Optimal defense traits in plants living in environments with different productivities: extending Coley, Bryant and Chapin's model

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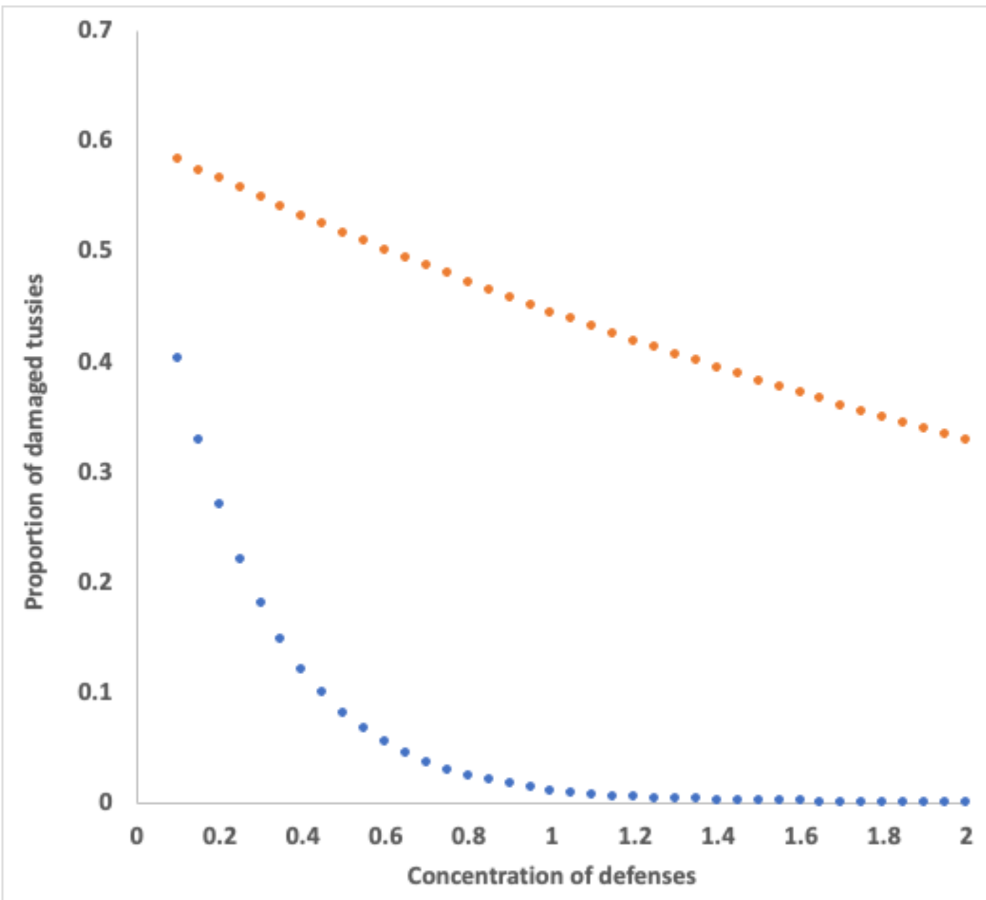
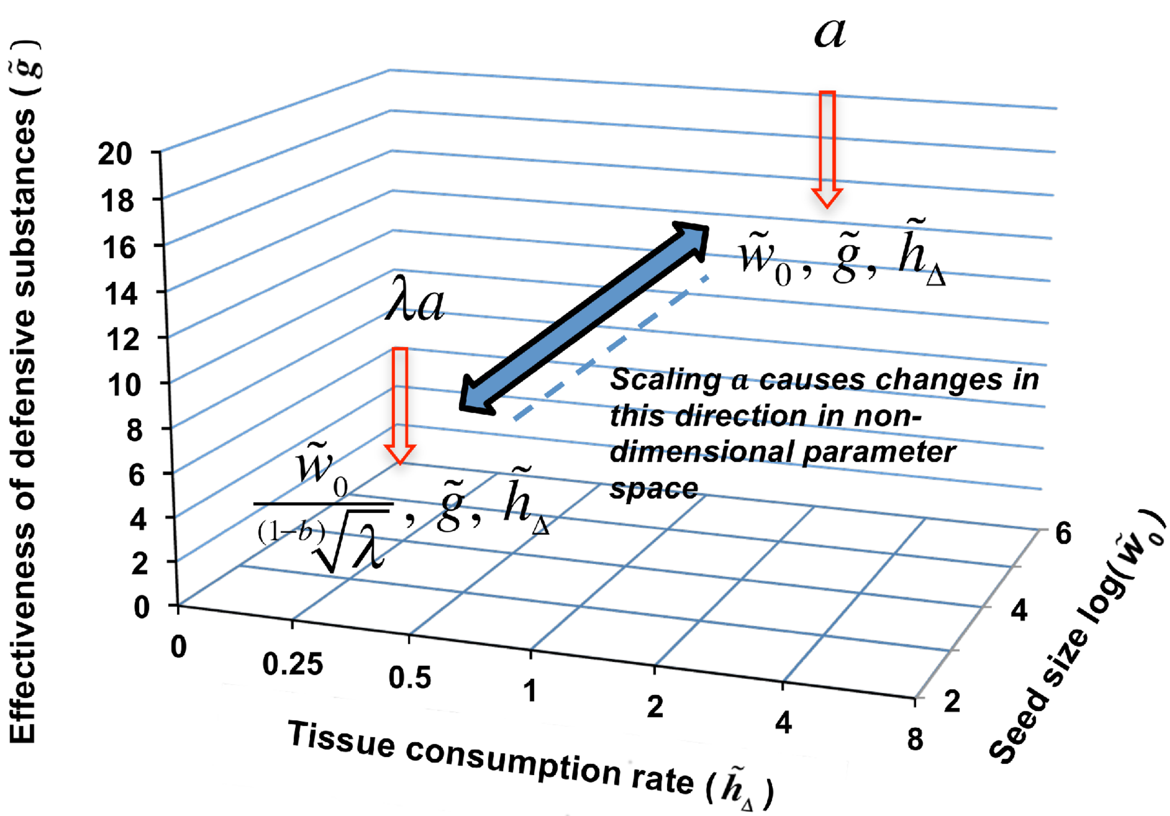
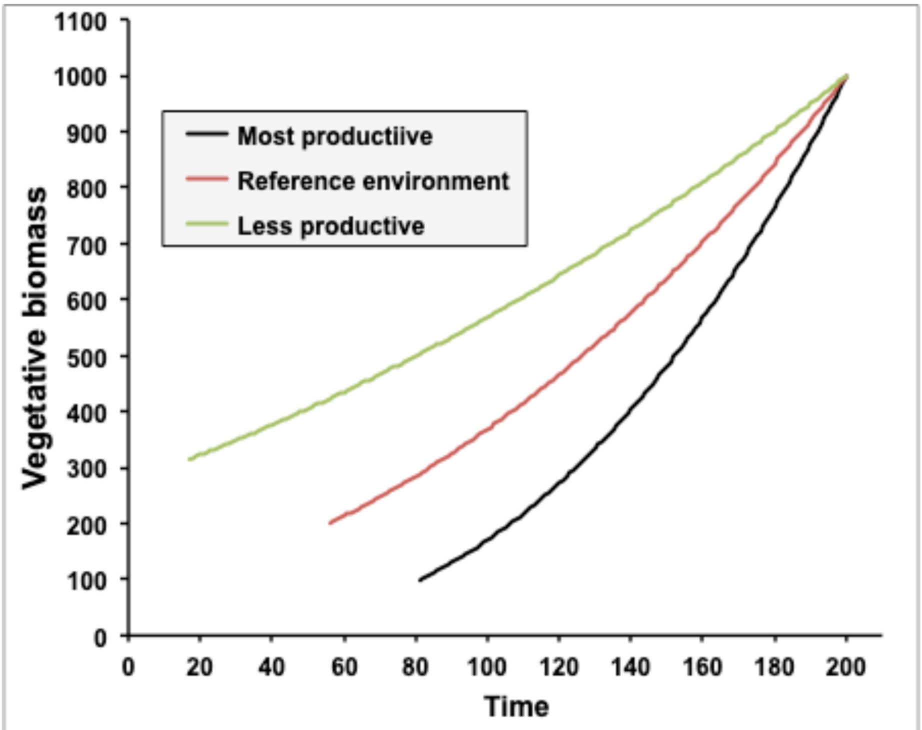
S1 Methods. Illustration of the defense equation $h(C) = h_{\Delta} e^{-gC}$, describing the rate of decrease of the maximum herbivory rate in relation to defense concentration (C). Blue dots correspond to a high value of g ($g = 4$) (efficiency of defensive substances to repel herbivores) and orange dots, to a small value of g ($g = 0.3$). In the latter case, a small value of g makes the relationship nearly linear; h_{Δ} is the maximum proportion of vegetative tissue removed when defense is absent. When $g \sim 0$ and positive, the decrease is nearly linear.



