (Wyka, 1999; Zimmerman & Whigham, 1992) and theory predicting that plants should use stored resources to produce m_0 at the maximum possible rate before switching to rely on newly acquired resources for biomass production (Iwasa & Cohen, 1989). It is possible that plants possess stored resources too large to exhaust by constructing m_0 at the maximum rate (Iwasa & Cohen, 1989) and

consequently retain a portion of $V(y)$ as storage during the growing season. Including this possibility in our model did not affect the qualitative predictions of our model (because it is rarely optimal for plants to keep such a large amount of resources), so we present results for the simpler scenario in which plants exhaust their storage to produce the initial above-ground structure. After constructing m_0, plants acquire new resources over time in the growing season $0 \leq t \leq T$, where t is time within the season and T the length of the growing season. These resources are used to maintain existing tissues, to grow the size of the above-ground photosynthetic structure $m(t)$, and to increase the pool of stored reserve resources $s(t)$. The expected stored reserves available for reproduction and overwinter storage at the end of the season, $S(y)$, equal the total reserves accumulated by the end of the season $s(T)$ weighted by the probability μ of surviving to T.

To determine $s(T)$, we modified the general ontogenetic growth model of West et al. (2001) to consider the seasonal re-growth of photosynthetic structures and accumulation of stored reserves by an herbaceous plant. Gross photosynthate production at time t in the growing season increases with above-ground biomass $m(t)$ as $am(t)^{3/4}$ (Enquist, Brown, & West, 1998), where a is a taxon-specific constant and $m(t = 0) = m_0(y)$. The rate at which photosynthate is used to maintain existing tissues increases in direct proportion to biomass $bm(t)$ (West et al., 2001). Because reserves $s(t)$ are in part stored within vacuoles and plastids within existing cellular structures (Chapin et al., 1990; Lewis & McCourt, 2004; Matile, 1987), we assume that the maintenance cost per unit of reserve resources (denoted c) is less than that of above-ground structures (denoted b). Thus, the net photosynthate $p(t)$ available to the plant at time t within the growing season is

$$p(t) = am(t)^{3/4} - bm(t) - cs(t), \quad 0 \leq t \leq T. \quad (4)$$

The amount of resources available to a plant at the end of the growing season $s(T)$ depends on a plant's investment into growing photosynthetic biomass, $m(t)$. Up to a point, greater investment in growing $m(t)$ increases $s(T)$ through compounding returns in terms of new resources gained (Chapin et al., 1990). However, plants investing everything into $m(t)$ have no reserves left at the end of the growing season. Thus, $s(T)$ should tend to be highest for intermediate investments in photosynthetic biomass. Let g be the proportion of net photosynthate allocated to $m(t)$, and the remainder $(1 - g)$ is allocated to reserves $s(t)$. Assuming g does not change over the growing season, the above-ground biomass $m(T)$ and reserve biomass $s(T)$ accumulated by the end of the season of length T are

$$m(T) = m_0 + g \int_0^T p(t)\, dt = m_0 + g \int_0^T \left[am(t)^{3/4} - bm(t) - cs(t) \right] dt, \quad 0 \leq t \leq T, \quad (5)$$

$$s(T) = (1 - g) \int_0^T p(t)\, dt = (1 - g) \int_0^T \left[am(t)^{3/4} - bm(t) - cs(t) \right] dt, \quad 0 \leq t \leq T. \quad (6)$$

In general, the change in m and s over t follows a logistic trajectory identical to that of the phenomenological von Bertalanffy growth

model (Von Bertalanffy, 1957), in which growth slows as maintenance costs of existing tissues approaches the rate at which new resources are produced (West et al., 2001).

The increase in initial photosynthetic biomass m_0 with spring storage $V(y)$ causes the relationship between $s(T)$ and g to differ among plants with different $V(y)$. Plants with greater spring storage $V(y)$ can, up to a point, accumulate greater $s(T)$ (Figure S1), provided they allocate a smaller proportion g of net photosynthate to $m(t)$ to avoid excessive maintenance costs. However, if $V(y)$ is too large the plant accumulates fewer reserves than plants with smaller $V(y)$ (Figure S1), even if no net photosynthate is allocated to increasing m (i.e. $g = 0$). Thus, the difference in the scaling exponents for gross photosynthesis $am(t)^{\frac{3}{4}}$ and maintenance $bm(t) + cs(t)$ causes the maximum quantity of reserves a plant can accumulate by T to be greatest for intermediate spring storage $V(y)$ (Figure S1) because net photosynthate production is maximized at intermediate values of total biomass (West et al., 2001).

The probability of plants surviving the growing season increases with the size of the plant's above-ground structures (Cain, 1990; Cook, 1980; Roach & Gampe, 2004; Schmitt et al., 1987; Shefferson, 2006; Solbrig, 1981; Tenhumberg et al., 2015; but see Goldstein, Meinzer, & Monasterio, 1985; Zhang et al., 2009). We model the survival probability of a sprouted plant μ as an increasing logistic function of initial above-ground biomass m_0 and the allocation to growth g because larger values of either result in greater biomass during the growing season (Figure S2). The effect of g depends on the length of the growing season, T. As T increases, μ increases more strongly with g because plants that allocate few resources to above-ground structures must survive a longer period of time at greater mortality risk. Thus

$$\mu = 1/\{1 + \exp[-(\mu_0 - \mu_1 \times m_0 - \mu_2 \times g - \mu_3 \times T - \mu_4 \times g \times T)]\}, \quad (7)$$

where μ_{0-4} represent the regression coefficients associated with the intercept (on the log odds scale), initial above-ground biomass m_0, allocation to growth g, season length T and the interaction between g and T respectively.

In summary, the proportion g of net photosynthate allocated to photosynthetic structures versus storage during the growing season affects both the total reserves accumulated by the end of the season $s(T)$ and the probability μ of surviving to the end of the season. In our model, we used values of g that produce the greatest possible expected reserves at the end of the season, $S(y)$, for a given $V(y)$ (i.e. the greatest product of $s(T)$ and μ; Figure 2; Figure S3).

