Herbivore population dynamics in response to plant allocation strategies

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Abstract
When herbivores feed, plants may respond by altering the quantity of edible biomass available to future feeders through mechanisms such as compensatory regrowth of edible structures or allocation of biomass to inedible reserves. Previous work showed that some forms of compensatory regrowth can drive insect outbreaks, but this work assumed regrowth occurred without any energetic cost to the plant. While this is a useful simplifying assumption for gaining preliminary insights, plants face an inherent trade-off between allocating energy to regrowth versus storage. Therefore, we cannot truly understand the role of compensatory regrowth in driving insect outbreaks without continuing on to more realistic scenarios. In this paper, we model the interaction between insect herbivores and plants that have a trade-off between compensatory regrowth and allocation to inedible reserves in response to herbivory. We found that the plant’s allocation strategy, described in our model by parameters representing the strength of the overcompensatory response and the rates at which energy is stored and mobilized for growth, strongly affects whether herbivore outbreaks occur. Additional factors, such as the strength of food limitation and herbivore interference while feeding, influence the frequency of the outbreaks. Overall, we found a possible new role of overcompensation to promote herbivore fluctuations when it co-occurs with allocation to inedible reserves. We highlight the importance of considering trade-offs between tolerance mechanisms that plants use in response to herbivory by showing that new dynamics arise when different plant allocation strategies occur simultaneously.

Keywords
Belowground allocation · Overcompensation · Plant-herbivore interaction · Population dynamics · Tolerance · Trade-off

Introduction
Many herbivorous insect populations show fluctuating dynamics over time (Elton 1924; Kendall et al. 1999; Turchin 2013), and ecologists have long worked to explain these fluctuations from both theoretical (Lundberg et al. 1994; Vos et al. 2004) and empirical (Underwood and Rausher 2000; Liebhold 2019) perspectives. Many mechanisms that can drive insect outbreaks (which, following Stieha et al. (2016), we define as intrinsically generated herbivore population fluctuations as opposed to eruptive outbreaks due to external factors) involve the plants’ own responses to herbivory. In one class of responses, plants alter the quantity of edible biomass available to herbivores, either increasing it through compensatory regrowth of edible tissues lost to herbivory (McNaughton 1983; Orians et al. 2011; Belsky 1986; Agrawal 2000), or decreasing it by allocating energy to the growth of inedible storage organs (Dyer et al. 1991; Briske et al. 1996). Given a finite amount of energy for growth, plants face a trade-off in their capacity to respond to herbivory in either of these ways. How plants allocate energy to different structures is known to influence insect dynamics (Miller et al. 2006), so the trade-off between compensatory regrowth of edible tissues and storage of biomass in inedible ones is likely to be consequential. How, though, remains unknown.

Overcompensation, one form of compensatory plant regrowth in response to herbivory, occurs when herbivore-damaged plants regrow more edible biomass than is needed to replace the losses to sufficiently mild herbivory (McNaughton 1979; Paige and Whitham 1987; Alward and Joern 1993;
We focus particularly on identifying the conditions that lead to dynamics, such as equilibrium population size and outbreak frequency. Overcompensation boosts the boom in the herbivore population, exaggerating the crash and making eventual stabilization to a point equilibrium more difficult to achieve.

For plants with inedible storage organs, such as perennial plants that experience above-ground herbivory during the growing season and have overwintering roots, the ability to reallocate energy to inedible storage in response to herbivory is another critical tolerance mechanism. It allows plant regrowth using stored energy after an acute bout of herbivory has passed (Zhou et al. 2015). Previous work has shown that allocation to inedible storage influences herbivore population dynamics and can lead to sustained oscillations, especially when the late-season allocation to storage tissue is high enough to support a large amount of above-ground biomass next year (Thomas et al. 2017).

Overcompensation and allocation to inedible reserves have been studied separately, where both processes can drive population cycles when acting on their own. However, because of the inevitable energetic trade-off between edible regrowth and inedible reserves in overcompensating plants, it is imperative that we consider both processes together when assessing their impact on herbivore dynamics. Past work on other plant responses to herbivory, such as food limitation, compensatory regrowth, and induced resistance, has revealed counter-intuitive effects: outbreaks can cease when two outbreak-promoting mechanisms are combined, or new outbreaks can arise from the combination of two processes neither of which drives outbreaks in isolation (Abbott et al. 2008; Stieha et al. 2016). The true effects of overcompensation and inedible storage on insect population dynamics can therefore only be understood by studying the two mechanisms, and their intrinsic trade-off, simultaneously.