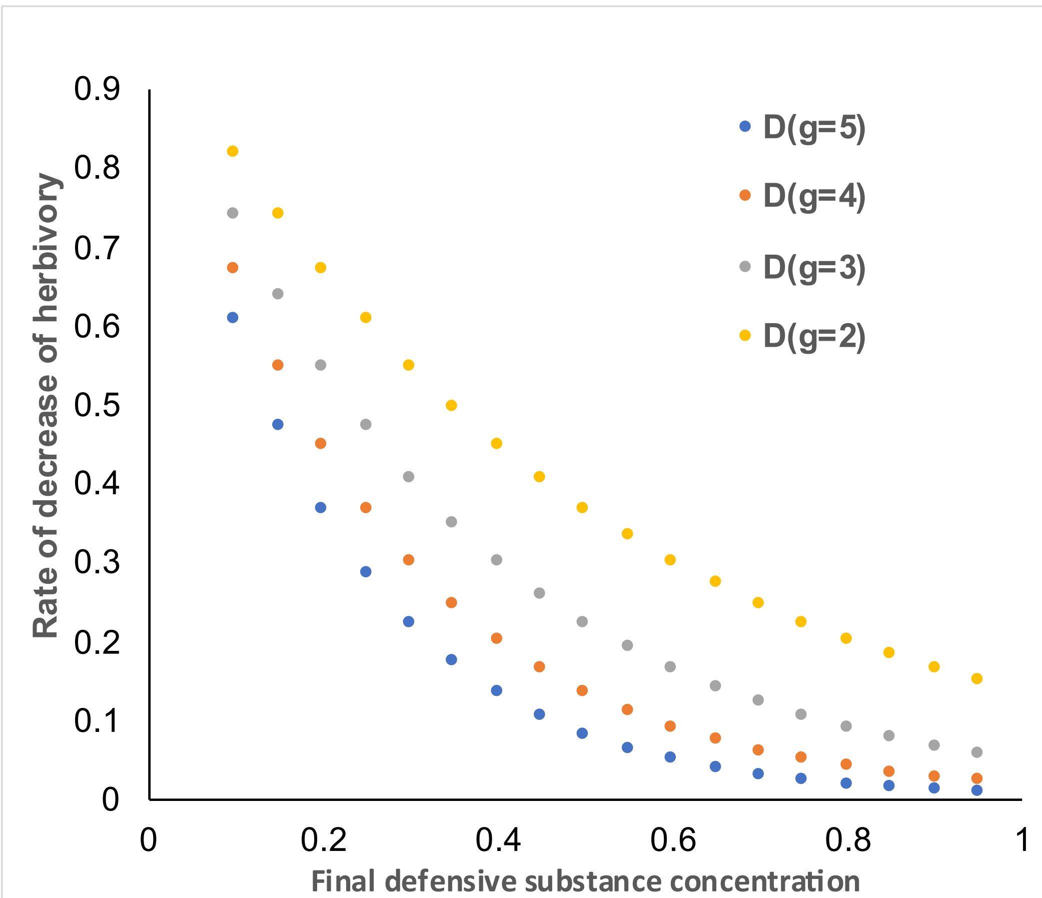
S1 Figure. The effect of the environmental productivity on fitness: scaling of the parameters. To study how the differences of the parameter *a* (environmental productivity) affect *ceteris paribus* the lifespan optimal strategy, we compare different strategies laying on the curve $\tilde{w}_0, \tilde{g}, \tilde{h}_\Delta$ parameterized by λ. Changing *a* affects $\tilde{w}_0$ but does not affect $\tilde{h}_\Delta$ and $\tilde{g}$.