2.3 | Within-season resource dynamics for dormant plants

How stored resources change during the growing season for plants that undergo prolonged dormancy is relatively poorly understood. While stored resources are known to decline during seasonal dormancy (Boyce & Volenec, 1992; Wyka, 1999), some
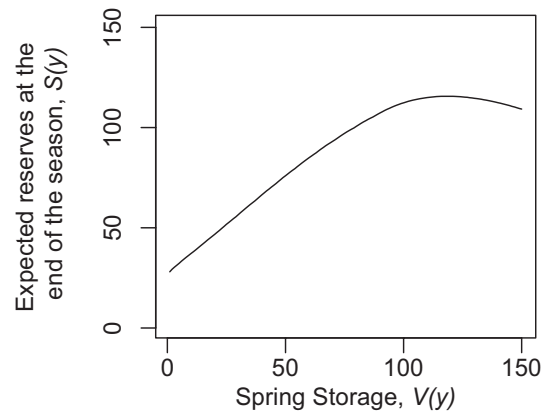

FIGURE 2 Relationship between spring storage $V(y)$ and the expected reserves available for reproduction and overwinter storage at the end of the growing season, $S(y)$. The expected reserves are equal to the total reserves accumulated, $s(T)$, weighted by the probability of survival μ. The reduction in $S(y)$ at high values of $V(y)$ is due to the costs of maintaining existing tissues

empirical evidence suggests that resource dynamics during prolonged dormancy may differ fundamentally from those during seasonal dormancy; indeed, plants undergoing prolonged dormancy may acquire similar quantities of resources as sprouted plants (Gremer et al., 2010). The underlying processes may include the remobilization of structural carbohydrates (Gremer et al., 2010) or the acquisition of new resources from mycorrhizal fungi (Shefferson, 2009; Shefferson et al., 2018). The net outcome of such processes is likely an increasing function of the spring storage $V(y)$, as plants with larger storage may have greater quantities of structural carbohydrate and more extensive fungal connections but also pay greater maintenance costs. Thus, the reserve biomass accumulated by the end of the growing season, given the spring storage $V(y)$, is

$$s(T) = [i \times V(y)]/[1 + i \times \lambda \times V(y)], \quad (8)$$

where i represents the maximum per unit storage rate of storage accumulation during prolonged dormancy and λ is the reciprocal of the theoretical maximum storage size. This parameterization allows us to consider scenarios in which $s(T)$ is relatively independent of $V(y)$ (i.e. high i), approximately a linear function of $V(y)$ (i.e. low i), or a saturating function of $V(y)$ (i.e. intermediate i). A plant in prolonged dormancy survives to the end of the growing season with probability ν. We assume that survival increases with spring storage $V(y)$, as plants with greater spring storage are more likely to meet metabolic demands during the growing season. Thus, the probability of survival for a dormant plant ν is

$$\nu = 1/\{1 + \exp[-\nu_0 - \nu_1 \times V(y)]\}. \quad (9)$$

The expected stored reserves available at the end of the season, $S(y)$, then equal the total reserves accumulated by the end of the season $s(T)$ weighted by the probability ν of surviving to T.

3 | RESULTS

The SDP uses expected values for all life history parameters (Table 1), which do not vary between growing seasons y to predict the optimal resource allocation to reproduction, r^*, and whether a plant should enter dormancy, D. Further, our model does not assume a deterministic life span Y. Hence, changes in a plant's allocation patterns over its lifetime are determined by changes in its storage $V(y)$, but are independent of y. To explore the conditions favouring the evolution of different life history strategies, we varied model parameters that influence (a) the relationship between overwinter storage and overwinter survival ξ, (b) the relationship between overwinter storage and expected future reserve availability $S(y + 1)$, (c) the relationship between the reserves allocated to reproduction $r \times S(y)$ and the number of offspring produced and (d) the benefits of entering prolonged dormancy. Default parameter values are provided in Table 1. We first describe the conditions under which the model predicts that a monocarpic life history should evolve. Monocarpic plants use all expected reserves $S(y)$ for a single reproductive event and die. If the flowering event happens after the first growing season, such plants are also annuals ($r^* = 1$ at $y = 1$), otherwise they are monocarpic perennial plants. We then describe the factors underlying quantitative differences in resource allocation for polycarpic plants (i.e. plants that flower in more than one growing season over their lifetime and thus keep overwinter storage [$r^* < 1$]). Finally, we explore the conditions under which prolonged dormancy can evolve in response to resource allocation trade-offs associated with sprouting.

3.1 | Monocarpic life histories

Our model predicts two situations in which plants should express a monocarpic life history in which all reserves $S(y)$ are used in a single, suicidal reproductive event (i.e. $r^* = 1$ for at least some $V(y)$).

In the first case, $r^* = 1$ for all $V(y)$; this implies that plants are obligate annuals, as $r = 1$ maximizes lifetime offspring production for any possible storage available in the seed $V(y = 1)$. This occurs if (a) the probability of surviving the winter ξ is low, (b) the expected reserves $S(y)$ that can be acquired during the growing season are low, or (c) a large proportion γ of storage is lost during the winter period.

In our model, the range of overwinter survival conditions for which an obligately annual strategy (i.e. $r^* = 1$ for all $V(y)$) is optimal depends strongly on the assumption that overwinter storage affects survival to the next growing season. This can be illustrated by comparing the trade-off between current reproduction (i.e. $R(r)$) and future reproduction {i.e. $\xi(1 - r) \times F[V(1 - r, y + 1), D, y + 1]$} for different minimum probabilities of surviving the winter (defined on the log-odds scale by ξ_0) to a scenario in which overwinter survival is independent of storage (i.e. ξ is fixed). While the precise shape of this trade-off varies with spring storage $V(y)$, the range of overwinter survival conditions for which $r^* = 1$ is the same for all $V(y)$; thus, we can infer changes in the range of survival conditions for which an obligately annual strategy is optimal by visualizing the trade-off between current and future reproduction for a single $V(y)$ (Figure 3).

If overwinter survival is independent of overwinter storage, then the trade-off between current and future reproduction is exceptionally weak (i.e. increasing current reproduction has little effect on future reproduction, Figure 3a). This is because the benefit of large $V(y)$, and thus m_0, is small due to the costs of maintenance (Figure 2). Hence, for most survival scenarios, the sum of current and future reproduction is maximized when individuals keep a small quantity of reserves as storage and invest any remaining reserves in current reproduction (filled circles on solid, dashed and dotted lines in Figure 3a). This implies that a perennial polycarpic strategy is optimal and, because the quantity of storage kept is small, even plants with low $V(y)$ (e.g. early in life) can generate enough reserves to reproduce. An annual life history (i.e. using
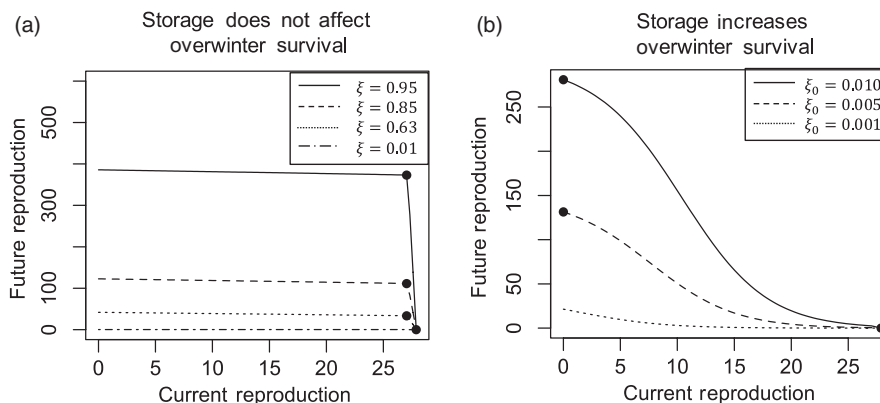