Here, we present a theoretical model to understand how overcompensation and allocation to inedible reserves interact to affect herbivore population dynamics. We assume that there is a trade-off between overcompensation and the ability to keep energy in inedible storage—that is, when plants use a certain portion of their energy for overcompensatory regrowth, they cannot keep the same energy in reserve for future growth. We use our model to examine properties of the insect population dynamics, such as equilibrium population size and outbreak frequency, as a function of the plant’s growth and allocation traits. We focus particularly on identifying the conditions that lead to sustained insect population fluctuations. Finally, we compare the behavior of our model to previous models of either overcompensation or inedible allocation alone (Stieha et al. 2016; Thomas et al. 2017), to determine which, if any, of our results arise from an interaction between these processes. We found that the equilibrium herbivore density increases when plants have strong overcompensatory regrowth or allocate more energy to inedible storage. Both high-frequency fluctuations characteristic of strong intraspecific density dependence (“single-species cycles” sensu Murdoch et al. (2002)) and lower-frequency fluctuations characteristic of consumer–resource feedbacks can happen when overcompensation and allocation to inedible stores occur simultaneously. In contrast, overcompensation acting on its own results only in single-species fluctuations and inedible allocation alone solely shows consumer–resource fluctuations. Overall, our results show that new dynamics arise when different plant allocation strategies occur simultaneously and suggest a new role of overcompensation to promote herbivore fluctuations when it co-occurs with allocation to inedible reserves. This knowledge is relevant to applications such as increasing crop yield in agriculture, pest control, and forest management.

Methods

For ease of presentation, we describe a folivorous insect herbivore population, and we refer to the plant’s pool of edible plant biomass as “aboveground” and its inedible stores as “belowground”, although the same model could be applied to any overcompensating perennial plant with separate pools of biomass accessible and inaccessible to a population of herbivores. We assume insects are univoltine and plants, though perennial with potentially long-lived belowground tissues, regrow aboveground structures each growing season. These assumptions match those used in one or more of the models presented in Abbott et al. (2008), Stieha et al. (2016), and Thomas et al. (2017), allowing us to combine well-understood elements of these past models to arrive at our new model.

We use \( H_t \) to represent herbivore population density in year \( t \) and divide the perennial plant population’s biomass into an aboveground pool \( (A_t) \) and a belowground pool \( (B_t) \). We model dynamics in discrete, annual time steps that are subdivided into sequential phases of growth, herbivory, etc. (see Fig. 1 for a schematic). Variables and parameters are listed in Table 1. Except where noted, our model follows Thomas et al. (2017), and additional justification for the functional forms used can be found therein.

Early in the growing season, while herbivores are still overwintering, plants begin aboveground growth. We assume that early spring allocation of energy from belowground to aboveground follows a saturating function, \( \frac{y_{B_{t-1}}}{1 + a_{B_{t-1}}} \).
Although we refer to $y$ in Sect. 2, is $y \leq yB$ because more herbivores per unit edible biomass interfere with each other’s ability to find edible biomass. When the value of $p_1$ is low, it indicates that interference between feeding adult herbivores is weak so that the damage caused by adult herbivores per unit biomass escalates quickly. After herbivory by adults, the remaining aboveground biomass, $A_i''$, is

$$A_i'' = A_i' (1 - d_i A_i').$$

(4)

Only a proportion, $h_1$ (Fig. 2c), of the adult herbivores survive the feeding period, so the herbivore population density updates to

$$H_i' = h_1 H_{i-1},$$

(5)

with a saturating survivorship

$$h_1 = \frac{A_i'}{k_1 + \frac{A_i'}{n_{i-1}}} = \frac{A_i'}{k_1 H_{i-1} + A_i'},$$

(6)

where $k_1$ determines the strength of food limitation in the adult herbivore population. Higher $k_1$ indicates stronger food limitation and thus lower adult herbivore survival at a given level of edible biomass per herbivore (Abbott et al. 2008).