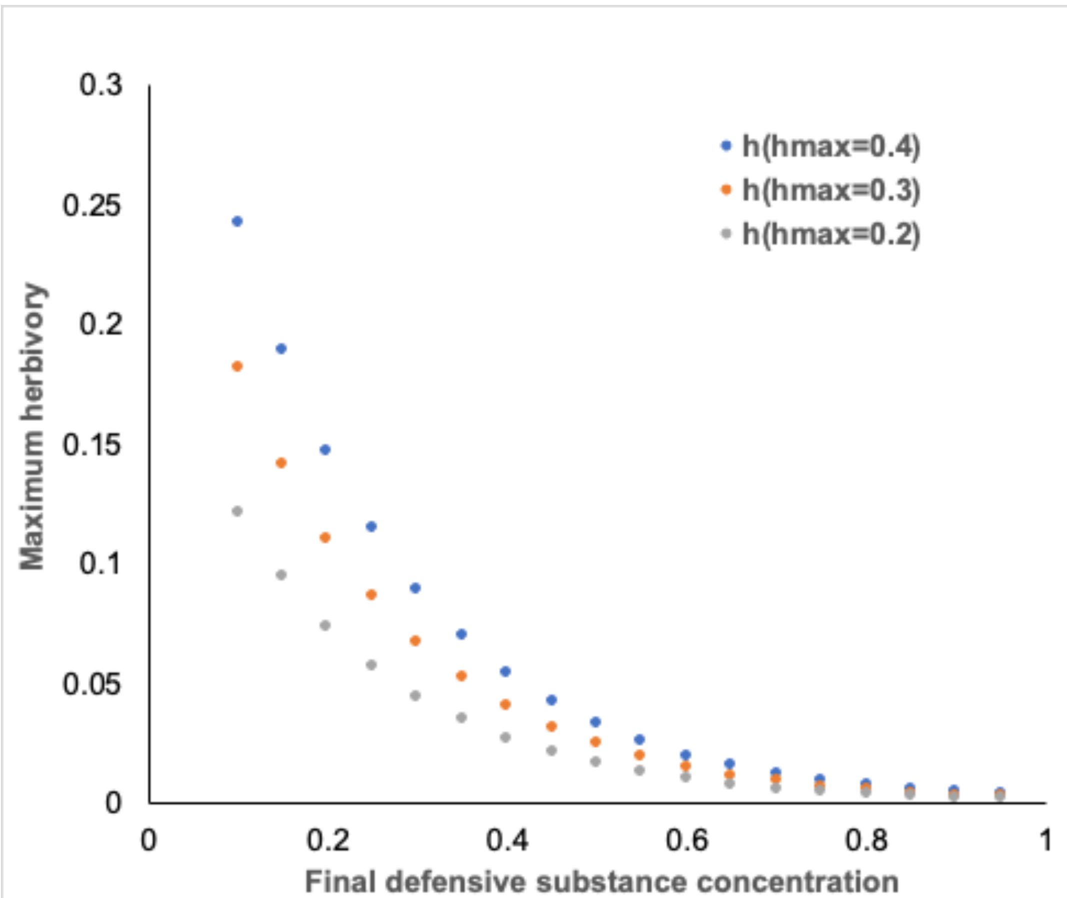


S2 Figure. Illustration of the idea of the scaling of the environmental productivity by referencing the seed size to the maximum possible vegetative biomass when there is no herbivory, and all production is allocated to growth. After scaling, growth rate is higher for plants with smaller seed and thus, such plants may begin growing later to achieve the same final vegetative biomass.

S1 Results. Illustration of the concept of the reduction of herbivory rate by the final concentration of defensive substance. After maturation, the plant only reproduces and defends with stable defensive substances produced earlier in life. The figure explains the concept of the effect of defenses on the reduction of herbivory rate ($D = e^{-\tilde{g}f_{t_c}}$.). We presented the reduction of herbivory rate for different intrinsic properties to repel herbivores; f_{t_c} is the final defensive substance concentration, and $\tilde{g}$ is the defensive substance repelling effectiveness.



S2 Results. Illustration of the concept of the effect of the final concentration of defensive substances on the reduction of the maximum herbivory rate. After maturation, the plant only reproduces and defends with stable defensive substances produced earlier in life. The figure shows to what extent the effective herbivory is reduced by the effect of the final concentration of the defensive substances ($\tilde{h} = \tilde{h}_{\Delta} e^{-\tilde{g} f_{t_c}}$,); $\tilde{h}_{\Delta}$ is the maximum proportion of the removed vegetative biomass, f_{t_c} is the final defensive substance concentration, $\tilde{g}$ is the defensive substance repelling effectiveness.



S3 Results. Numerical solution of growth equations of plants growing in environments with different productivities, either exposed or not exposed to tissue loss exerted by herbivores. The numerical solutions show that there is possible to find values of both constant and proportional biomass removal that bring about similar plant growth curves.

1. For the vegetative biomass w its production rate is $dw/dt = aw^b$, where w – vegetative biomass, a and b parameters of the growth rate (a – proportional to habitat productivity), t – time, Δt – time interval.

2. The numerical solution for this rate is $w(t + 1) = w(t) + aw(t)^b\Delta t$ when herbivory is absent.

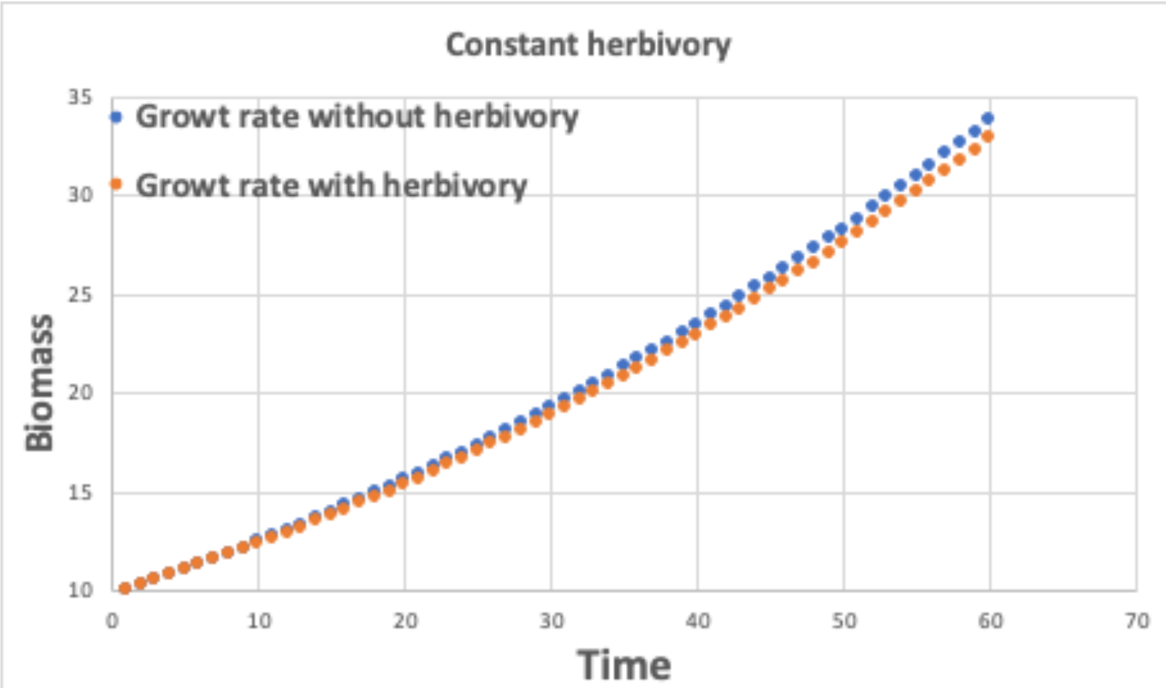
3. When herbivory is constant (a plant loses a constant biomass in a time unit), this rate is: $w(t + 1) = (w(t) - c) + a(w(t) - c)^b\Delta t$, where c – constant vegetative mass loss.