FIGURE 3 The effect of overwinter survival on the trade-off between current and future reproductive success for scenarios in which the probability ξ of surviving over the winter (a) is independent of overwinter storage or (b) increases with overwinter storage. Note that in (b) line types correspond to different minimum probabilities of survival ξ_0. Points represent the allocation of resources to current reproduction that maximizes the sum of current and future reproductive success. Note that the precise shape of the curves, and thus the optimal allocation of resources, depends on spring storage $V(y)$; results are shown for $V(y) = 20$

all reserves for current reproduction, filled circle on dash-dotted line in Figure 3a) is predicted to evolve only if overwinter survival is exceptionally low (e.g. $\xi = 0.01$). In contrast, if plants can use storage to increase overwinter survival, then allocating resources to current reproduction drastically reduces future reproductive success (Figure 3b) and, for most survival scenarios, plants should keep large quantities of storage to capitalize on future reproductive potential. This once again implies a perennial polycarpic strategy is optimal. However, because the quantity of storage kept is very large, plants with lower $V(y)$ may forego reproduction in the current growing season entirely (filled circles on solid and dashed lines in Figure 3b). An obligately annual strategy becomes optimal if the minimum survival probability is low (filled circle on dotted line in Figure 3b), but this occurs at values of minimum overwinter survival (ξ_0) for which a plant foregoing reproduction would still achieve a relatively high probability of survival (e.g. $\xi = 0.63$). In fact, a plant foregoing reproduction would experience the same probability of survival ($\xi = 0.63$) for which a perennial strategy is optimal if overwinter survival is independent of storage (cf. Figure 3a,b). Thus, when accounting for maintenance costs, the effect of storage on overwinter survival causes our model to predict an obligately annual strategy even if overwinter survival is relatively large.

Conditions leading to low expected reserves at the end of the season $S(y)$ generally decrease the benefit of allocating reserves to overwinter storage because $S(y)$ determines the maximum quantity of storage as well as the expected reserve acquired in the next growing season (Notes S1). In contrast to previous models that ignore maintenance costs, we find that the per-unit-biomass costs of maintaining reserves c is a key parameter influencing $S(y)$ and, thus, the conditions under which an obligately annual life history evolves. As maintaining storage becomes more expensive (i.e. c increases), $S(y)$ decreases, particularly for plants with high spring storage $V(y)$ (Figure S4a). Consequently, the minimum overwinter survival probability ξ_0 at which an annual strategy becomes optimal (i.e. the switchpoint value) increases with c (Figure 4). For a given c, the range of overwinter survival conditions for which an annual strategy is optimal increases further if the probability of surviving growing season is lower (illustrated by different μ_0 values, in Figure 4), as this further decreases $S(y)$ (Figure S4b). Previous theory suggests that short growing seasons can also decrease $S(y)$, thereby favouring an annual life history (Iwasa & Cohen, 1989); our model corroborates this result to a point (Figure S5), but also suggests that $S(y)$ may decrease if growing seasons are very long due to a lower probability of surviving to the end of the season (not shown). Our model also reinforces previous theory (Iwasa & Cohen, 1989) predicting that high losses of storage over winter γ may also favor an annual strategy ($r^* = 1$ for $(1 - \gamma) > 0.7$, Figure S6) by increasing the quantity of overwinter storage necessary to begin the next season with a given quantity of spring storage $V(y)$.

The second case in which our model predicts plants should express a monocarpic life history occurs if the number of
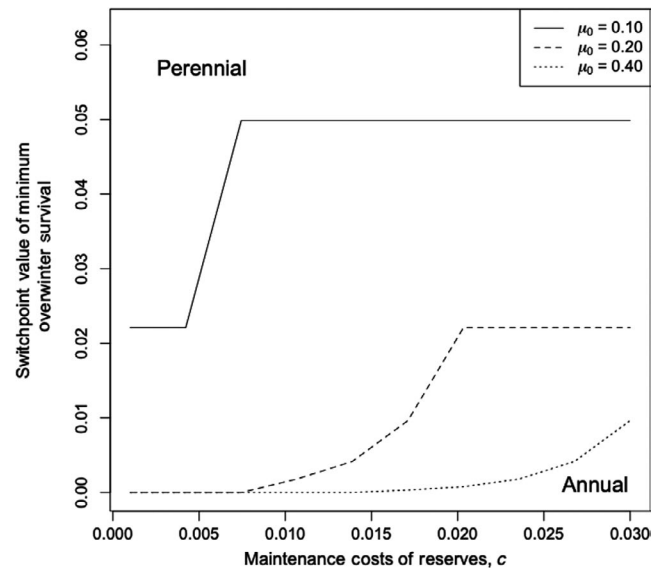

FIGURE 4 The minimum overwinter survival probability $\{1/[1 + \exp(-\xi_0)]\}$ below which an annual strategy becomes optimal (the 'switchpoint value') plotted against the maintenance costs of reserves, c for different values of minimum within-season survival probabilities μ_0. Note that for intermediate and high μ_0 the switchpoint value approaches but is not exactly equal to 0 at low c