Next, adult herbivores lay eggs and then die. In the meantime, plants respond to herbivory by allocating more energy from belowground stores to aboveground biomass for compensatory regrowth. After this allocation, the aboveground biomass becomes

$$A_i''' = A_i'' + \min \left\{ \frac{(1 - zd_i) A_i'}{B_i'}, \frac{(1 - zd_i) A_i'}{A_i'' + B_i'} \right\}.$$

(7)

That is, plants regrow a fraction $1 - z$ of the biomass lost to herbivores ($d_i A_i'$) up to a maximum of $B_i'$ units of regrowth since only $B_i'$ remains in the belowground stores. As the final equality in Eq. (7) shows, as long as sufficient belowground stores remain, the quantity $1 - zd_i$ (Fig. 2d) can be thought of as the fraction of pre-herbivory aboveground biomass ($A_i'$) that is present after adult herbivory and compensatory regrowth ($A_i'''$). Although we refer to $1 - z$ and $1 - zd_i$ as fractions, note

![Fig. 1](image-url)
that they need not to be proper fractions; $z$ will be negative, and $1 - z$ and $1 - zd_l$ will be larger than 1, when regrowth is overcompensatory (as in Stieha et al. (2016)). The addition of an overcompensatory response between two feeding insect life stages in our model is distinct from Thomas et al. (2017), who deliberately chose a partial regrowth function with parameter settings that disallowed overcompensation.

Following Stieha et al. (2016), $z$ has the form,

$$z = 1 - \frac{1 + \frac{vH_{t-1}}{A_t'}}{1 + (\frac{vH_{t-1}}{A_t'})^2}. \quad (8)$$

We use $v$ to control the relationship between the herbivore density per unit edible plant biomass ($H_{t-1}/A_t'$) and the plant compensatory response. Small values of $v$ mean that overcompensation is strong, with a high maximum $1 - zd_l$ and overcompensatory regrowth ($1 - zd_l > 1$) occurring for a broader range of herbivore per unit edible biomass (Fig. 2d). Larger values of $v$ indicate weaker overcompensation, and with infinitely large $v$, plants have no regrowth in response to herbivory.

After allocating energy for aboveground compensatory regrowth in response to adult herbivory, belowground biomass becomes,
Next, herbivore eggs hatch into larvae. If $r_p$ is the net reproductive rate, herbivore population density at the larval stage is,

$$H''_t = r_p H'_t. \tag{10}$$

Larval herbivores then begin feeding, and a proportion of aboveground biomass $d_2$ is removed. The remaining biomass grows by a factor of $r$ from photosynthetic energy until the end of the growing season. The aboveground biomass at the end of the growing season is thus,

$$A_t = (1 - d_2) r A''_t, \tag{11}$$

with

$$d_2 = \frac{H''_t}{P_2 + H''_t} = \frac{H''_t}{p_2 A''_t + H''_t}. \tag{12}$$

Similar to Eq. (3), $p_2$ indicates how strongly larval herbivores interfere with each other when feeding.

Prior to the onset of winter, energy is allocated to belowground storage before aboveground biomass dies back. Belowground biomass after end-of-year allocation is

$$B_t = B''_t + \frac{q A_t}{1 + m B''_t}. \tag{13}$$

$q$ is the maximum fraction of energy allocated from aboveground to belowground for storage and $m$ indicates the density dependence of allocation (Fig. 2e). When $m$ is large, the allocation rate drops quickly due to strong belowground density dependence as there is limited space in belowground environment. Note that we slightly depart from the assumptions in Thomas et al. (2017) here. While they modeled density dependent belowground allocation using a discrete logistic function, we instead use Beverton–Holt density dependence in Eq. (13) to eliminate the possibility of negative values of $B_t$.

After larval feeding, herbivores overwinter in the pupal stage with population density

$$H_t = h_2 H''_t, \tag{14}$$

with survival fraction, $h_2$, written as

$$h_2 = \frac{A''_t}{A''_t + h_1} = \frac{A''_t}{k_2 H''_t + A''_t}, \tag{15}$$

where $k_2$ determines the strength of food limitation in the larval herbivore population.

### Analysis

All the analyses were done in MATLAB R2019a. Model realizations were run for 10,000 annual time steps with the parameter values and initial conditions given in Table 1. The parameter ranges were chosen both for comparability to previous models (Stieha et al. 2016; Thomas et al. 2017) and to highlight noteworthy behaviors in our model.