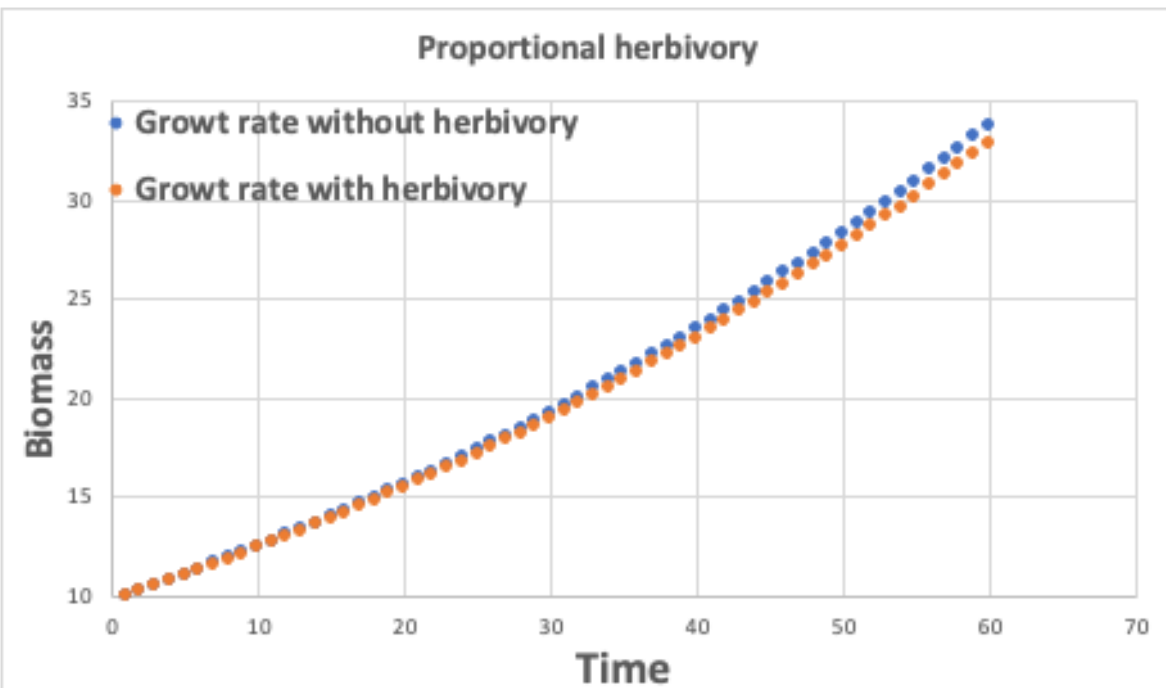
4. When herbivory is proportional to vegetative biomass: $w(t + 1) = (w(t) - zw(t)) + a(w(t) - zw(t))^b\Delta t$.

5. In both models we assumed that first the biomass is eaten by herbivores and then it grew during the time interval Δt.

6. In both cases it is possible to find such parameters that produce very similar growth curves with herbivory present ($a = 0.05$, $b = 0.7$, $c = 0.01$, $z = 0.00055$, $\Delta t = 1$; initial biomass $w(0) = 10$):

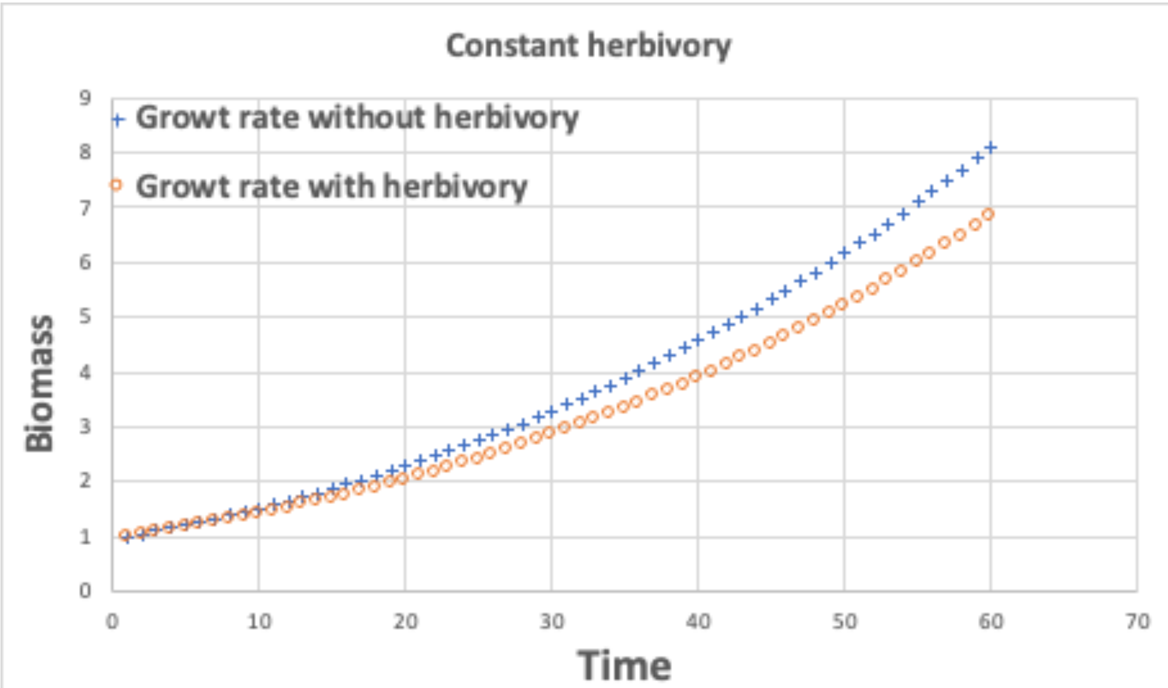
Small herbivory rates produce similar effect (small difference between growth with and without herbivory) for constant and fractional herbivory rate:

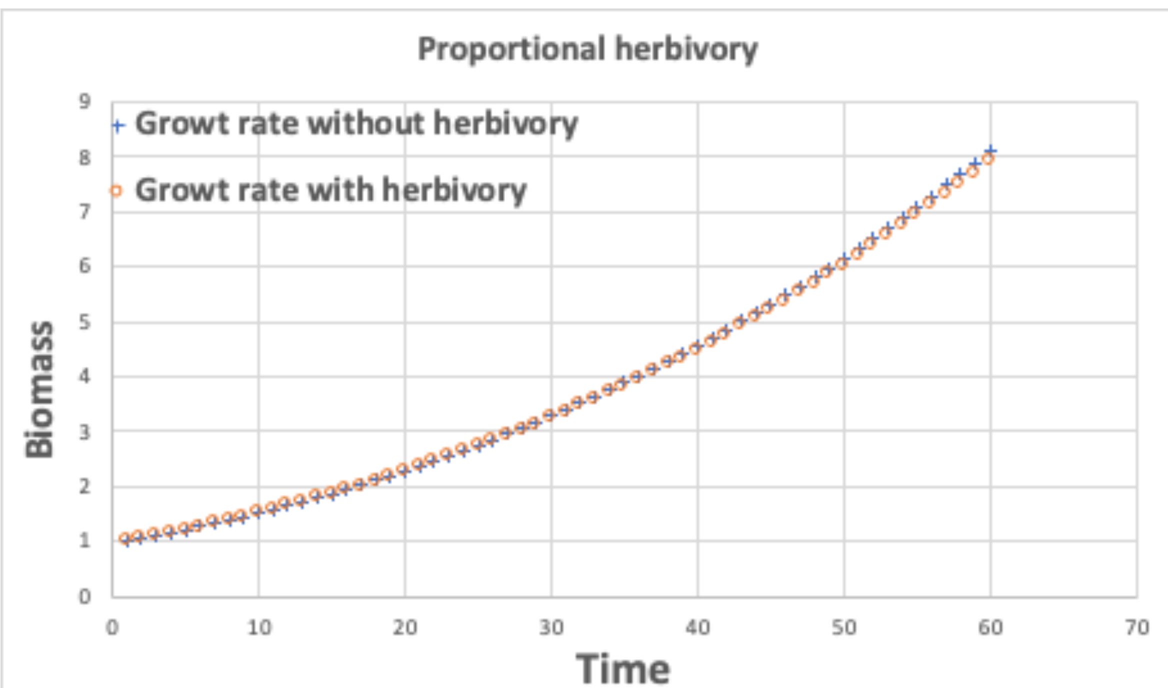




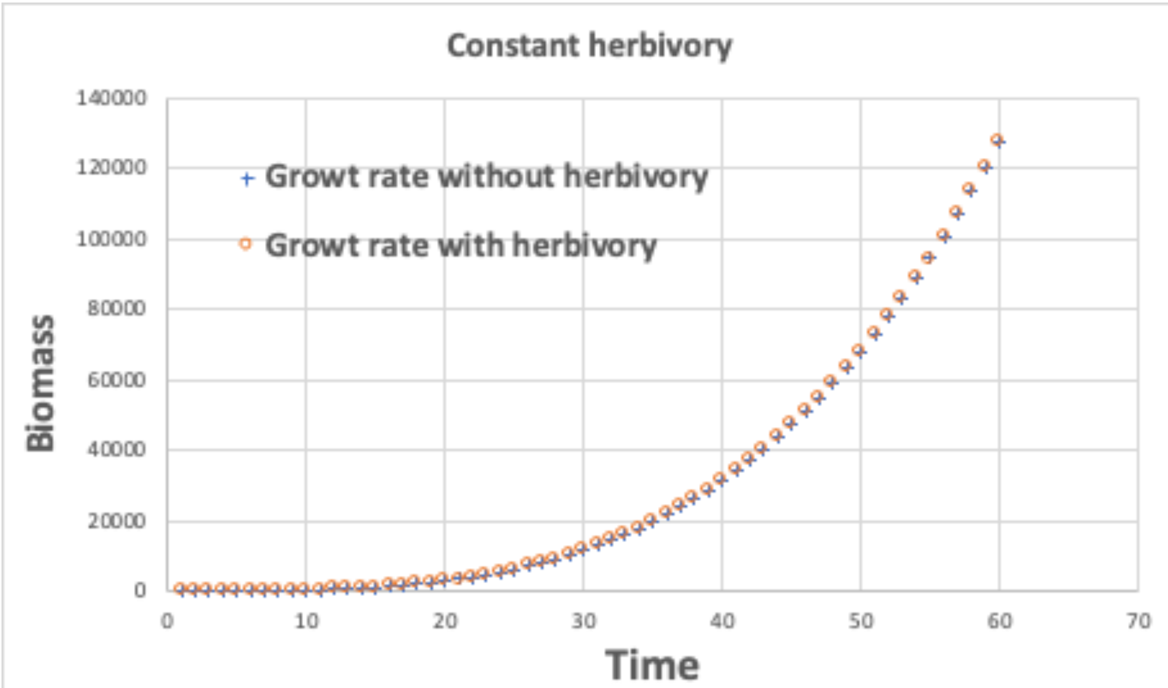
These simulations did not show that both equations are equal but rather that it is possible to find such parameters that produce similar solutions. In this simulation, the initial tissue loss in the constant herbivory is 1000 times lower than the initial plant size. Assuming the fractional herbivory, the initial tissue loss is 22222 times lower than the initial size. That is, lower initial damage assuming fractional herbivory, produced at the same time a similar tissue loss as a constant tissue loss.