offspring produced is an increasing exponential function of the resources allocated to reproduction, consistent with previous theory (Janzen, 1976; Klinkhamer et al., 1997; Schaffer, 1974). In this case, $r^* = 1$ for all $V(y)$ above a threshold value of $V(y)$ and $r^* = 0$ for all $V(y)$ below this threshold (Figure 5a). Whether the predicted monocarpic life history is annual or perennial depends on the storage within the seed $V(y = 1)$. If the storage within the seed $V(y = 1)$ exceeds the threshold above which reproduction is optimal, then plants will use all resources for reproduction at the end of the first season and die. This implies that plants are facultatively annual. If $V(y = 1)$ is lower than the threshold, then individuals are monocarpic perennials. The number of growing seasons needed to reach the threshold value of $V(y)$, reproduce, and die depends on the seed storage $V(y = 1)$ and the relationship between $V(y)$ and the reserves accumulated by the plant in each growing season $S(y)$. For our default parameter values (Table 1) and $V(y = 1) = 1$, for example, a plant would accumulate $S(y = 1) \approx 30$ units of reserves in the first growing season (Figure 2), all of which would be saved as storage for the second season (Figure 5a). In the second season, the plant would possess spring storage $V(y = 2) \approx 30$ and accumulate $S(y = 2) \approx 55$ (Figure 2), again saving all as storage (Figure 5a). In the third season, $V(y = 3)$ would exceed the threshold for reproduction (Figure 5a), and the plant would use all reserves $S(y = 3)$ for reproduction and die. If we assume a linear relationship between seed production and the resources allocated to reproduction, the model predicts either an obligately annual strategy (see above) or a polycarpic perennial strategy (see below), but never a monocarpic perennial strategy.
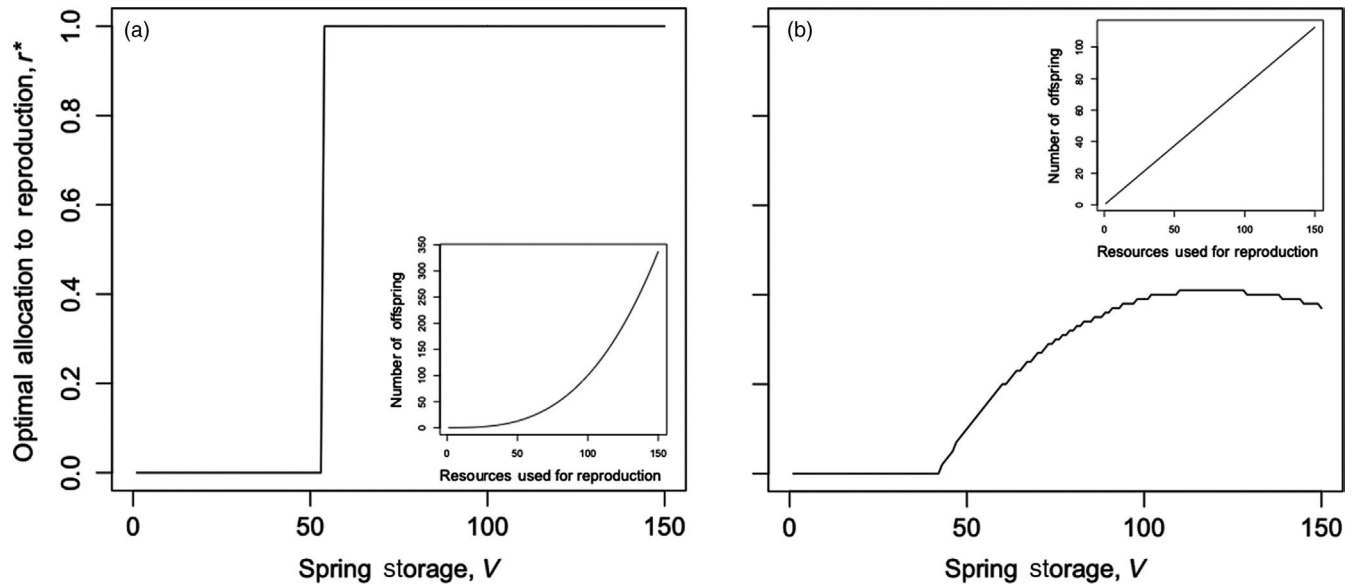
FIGURE 5 The optimal proportional allocation of reserves to reproduction r^* for different values of spring storage $V(y)$. Predictions are shown for (a) an exponential relationship and (b) a linear relationship between seed production and the quantity of reserves allocated to reproduction as shown in the inset figures

3.2 | Polycarpic life histories

If the optimal allocation of reserves to reproduction $r^* < 1$ for all $V(y)$, then reproduction is never suicidal, and plants are therefore polycarpic. For polycarpic plants, the optimal allocation of reserves to reproduction r^* changes with spring storage $V(y)$. This is because the model predicts that there is a target amount of storage that plants should keep overwinter (see below), yet the total quantity of reserves available to the plant $S(y)$ depends on $V(y)$ (Figure 2). If $V(y)$ is small, plants cannot accumulate enough reserves by the end of the season to reach the target, so they forego reproduction and allocate all reserves to storage (e.g. for $V(y) < {\sim}45$ in Figure 5b). Plants with larger $V(y)$ accumulate enough reserves to reach this target and allocate any excess reserves to reproduction (i.e. $0 < r^* < 1$, Figure 5b). The expected change in storage and reproduction over a polycarpic plant's life therefore depends on seed storage $V(y = 1)$. Plants with little seed storage $V(y = 1)$ may need to accumulate storage for one or more seasons before the target storage is reached. Once the target storage is reached, individuals reinvest the same quantity of reserves into storage each season and use the excess for reproduction, resulting in a stable schedule of reserve production and reproductive output over the remainder of the plant's lifetime. In contrast, plants with large $V(y = 1)$ may generate enough reserves to begin reproducing in the first season. In this case, storage and reproductive output may be relatively constant over a plant's lifetime.

The optimal reproductive allocation of a polycarpic perennial can be understood in terms of the conditions that affect the target overwinter storage. In previous models, the target overwinter storage increases with overwinter survival and the reserves available to a plant at the end of the season (Iwasa & Cohen, 1989).

These factors also affect the target overwinter storage in our model; however, the effect of overwinter survival is qualitatively different. In our model, plants can use overwinter storage to increase overwinter survival. As shown above (see Section 3.1), if maintaining tissues is costly, this effect of storage on overwinter survival can cause plants to forego reproduction entirely when they possess little spring storage (cf. Figure 3a,b). With decreasing minimum probability of surviving the winter ξ_0, polycarpic plants allocate a greater amount of resources to storage because it improves their chances of surviving the winter (Figure 6a). The increase in overwinter storage necessarily decreases the excess reserves that can be used for reproduction; therefore, decreasing ξ_0 leads to a decrease in reproduction (Figure 6d). The prediction that plants should evolve larger allocations to storage and decreased allocations to reproduction in environments characterized by lower overall survival is opposite the predictions of previous theory (Iwasa & Cohen, 1989).