To quantify long-term equilibrium dynamics, we calculated the mean and coefficient of variation (CV) of the population densities over the last 200 annual time steps. Our use of continuous-valued variables allows the possibility that populations drop to unrealistically low levels, and potentially recover, without technically becoming extinct. To prevent this, we assumed that plant populations with mean belowground biomass $B_t < 10^{-6}$, or herbivore populations with mean density $H_t < 10^{-6}$, were extinct. We used the CV of belowground biomass as an automated method for identifying whether populations are fluctuating at equilibrium (following Thomas et al. (2017)). After preliminary trials, we chose CV = 0.02 as the cutoff between a stable equilibrium and persistent fluctuations, although a slightly larger or smaller cutoff did not change our conclusions (F. Ji, unpublished results). Visual inspection of simulated time series confirmed that when CV < 0.02, both plant and herbivore populations reach a stable equilibrium point, and when CV > 0.02, the asymptotic dynamics were cyclic or chaotic. To understand the influence of different parameters on the resulting population dynamics, we map these qualitative outcomes (stable nonzero equilibrium, fluctuations, or extinction) across two-dimensional “parameter space”: combinations of two varying parameters, with all other parameter values held fixed.

Murdoch et al. (2002) describe the distinction between shorter-period cycles due to intraspecific density dependence (what they called “single-species cycles”) and longer-period cycles due to the interaction between tightly coupled consumers and resources. We found local maxima in the simulated herbivore time series and measured the period of fluctuations as the modal interval between maxima during the last 200 annual time steps. We categorized the population as exhibiting the typically jagged 2$n$-point cycles stemming from discrete-time intraspecific density dependence if the mode was equal to 2 years, and as the more gradual periodic or quasi-periodic consumer–resource fluctuations if the mode was larger than 2 years.

Because we are ultimately interested in understanding how two plant defensive strategies—overcompensation and allocation to inedible structures—interact, our final step was to compare our model to models representing just one of these strategies (Stieha et al. 2016; Thomas et al. 2017). To understand the interaction, we need to pinpoint
which features of our model gave rise to which new behaviors not seen in either of the previous models. To do this, we made a series of modified models that turned off overcompensation, juvenile herbivory (when herbivores respond to overcompensation), and/or allocation between above- and belowground biomass pools. We considered both Beverton–Holt (as in our Eq. (13)) and discrete logistic (as in Thomas et al. (2017)) density dependence during fall biomass allocation. With the right set of modifications (Supporting Information), we were able to convert our model to (a) one with overcompensation only, without a cost to belowground biomass stores, equivalent to Stieha et al.’s (2016) overcompensation model (their Eq. 8); and (b) one with belowground allocation but no overcompensation, equivalent to Thomas et al.’s (2017) model. By adding or removing one modification at a time, we can identify which of our results are due to the interaction between overcompensation and belowground storage, and which arise from just one mechanism or the other.

### Interpretation

We use our model to explore how plant’s allocation strategies influence the shape of population cycles, highlighting the distinction between single-species and consumer resource cycles. Single-species cycles result from delayed intraspecific density dependence—a high enough reproductive rate allows the population to boom, resulting in a decrease in the total number of offspring in the next time step. The characteristic 2-, 4-, ..., or $2^n$-point cycles are recognized by a local population peak in alternate years (Stevens 2009). When we see biannual herbivore outbreaks, we therefore infer that intraspecific density dependence (either in the herbivore population itself, or in the plant population to which the herbivore is responding) is the primary driver of outbreaks. On the other hand, when we have a buildup of plant biomass over several years, tracked by an herbivore buildup and eventual crash, we take this as evidence that the consumer–resource interaction is primarily responsible for herbivore outbreaks.