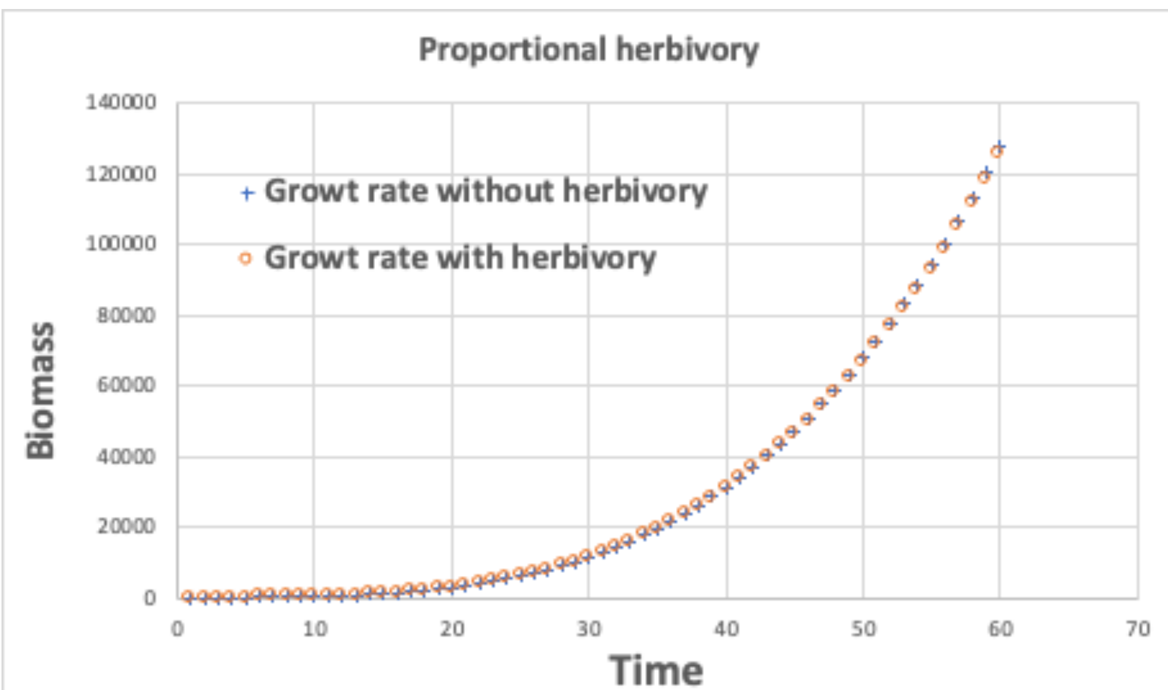
For a = 0.05 (less productive environment), b = 0.7, c = 0.01, z = 0.00055, Δt = 1; initial biomass w(0) = 1 (lower than in the previous example):



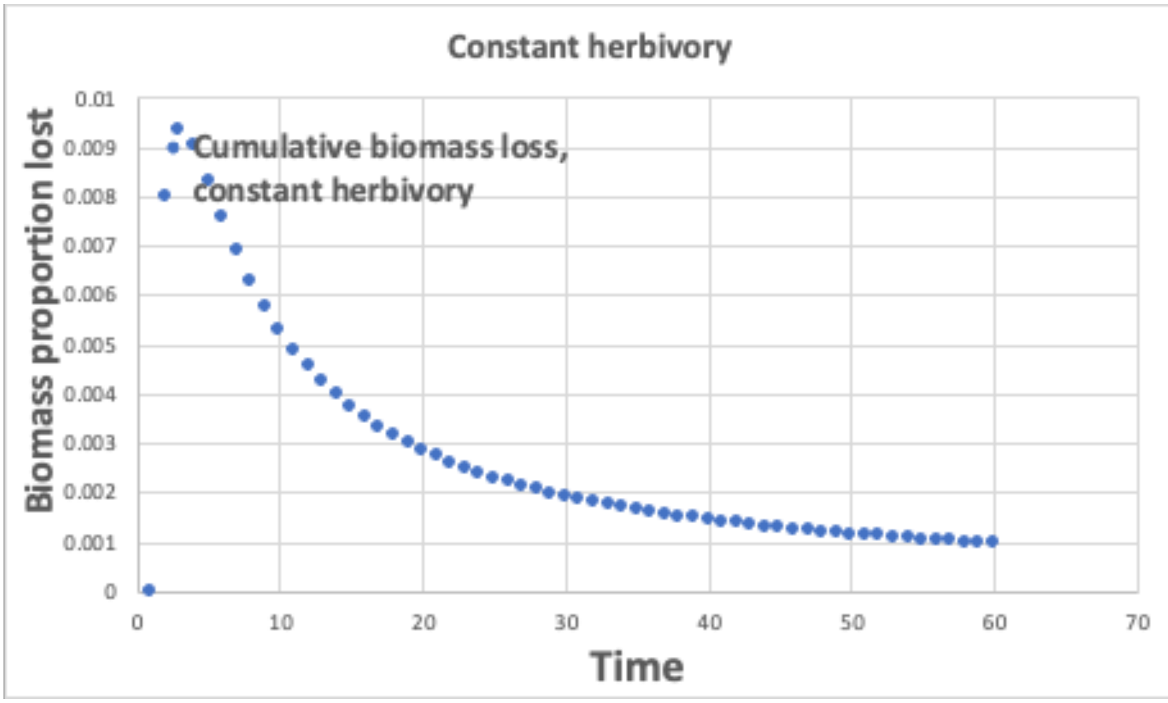


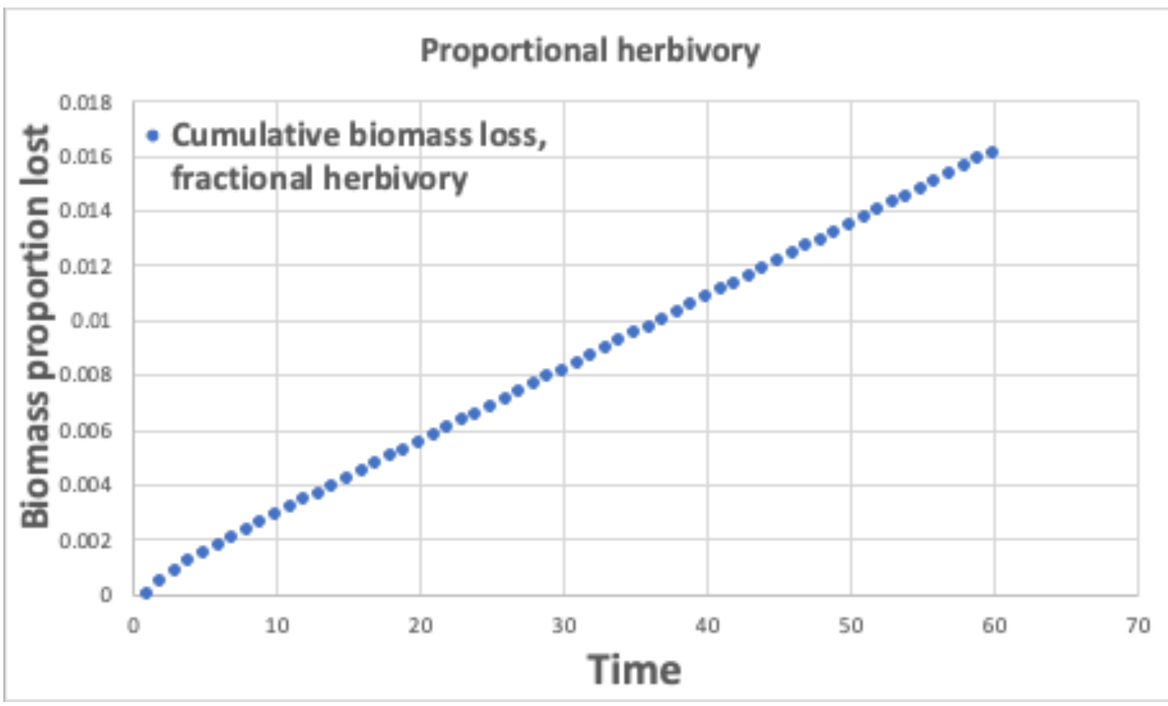
For a = 0.2 (more productive environment than in the previous example), b = 0.7, c = 0.01, z = 0.00055, Δt = 1; initial biomass w(0) = 1 (lower than in the previous example:





….and the corresponding cumulative relative to non-damaged plant biomass losses:

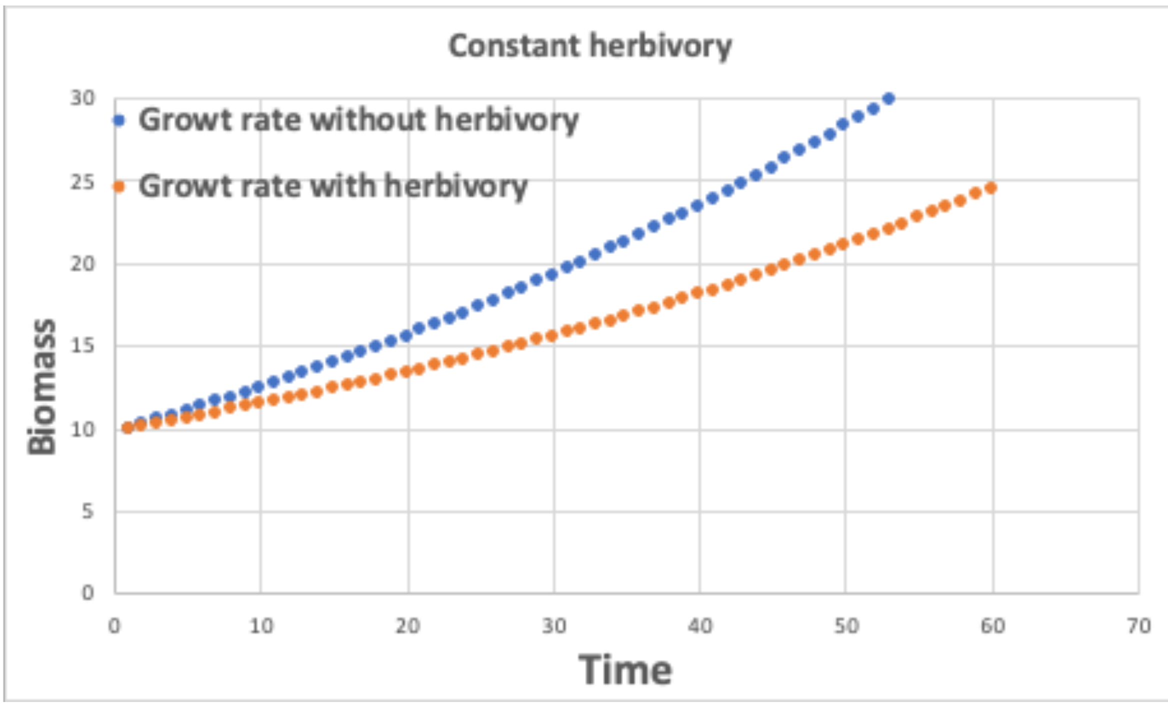


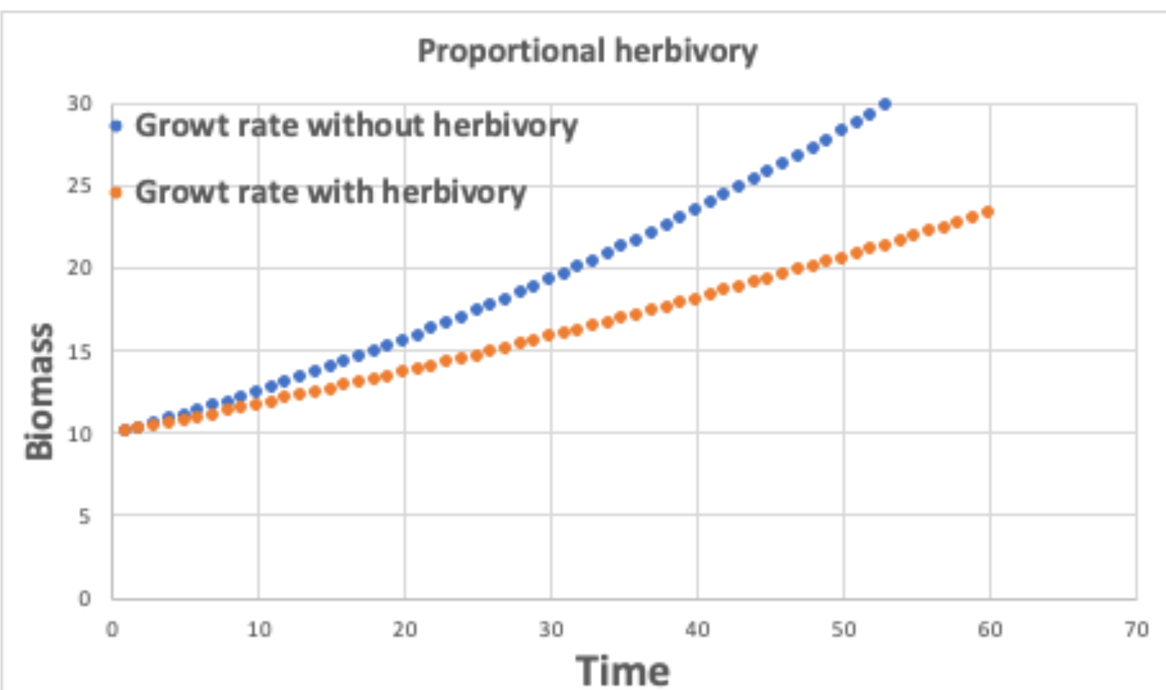


The comparison of the numerical solution for less productive and more productive environment shows that faster plant growth will not produce more biomass to reduce the proportional amount consumed assumed in the model. Notice that the values of biomass losses are very small. Here, we showed that this is easy to find solutions that contradict the Coley's hypothesis [1].