Conditions leading to low $S(y)$ generally decrease the target overwinter storage, as predicted by previous theory (Iwasa & Cohen, 1989). This is because lower $S(y)$ decreases the amount of reserves the plant can accumulate in the next season and, in our model, also limits how much plants can store to improve overwinter survival. In contrast to previous theory, however, the magnitude of the decrease in overwinter storage and its consequences for reproduction depend on whether decreases in $S(y)$ are caused by an increase in the maintenance costs of storage c or a decrease in the minimum probability of surviving the growing season μ_0. Decreases in $S(y)$ due to greater maintenance costs of reserves c are largest for those plants with high spring storage $V(y)$ and thus large m_0 (Figure S4a). Thus, greater maintenance costs limit the increase in future reserve production a plant can achieve by increasing overwinter storage,
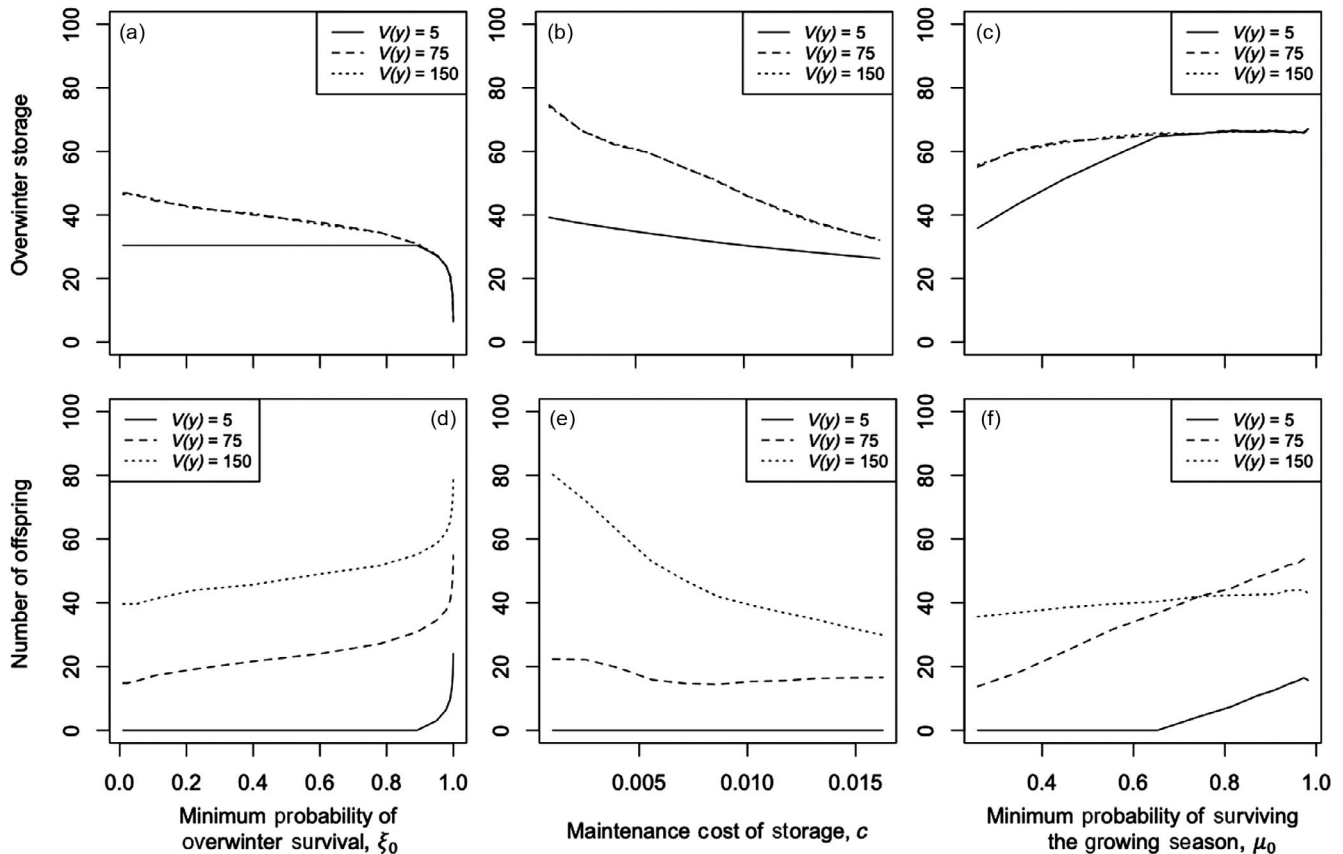
FIGURE 6 Model parameters determining the optimal allocation of resources to overwinter storage (a–c) and reproduction (expressed as the number of offspring, d–f) for polycarpic plants. Shown are the effects of the minimum probability ξ_0 of surviving over winter (a, d), the maintenance cost of storage c (b, e) and the minimum probability μ_0 of surviving the growing season (c, f). Panels in the top row share an x-axis with the corresponding panel in the bottom row. Line types denote different values of spring storage $V(y)$ as indicated in the legend. Note that overwinter storage for individuals with $V(y) = 75$ (dashed lines) overlaps that of individuals with $V(y) = 150$ (dotted lines)

drastically decreasing the target overwinter storage (Figure 6b). For those plants with high $V(y)$, $S(y)$ decreases more quickly with increasing costs of maintaining reserves c than does the target overwinter storage. Higher maintenance costs therefore lead to a decrease in both reproduction (Figure 6e, dotted line) and overwinter storage (Figure 6b, dotted line) for plants with high $V(y)$. For plants with intermediate $V(y)$, $S(y)$ and overwinter storage decrease at approximately the same rate with increasing maintenance costs c, causing reproductive output to be relatively independent of c (Figure 6e, dashed line). Thus, decreases in $S(y)$ decrease the target overwinter storage as in previous models (Iwasa & Cohen, 1989), but, if decreases in $S(y)$ are due to greater maintenance costs, the consequences for reproductive output depend on a plant's spring storage $V(y)$.

Decreases in $S(y)$ due to a lower minimum probability of surviving the growing season μ_0, however, are greatest for plants with small $V(y)$ because they begin the season with smaller m_0 and therefore experience greater mortality risk (Figure S4b). Because $S(y)$ for large plants is relatively unaffected by μ_0, the target overwinter storage changes little with μ_0 (Figure 6c). Thus, reproduction is largely independent of μ_0 for plants with large $V(y)$, but decreases at lower μ_0 for plants with intermediate or low $V(y)$ because there are fewer reserves $S(y)$ (Figure 6f) available to meet the target overwinter

storage. At sufficiently large μ_0 even plants with the smallest $V(y)$ can reach the target overwinter storage and allocate excess reserves to reproduction (Figure 6f, solid line).