| Notation | Description | Value or range |
|----------|-------------|----------------|
| Initial conditions: | | |
| $H_0$ | Initial herbivore population density | 20 |
| $A_0$ | Initial amount of $AG$ biomass | 0 |
| $B_0$ | Initial amount of $BG$ biomass | 100 |
| Variables: | | |
| $A'_s$ | $AG$ biomass after spring growth | |
| $A''_s$ | $AG$ biomass after adult herbivore feeding | |
| $A'''_s$ | $AG$ biomass after compensatory regrowth | |
| $A_j$ | $AG$ biomass after juvenile herbivore feeding and photosynthetic growth | |
| $B'_s$ | $BG$ biomass after allocating resources to initiate spring growth | |
| $B''_s$ | $BG$ biomass after allocating energy for $AG$ compensatory regrowth | |
| $B_j$ | $BG$ biomass after end-of-year allocation | |
| $H'_h$ | Adult herbivore density after feeding on aboveground biomass | |
| $H''_h$ | Juvenile herbivore density after hatching | |
| $H_i$ | Density of herbivores in the pupal stage prior to the onset of winter | |
| Parameters: | | |
| $r$ | $AG$ photosynthetic growth factor | 1-7 |
| $y$ | Maximum fraction of energy allocated from $BG$ to $AG$ in spring | 0.1-1 |
| $b$ | Density-dependence in spring biomass allocation | 0.01-1 |
| $v$ | Strength of plant compensatory regrowth (lower is stronger) | 0.1-10 |
| $q$ | Maximum fraction of energy allocated from $AG$ to $BG$ in fall | 0.1-1 |
| $m$ | Density-dependence in fall energy allocation | 0.01-1 |
| $p_1$ | Degree of adult herbivore interference during feeding | 0.5-10 |
| $p_2$ | Degree of juvenile herbivore interference during feeding | 0.5-10 |
| $k_1$ | Strength of adult herbivore’s food limitation | 0.5-5 |
| $k_2$ | Strength of juvenile herbivore’s food limitation | 0.5-5 |
| $r_p$ | Herbivore net reproduction ratio | 1-4 |
In interpreting the effects of the parameter $v$, which governs the relationship between herbivore population density and plant compensatory regrowth, care is required. Smaller values of $v$ indicate an ability to overcompensate for greater degrees of herbivory (Fig. 2d). Note, however, that our model always assumes a finite ability to overcompensate: beyond some ratio of herbivores to plant biomass (i.e., where the curves cross the dashed horizontal 1 line in Fig. 2d), plants cannot fully make up for biomass lost to herbivory. Plants that are capable of overcompensation up to a higher threshold ratio, and those that can achieve higher levels of partial compensation when this ratio is exceeded, will be characterized by a lower $v$ value. However, even a plant that is capable of strong overcompensation (small $v$) may or may not actually exhibit overcompensation at equilibrium, depending on the equilibrium $H$ to $A$ ratio (in prep.). In the following discussion of our results, we therefore use $v$ as a measure of the plant’s overcompensatory response, but we also specify whether or not overcompensation actually occurs ($A'''' > A'$) at equilibrium. For example, for the parameter set used to create Fig. 3a, overcompensation occurs at equilibrium only within the hatched region.

**Results**

The plant’s overcompensation and belowground allocation strategies will determine the equilibrium aboveground biomass after initial spring growth ($A'$) and after compensatory regrowth ($A''''$), as well as the belowground biomass after overcompensation ($B'''$) and after end-of-year belowground allocation ($B$). These changes in plant biomass in turn affect equilibrium herbivore population density ($H$; Fig. 3). Equilibrium aboveground biomass after early-season growth and herbivory, $A'$, is only very weakly influenced by the plant’s overcompensatory response (Fig. 3a) and is much more strongly determined by the plant’s allocation strategy to belowground storage (Fig. 3b). Intuitively, we see a much stronger effect of overcompensation on later parts of the plant’s seasonal progression. Post-compensation aboveground biomass, $A''''$, is highest at equilibrium when overcompensation is quite strong (though not so strong as to diminish end-of-year stored biomass; Fig. 3a). As a consequence of these effects on plant biomass, equilibrium herbivore density is also maximized when the plant has a strong (small $v$) overcompensatory response and allocates heavily ($q = 1$) to belowground stores at the end of each growing season.