3.3 | Prolonged dormancy

Our model predicts that prolonged dormancy is part of an optimal life history strategy if dormant plants accumulate reserves and there is a high probability of surviving the season as a dormant plant ν (Figure 7). We explored the effect of varying the maximum increase in $s(T)$ with $V(y)$ during dormancy, i and the minimum probability of surviving prolonged dormancy ν_0. The value of i required for dormancy to occur is lower at higher ν_0; however, high ν_0 alone does not result in dormancy. If dormancy occurs, then sprouted plants enter dormancy in the following growing season regardless of their spring storage $V(y)$ (Figure 7a). However, dormant plants only remain dormant in the following season if they possess intermediate or low $V(y)$ (Figure 7b). Thus, whether a plant remains dormant for only a single season or multiple consecutive seasons depends on the overwinter storage retained by sprouted plants and the change in storage during prolonged dormancy, as either can
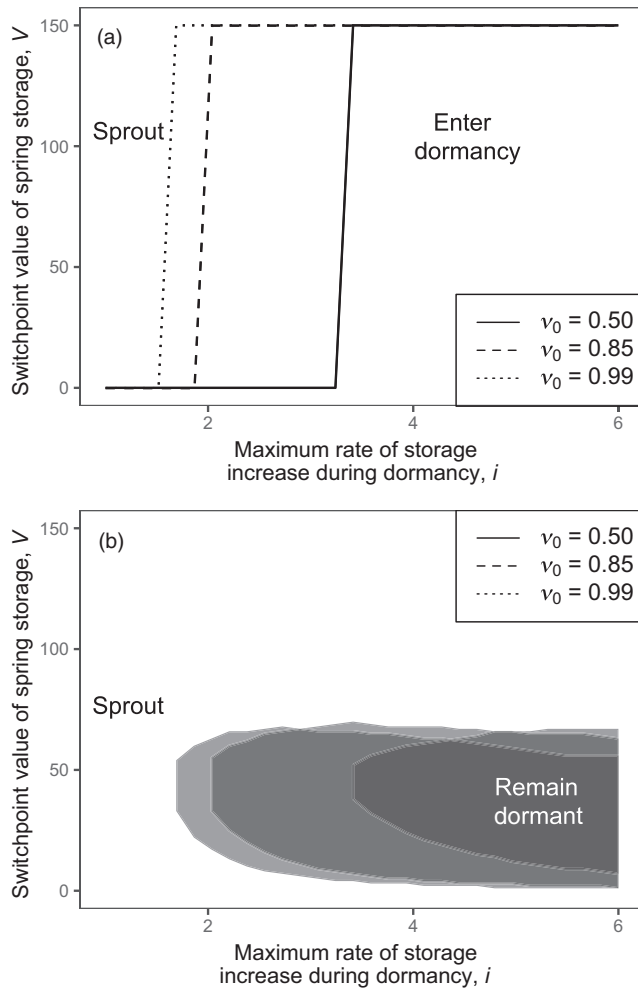
FIGURE 7 The minimum spring storage $V(y)$ for (a) sprouted plants and (b) dormant plants below which prolonged dormancy in the next season becomes optimal (the 'switchpoint value') plotted against the maximum change in storage during prolonged dormancy i for different values of minimum within-season survival probabilities v_0. For those cases in which the switchpoint equals the maximum $V(y)$, prolonged dormancy maximizes fitness for all possible spring storage values. Note that in (b) there are two switchpoints (i.e. boundaries of the shaded regions) for each combination of i and v_0

determine the storage available to the plant at the onset of prolonged dormancy.

4 | DISCUSSION

Previous models of resource allocation by herbaceous plants assume that net photosynthate production increases monotonically with the size of the plant's photosynthetic structures such that greater over-winter storage (and thus larger initial photosynthetic structures) always increases future resource availability (Iwasa & Cohen, 1989; Klinkhamer et al., 1997). Moreover, previous models typically do not consider that the amount of stored resources may affect survival, or that plants may undergo periods of prolonged dormancy. Our model expands on this foundation by exploring the consequences of (a) net

resource production being greatest at intermediate plant size due to differences in the scaling of gross photosynthate production and maintenance costs with size, (b) the effect of plant size on survival during the growing season, (c) the effect of resource allocation decisions on overwinter survival and (d) the benefits of periods of prolonged dormancy in terms of increased survival and storage.

By incorporating theory on the allometric scaling of gross resource production and maintenance costs (Enquist et al., 1998; West et al., 2001), we find that the benefit of storage for future resource production is generally limited by the cost of maintaining existing tissues. Consequently, maintenance costs are critical for determining the conditions under which selection favours a monocarpic or polycarpic life history as well as the optimal allocation of resources to reproduction by polycarpic plants. Moreover, by incorporating these limits to the benefits of storage, we find that our model never predicts significant investment into storage unless plants can increase subsequent survival by allocating a larger proportion of resources to storage. Thus, in contrast to previous theory that does not consider maintenance costs (Iwasa & Cohen, 1989; Klinkhamer et al., 1997), our model suggests that the ability of plants to compensate for low survival by increasing storage is a critically important ecological mechanism for predicting large investments in storage consistent with empirical observations. The effect of storage on overwinter survival can also result in seemingly counterintuitive relationships between overwintering conditions and resource allocation, as plants inhabiting environments with harsher winters (i.e. lower ξ_0) should allocate fewer reserves to current reproduction to increase survival. Finally, we demonstrate that a life history in which plants undergo prolonged dormancy [i.e. spend at least one growing season below ground, foregoing sexual reproduction (Lesica & Steele, 1994)], can evolve in response to resource allocation trade-offs alone if plants can increase storage during dormancy (e.g. through reallocation of structural carbohydrates or uptake from mycorrhizal fungi), particularly if dormancy also increases survival relative to sprouting.

4.1 | Monocarpic life histories

Our model corroborates previous theory predicting that herbaceous plants growing in seasonal environments may evolve a monocarpic perennial life history if offspring production is an accelerating (e.g. exponential) function of the resources allocated to reproduction (Janzen, 1976; Klinkhamer et al., 1997; Schaffer, 1974). Several mechanisms have been proposed for how such relationships arise, including saturation of seed predators and attraction of pollinators, although empirical evidence for such mechanisms in monocarpic perennials remains equivocal (Klinkhamer et al., 1997). Moreover, because the reserves that can be accumulated during a growing season depend on maintenance costs, these costs may be critical in determining the number of growing seasons needed before a monocarpic perennial accumulates enough reserves to reproduce and die.

The predictions of our model are also consistent with previous theory suggesting that an annual life history should evolve if survival

is low, growing seasons are unproductive, or overwinter losses of storage are large (Iwasa & Cohen, 1989). This is largely unsurprising; for a given relationship between storage and subsequent reserve production, a sufficiently large average loss due to mortality or storage efficiency will prevent any possible allocation to storage from producing a return of equivalent (or greater) reserves in the next season (Iwasa & Cohen, 1989). For herbaceous plants, these vital rates likely depend on abiotic environmental factors such as temperature and precipitation (e.g. Tenhumberg, Crone, Ramula, & Tyre, 2018 and citations therein) as well as biotic factors such as competitor density (Tenhumberg et al., 2015). For example, in the common yellow monkeyflower *Mimulus guttata*, annual ecotypes occurs more frequently in environments with less late-summer precipitation (Hall & Willis, 2006) in which individuals experience decreased survival (Hall & Willis, 2006) and are likely to be less productive. Similar differences in water availability, and thus presumably survival and productivity, are associated with variation in the frequency of annual ecotypes in wild rice (Morishima, Sano, & Oka, 1984). In the forb *Streptanthus tortuosus*, variation within and among populations in the frequency of an annual life history correlates with germination date, which in turn influences survival to subsequent growing seasons (Gremer, Wilcox, Chiono, Suglia, & Schmitt, 2019).

While our model aligns with previous theory and empirical data on the general conditions under which an annual life history should evolve, our model provides new perspectives on the mechanisms underlying these predictions. Specifically, our model predicts that if maintaining existing tissues is costly, an annual life history should evolve only if the chances of surviving to future growing seasons are exceptionally low (Figure 3a). This is because the benefit of large quantities of storage in terms of future resource production is limited by the costs of maintaining existing tissues; therefore, plants can virtually maximize future reproductive success by allocating only a tiny fraction of resources to storage. The chances of surviving overwinter must be very low for this strategy to become less profitable than an annual strategy. However, for many plants, storage likely increases overwinter survival, for example by increasing cold hardiness (Boyce & Volenec, 1992). Our model predicts that the effect of storage on overwinter survival can restore strong trade-offs between current and future reproductive success (Figure 3b). As a result, an annual life history may be optimal even when a plant has the capacity to achieve a relatively high probability of surviving the winter because doing so comes at a large cost to current reproduction. Of course, it is possible that in some cases the evolution of annual life histories is associated with extremely low survival or low costs of maintenance (which should result in stronger effects of storage on future resource production). Nevertheless, our model predicts that, all other things equal, taxa in which storage more strongly affects overwinter survival should generally show greater variation in the frequency of annual life histories among environments differing in overall survival or productivity. Testing this prediction will ultimately require the ability to disentangle the relative contributions of the effect of storage on future resource production and on survival to the trade-offs between current and future reproduction (e.g. cf.

Figure 3a,b) in a variety of taxa. Such studies would undoubtedly be challenging, but may ultimately resolve the physiological and ecological mechanisms underlying the evolution of annual life histories predicted by our model.

Our model predicts that the overwinter survival conditions in which an annual strategy is optimal depend strongly on the costs of maintaining existing tissues (Figure 4), as these costs determine the reserves the plant can acquire (Figure S4a). This contrasts previous models in which the reserves accumulated by the end of the season depend only on the spring storage, the size-specific rate of net photosynthate production, and the length of the growing season (Iwasa & Cohen, 1989; Klinkhamer et al., 1997). Factors affecting the costs of maintaining tissues (e.g. temperature, plant architecture) may therefore represent a fundamental, yet underappreciated, source of life history variation within and among plant taxa. In particular, empirical studies exploring the effects of environmental conditions on maintenance costs may be critical for understanding spatial and temporal patterns of life history variation and for predicting consequences of environmental change at the individual and population levels. Future theoretical work would benefit from exploring the extent to which the constraints imposed by maintenance costs depend on other limiting resources that influence the plant's trade-off between survival and reproduction (e.g. water, micronutrients; Cohen, Isaksson, & Salguero-Gómez, 2017).

4.2 | Polycarpic life histories

Under conditions favourable for reserve accumulation, storage efficiency and survival, our model predicts that plants maximize their fitness by expressing a polycarpic strategy (i.e. reproducing in multiple growing seasons). However, our model suggests that the relationship between the optimal allocation of resources to reproduction and the dynamics of survival and reserve production is more complex than previously appreciated. Specifically, our model predicts that overwinter survival and reserve production have contrasting influences on the optimal allocation of reserves to reproduction. Increases in overwinter survival favour greater reproductive allocation and less storage because a smaller amount of stored reserves in a favourable environment (high ξ_0) achieves the same survival probability and, therefore, the same future reproductive success, as a plant growing in less favourable environments (low ξ_0) that allocates more resources to storage. This result is in direct contrast to previous theory on plant life history evolution that predicts that greater overwinter survival should favour decreased investment in current reproduction (Iwasa & Cohen, 1989). Thus, our model predicts that greater overwinter survival favours a polycarpic perennial strategy over an annual strategy (see above), but greater overwinter survival also favours increased allocations to reproduction and less storage over the range of conditions in which a polycarpic life history is optimal. In contrast, our model predicts that increases in reserve production favour the evolution of greater allocation to storage due to greater

future fitness expectations, though the corresponding change in current reproduction depends on the underlying cause of increased reserve production and on the plant's spring storage. This leads to the seemingly counterintuitive prediction that in some cases the optimal allocation of reserves between reproduction and storage for polycarpic plants might be relatively independent of environmental conditions (e.g. temperature, precipitation) if those conditions have similar effects on survival and reserve production. However, there are probably many examples in which environmental conditions have somewhat different effects on survival versus resource production. For example, environments differing in winter precipitation may differ more strongly in overwinter survival than in productivity during the growing season. In these cases, our model would predict the evolution of increased storage in environments where reserve production is increased to a greater extent than survival or survival is decreased to a greater extent than reserve production.