Various other parameters also affect how plants respond to herbivory, and the herbivore dynamics that result. For example, Fig. 4 shows that plant dynamics transition from extinction to fluctuations to stable equilibrium as we increase the strength of food limitation experienced by juvenile herbivores, $k_2$. Plant dynamics in turn influence the behavior of herbivore populations, which can show (1) consumer–resource cycles, (2) consumer–resource chaos, (3) single-species chaos, (4) period 3 cycles (a periodic window within the chaotic regime), (5) single-species (period 2) cycles, and stable equilibrium. Generally, population fluctuations tend to be of the consumer–resource type with weaker food limitation and of the single-species type with stronger food limitation (this can also be seen in Figs. 5b, c and 6c). Competition for food is the direct mechanism of
density dependent regulation in the herbivore population, so this result makes intuitive sense. It is also possible for plants to persist while herbivores go extinct, though we only saw this for unrealistically strong food limitation (many orders of magnitude higher than what is shown in Fig. 4).

In sum, our model shows how the balance of overcompensation ability and belowground allocation in the plant population drives herbivore population dynamics. Intermediate levels of food limitation promote fluctuations ranging from classic consumer–resource cycles to intraspecific overcompensatory cycles, and both strong overcompensatory ability and large end-of-season allocation to storage lead to higher herbivore densities at equilibrium. These are important insights, but our complete model does not allow us to understand which features stem from the plant’s overcompensatory response, versus its allocation strategy, versus the interaction between these two processes. We therefore conclude our analysis by comparing our model to earlier models with overcompensation only (no belowground storage; Stieha et al. 2016) and belowground allocation only (no overcompensation; Thomas et al. 2017). We focus in particular on the conditions that lead to herbivore cycles in each of these models, and the nature of those cycles.

The overcompensation-only model solely exhibits single-species fluctuations (Stieha et al. 2016 and Fig. 5a) because there is no long-term cost to the plant of compensatory regrowth (that model was built to represent crop plants whose density is reset each year via planting). With the addition of the

Fig. 4 Bifurcation diagram of belowground plant biomass during the last 200 annual time steps over a range of food limitation ($k_2$). Time-series plots show different types of herbivore population dynamics (the last 25-100 time steps) at varying $k_2$: consumer–resource cycles at $k_2 = 1.19$, consumer–resource chaos at $k_2 = 1.2$, single-species chaos at $k_2 = 3.2$, period 3 cycles (a periodic window within the chaotic regime) at $k_2 = 3.7$, and single-species (period 2) cycles at $k_2 = 5.5$. Other parameters for the bifurcation diagram are: $r = 8$, $y = 0.9$, $b = 0.01$, $v = 1.2$, $q = 0.6$, $m = 0.01$, $p_1 = 0.05$, $p_2 = 10$, $r_p = 50$, $k_1 = 0.5$
trade-off between regrowth and overwinter biomass storage, both single-species and consumer–resource fluctuations are possible in our model. Our model also shows that herbivore cycles can occur when the plant exhibits actual overcompensation at equilibrium, as opposed to just having the ability to overcompensate at lower-than-equilibrium levels of herbivory. This again is in contrast to the overcompensation-only model (Fig. 5), in which herbivory is too strong in the cyclic regime for overcompensation to occur at equilibrium. In other words, in the overcompensation-only model, overcompensation does not lead to outbreaks per se (Abbott and Ji, in prep.). In our model, single-species fluctuations may be triggered by overcompensation, whereas longer period consumer–resource fluctuations mostly occur outside the overcompensation region (Fig. 5). By imposing a trade-off with belowground allocation, our model reveals a potentially new role of overcompensation per se (not just ability to overcompensate) to promote herbivore fluctuations.

To convert our model to a belowground allocation-only model comparable to Thomas et al. (2017), we remove overcompensation and the second round of herbivory within a season from our model (Supporting Information). Our resulting belowground allocation-only model can exhibit consumer–resource fluctuations but not single-species fluctuations (Fig. 6a). Thomas et al. (2017) reported single-species cycles in their belowground-allocation-only model, but these appear to be simply to their
use of discrete logistic density dependence in the plant population, as opposed to the Beverton–Holt form we used here.)
We also only see consumer–resource fluctuations in our model when overcompensation ability is weak (Fig. 6b). In this case, overcompensation only occurs at equilibrium when belowground allocation is just barely strong enough to support extant plant and herbivore populations (i.e., along the border of the fluctuation region and the extinction region; Fig. 6b). When the overcompensation is strong, weaker food limitation leads to consumer–resource fluctuations and stronger food limitation leads to single-species fluctuations; overall, overcompensation occurs throughout the fluctuation region (Fig. 6c). Again, this suggests a possible role of overcompensation in promoting some of the cycles we observe in our model.

To summarize the joint effects of overcompensation and belowground allocation on population dynamics when these two processes occur simultaneously, we plot dynamical outcomes across the \(\nu - q\) parameter space (Fig. 7). Strong overcompensation (small \(\nu\)) combined with low to medium levels of belowground allocation (low to moderate \(q\)) leads to population fluctuations. A higher belowground allocation rate or weaker overcompensatory ability stabilizes the system. When overcompensatory ability is strong enough, population fluctuations may be driven by overcompensation per se (Fig. 7, hatched region).

**Fig. 7** Regions of \(\nu - q\) parameter space where herbivores and plants maintain a stable equilibrium (white), undergo single-species fluctuations (orange), undergo consumer–resource fluctuations (blue), or go extinct (grey) in our model. Parameter \(\nu\) governs the relationship between herbivore population density and plant compensatory regrowth. Smaller \(\nu\) indicates that plants are capable of overcompensating for greater degrees of herbivory. The black hatched area indicates where overcompensation occurs at equilibrium. The other parameters are: \(r = 6, y = 0.7, b = 0.05, m = 0.5, p_1 = 0.5, p_2 = 1.5, r_p = 2.5, k_1 = k_2 = 1.5\).

**Discussion**

In this paper, we considered the trade-off between overcompensatory regrowth and allocation of energy to inedible reserves and its influence on herbivore population dynamics. Using our model, we examined how different plant allocation strategies influence the properties of insect population dynamics. The equilibrium herbivore density increases when the overcompensatory response is strong (small \(\nu\)) and when the belowground allocation rate is high (large \(q\)). The plant’s response to herbivory and the resulting herbivore population dynamics are affected by parameters such as strength of food limitation \((k_2, k_3)\) and degree of herbivore interference \((p_1, p_2)\). If herbivores are less food limited (small \(k_i\) and/or \(k_j\)) or if they interfere less with each other during feeding (small \(p_i\) and/or \(p_j\)), they are able to consume more edible plant biomass when the biomass is scarce, driving the edible biomass to even lower levels and promoting consumer–resource fluctuations. These findings are consistent with the results of the classic Rosenzweig–MacArthur model, where a low half-saturation constant in predation destabilizes the system and leads to cycles (Rosenzweig 1971).

By comparing our model to the overcompensation-only model, we have shown that consumer–resource oscillations are only possible when we additionally consider a long-term cost to plant’s compensatory regrowth. In Stieha et al.’s (2016) overcompensation-only model, because the plant biomass is reset to its carrying capacity at the beginning of every year, herbivores can never overexploit the edible biomass in a way that carries over to the next time step. Adding long-term cost to the plant’s compensatory regrowth enables a feedback between herbivore feeding and future years’ edible biomass, therefore making consumer–resource cycles possible.

The comparison between our model and the belowground allocation-only model (with Beverton–Holt density dependence in belowground stores) shows that single-species fluctuations are only possible when we additionally incorporate strong enough overcompensation. Overcompensating plants regrow more aboveground biomass in response to moderate herbivore damage, resulting in a decrease in the energy reserved for future growth, therefore the total amount of aboveground biomass decreases in the next time step. This delayed density dependence in resource allocation is the primary driver of cycles. As a consequence, when there is a trade-off between overcompensation and long-term storage, we are more likely to see single-species cycles when overcompensation is strong.

Our model provides a deeper understanding of the role of overcompensatory regrowth in regulating herbivore population dynamics. Plants only exhibit overcompensation at equilibrium in response to sufficiently mild herbivory. In the
overcompensation-only model, herbivory is too strong in the cyclic regime for overcompensation to occur at equilibrium and therefore, herbivore fluctuations are not driven by this mechanism per se. In contrast, our model shows that when there is a cost to overcompensatory regrowth, plants exhibit actual overcompensation at equilibrium in most of the single-species cyclic regime and some of the consumer–resource cyclic regime, suggesting that overcompensation itself may directly contribute to the cyclic dynamics.