It is difficult to compare these model predictions to empirical patterns because current studies on resource allocation among polycarpic plants occupying different environments typically do not link ecological factors (e.g. temperature, precipitation) or large-scale environmental gradients (e.g. latitudinal gradients) to resource production and survival. For example, in purple loosestrife *Lythrum salicaria*, individuals from higher latitude populations produce larger storage organs (Olsson & Ågren, 2002). This pattern is consistent with our model prediction if individuals can increase overwinter survival by increasing storage, and if high latitude conditions result in a greater decrease in survival than reserve production. In the winter rainfall region of South Africa, plants invest more heavily in overwinter storage organs if they grow in habitats with lower precipitation during the winter (Proche, Cowling, & Du Preez, 2005). Low winter precipitation likely decreases survival (low ξ_0 in our model). If plants can improve survival by allocating resources to storage, larger storage organs in drier habitats would be consistent with our model predictions. Low winter precipitation may also decrease reserve production in the subsequent growing season; nevertheless, the observed patterns are consistent with our model, provided that any decreases in reserve production are not large enough to outweigh the effect of decreasing survival. It is of course possible that these storage organs store mostly water, which our model does not consider explicitly. Additionally, few studies disentangle the relative contribution of absolute resource availability and relative resource allocation. In one such study of the perennial sunflower *Helianthus maximiliani*, higher latitude population produce a greater number of flowers per unit biomass, suggesting reproductive allocation increases with latitude (Kawakami et al., 2011). This pattern is consistent with our model provided that high latitudes are associated with greater decreases in reserve production than survival (e.g. because of lower herbivore pressure). In summary, resolving the potentially differential effects of environmental conditions on survival and reserve production will be essential in assessing the adaptive significance of differences in resource allocation by polycarpic perennials.

4.3 | Prolonged dormancy

Our model demonstrates that resource allocation trade-offs associated with sprouting are sufficient for the evolution of prolonged dormancy, provided that individuals accumulate resources during dormancy. These findings support recent verbal arguments suggesting that resource allocation trade-offs can contribute to the adaptive value of prolonged dormancy in the absence of temporal variation in environmental conditions (Lesica & Crone, 2007; Shefferson et al., 2014, 2018), but also predict that increases in resource availability during dormancy should be a general characteristic of plants in which such trade-offs favour prolonged dormancy. There is growing evidence that herbaceous plants may accumulate resources during prolonged dormancy (Gremer et al., 2010; Shefferson et al., 2018), and thus it is possible that resource allocation trade-offs associated with sprouting may often contribute to the adaptive value of prolonged dormancy. Additional studies providing direct evidence of changes in resource availability during dormancy (e.g. Gremer et al., 2010) will be instrumental in determining whether adaptive responses to trade-offs associated with sprouting per se provide a general explanation for patterns of prolonged dormancy in herbaceous plants or operate only under relatively restrictive taxonomic or ecological contexts.

Our model also predicts that the accumulation of resources by dormant plants should more strongly favour the evolution of prolonged dormancy if plants experience high survival during dormancy. While some observational studies suggest that dormancy may instead decrease survival relative to sprouted plants (Hutchings, 1987; Shefferson, Proper, Beissinger, & Simms, 2003), these patterns may reflect the tendency for plants at a survival disadvantage to enter prolonged dormancy. In at least some cases, the apparent survival costs of prolonging dormancy appear to be due to correlations between traits impacting survival (e.g. size) and the tendency to prolong dormancy rather than a detrimental effect of dormancy on survival per se (Jäkäläniemi et al., 2011; Shefferson, 2006). Other observational and experimental studies have found no effects of prolonged dormancy on survival (Lesica & Crone, 2007; Shefferson, Kull, & Tali, 2005). However, high survival during prolonged dormancy is also a key prediction of the hypothesis that dormancy functions as a bet-hedging strategy to circumvent temporal variation in environmental conditions (Gremer et al., 2012; Gremer & Sala, 2013; Hawryzki et al., 2011; Jäkäläniemi et al., 2011; Shefferson, 2009). Empirical studies that compare the relative survival of sprouted versus dormant plants during periods of favourable and stressful environmental conditions may help to disentangle the relative contributions of trade-offs associated with sprouting per se and bet hedging to patterns of prolonged dormancy. If prolonged dormancy results in high survival relative to sprouted plants only under periods of environmental stress, bet hedging may be a more likely explanation for the prolonged dormancy. Studies explicitly testing the relative importance of trade-offs associated with sprouting and environmental variation in explaining observed demographic patterns (e.g. Shefferson et al., 2014) will also be of critical importance in

determining the relative importance of these non-exclusive benefits of prolonged dormancy in natural populations.

The demographic patterns of dormancy predicted by our model, however, differ from those often described for natural populations, suggesting that our model does not consider all factors influencing dormancy. Our model predicts that for the parameter range where prolonged dormancy is adaptive individuals should always enter prolonged dormancy following a growing season in which they sprouted. Whether a plant remains dormant for more than one growing season depends on the levels of storage when they first entered dormancy. However, in nature, plants do not always enter prolonged dormancy following a growing season in which they sprouted. The probability that sprouted plants enter dormancy in any given year is often affected by short-term environmental stress such as shading, defoliation and weather anomalies (e.g. precipitation, spring temperature; Ehrlén, 2003; Knight, 2003; Lesica & Crone, 2007; Mceachern, Thomson, & Chess, 2009; Reintal, Tali, Haldna, & Kull, 2010; Shefferson et al., 2005; Shefferson, Sandercock, Proper, & Beissinger, 2001). Our model did not consider responses to such stressors but explored how expected average survival and productivity in different environments influence the evolution of prolonged dormancy. Further, we have limited understanding of the underlying dynamics of storage changes during dormancy, and therefore how an individual's spring storage is related to the storage available following prolonged dormancy. Future efforts to explicitly incorporate such stressors into our model and to resolve the dynamics of storage changes during prolonged dormancy will be particularly helpful in understanding the role of resource allocation trade-offs in the evolution of prolonged dormancy.

5 | CONCLUSIONS

In summary, our model demonstrates that relatively simple resource allocation trade-offs are sufficient to explain the evolution of different life history strategies observed in natural populations of herbaceous plants, including strategies that incorporate bouts of prolonged dormancy. We find that differences in how resource production and maintenance costs increase with biomass introduce additional constraints on storage accumulation and reserve production, fundamentally altering the nature of the trade-off between current and future reproduction. Consequently, we find that, in contrast to previous theory, the ability of plants to compensate for low survival conditions by allocating a larger proportion of resources to storage is critically important because without it our model never predicts significant investment into storage. Finally, we demonstrate that resource allocation trade-offs alone may be sufficient to favor the evolution of prolonged dormancy.

AUTHORS' CONTRIBUTIONS

B.T. conceived the study; J.C.W. and B.T. developed the model; J.C.W. took the lead on model programming, model analysis and manuscript preparation; J.C.W. and B.T. participated in manuscript revisions.

ORCID

J. Colton Watts https://orcid.org/0000-0003-1805-2901

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