In this paper, we focused on plants with a pool of edible aboveground biomass and inedible belowground storage, as this situation describes some overcompensating perennial plants. For example, leaf beetle (Galericella calmarensis) herbivory changes the branching patterns and increases the number of shoots in purple loosestrife (Lythrum salicaria; Schat and Blossey 2005). Broad-leaved paperbark trees (Melaleuca quinquenervia), when attacked by the melaleuca leaf weevil (Oxyops vitiosa), produce greater number of terminal branches and vegetative buds than undamaged trees (Pratt et al. 2005). Rosinweed (Silphium integrifolium, Asteraceae), when attacked by gall-insect Antistropheus silphii (Hymenoptera: Cynipidae), produces larger axillary leaf area than was lost to gall formation (Fay et al. 1996). Moving beyond such examples of aboveground herbivory and belowground storage, though, our model can actually be applied to any overcompensating perennial plant with separate pools of biomass accessible and inaccessible to a population of herbivores. For example, turfgrasses (Poaceae spp.) increase their aboveground biomass in response to root damage by Japanese beetle grubs (Popillia japonica; Crutchfield and Potter 1995). Moreover, while we only consider herbivory damage and compensatory regrowth in the plant’s vegetative organs in our model, oftentimes plants experience damage or regrowth in reproductive organs. For example, cotton plants (Gossypium spp.) increase leaf and root mass in response to early-season flowerbud loss, then they can use the stored energy in roots as well as the energy from photosynthesis to support fruit growth later in the growing season (Sadas 1996). For cases such as this, our model could be extended to incorporate reproductive damage or regrowth.

Besides the compensatory regrowth discussed in our study, herbivory may also lead to changes in the quality of edible plant biomass (Kessler and Baldwin 2002; DuToit et al. 1990), which in turn can affect herbivore population cycles (Abbott et al. 2008; Anderson et al. 2009). The effect of plant quality reduction via inducible defenses could readily be added to our model following the same approach as Stieha et al. (2016). This approach treats overcompensation and quality reduction as two simultaneous but separate responses to herbivory. If these responses are not separate—for example, if the biomass that is regrown during overcompensation is of lower quality than what it replaced—then a more nuanced model would be needed. This is an intriguing possibility, but it is unclear whether it would be warranted (for instance, there is no clear evidence for it in the recent meta-analysis on overcompensation by Garcia and Eubanks (2019)). On the other hand, the grazing optimization hypothesis states that a low to moderate rate of herbivory could increase plant primary productivity through nutrient cycling (De Mazancourt et al. 1998), suggesting it could be possible for the nutrient level in plant biomass after overcompensation to be affected. The potential interaction between compensatory regrowth and edible biomass quality therefore appears to be an open area for further research.

In our study, we exclusively focus on the intrinsically generated herbivore population fluctuations. However, many other factors, such as external environmental conditions as well as natural enemies, can also influence herbivore outbreaks (Berrigan 1987). Under different environment conditions, varying availability of resources such as water, nutrients, and light can greatly affect the net outcome of compensatory regrowth (Fay et al. 1996; Nabeshima et al. 2001). This in turn will influence the intensity of food limitation experienced by herbivores, as well as the resulting population dynamics of both species. Likewise, vertebrate herbivores, plant pathogens, and natural enemies of the insect herbivores are all expected to influence insect population dynamics in a nonlinear manner. Therefore, future work is needed to fully understand our findings in the context of these broader mechanisms.

Overall, our analysis reveals factors that determine the equilibrium population density of herbivores or plants, that promote population fluctuations, and that affect outbreak frequency. This knowledge is relevant to applications such as increasing crop yield in agriculture, pest control, and forest management. By showing that new dynamics arise when different plant allocation strategies occur simultaneously, we highlight the importance of considering trade-offs between different plant tolerance mechanisms in response to herbivory when studying plant-herbivore interactions.

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Author contributions Karen Abbott, Christopher Stieha, and Fang Ji conceived the ideas and designed methodology; Fang Ji and Christopher Stieha constructed the model; Fang Ji analyzed the model; Fang Ji and Karen Abbott led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability There were no data collected for this study.

Code availability Code is available at https://github.com/fang-ji/modeling_projects/tree/main/insect_outbreaks.

Declarations

Conflicts of interest/Competing interests The authors have no relevant financial or non-financial interests to disclose.

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