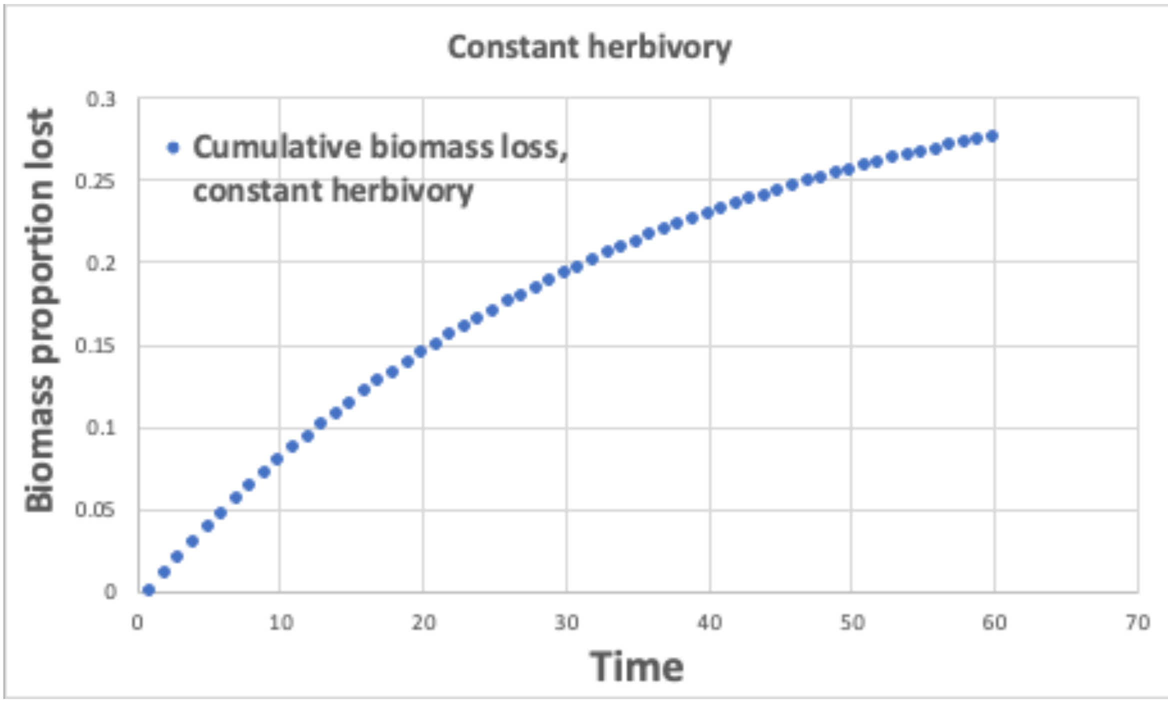
Numerical demonstration that both kinds of herbivory (constant and proportional) can produce similar functional response, analogous to the intake rate of a consumer as a function of food density, assuming that longer time of plant growth is positively correlated with food density (longer growing time → larger plant ≈ higher food density).

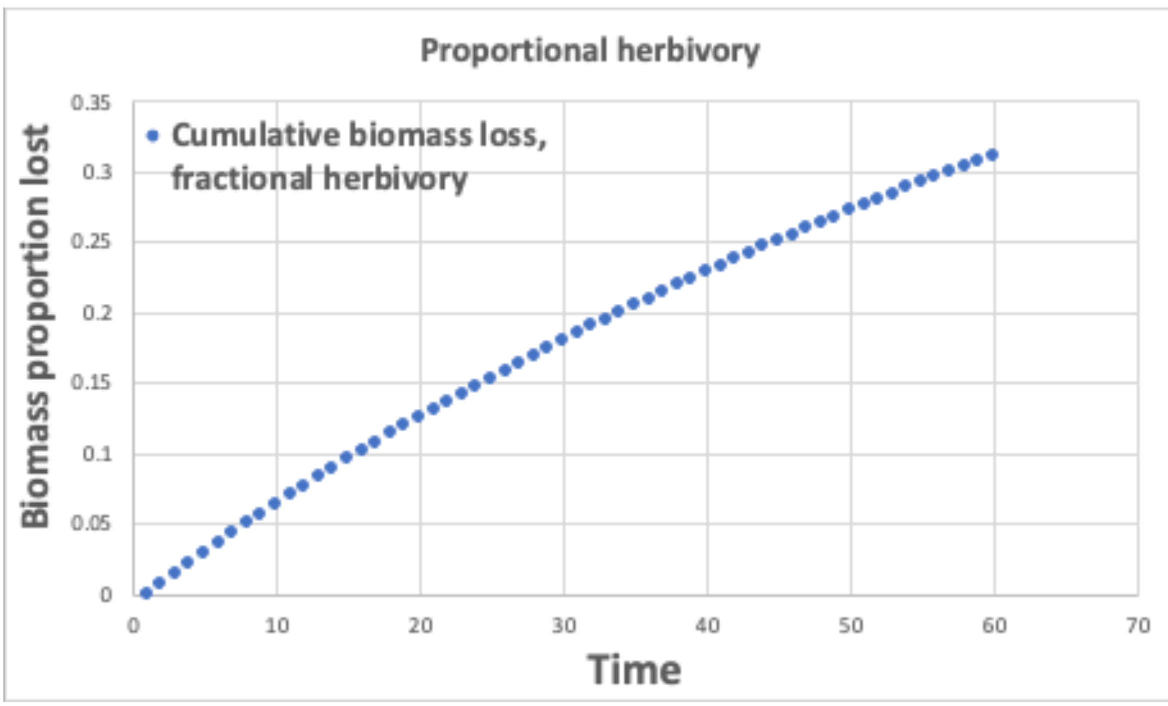
In both kind of herbivory it is possible to find such parameters that produce very similar growth curves with herbivory present ($a = 0.05$, $b = 0.7$, $c = 0.1$, $z = 0.0075$, $\Delta t = 1$; initial biomass $w(0) = 10$):



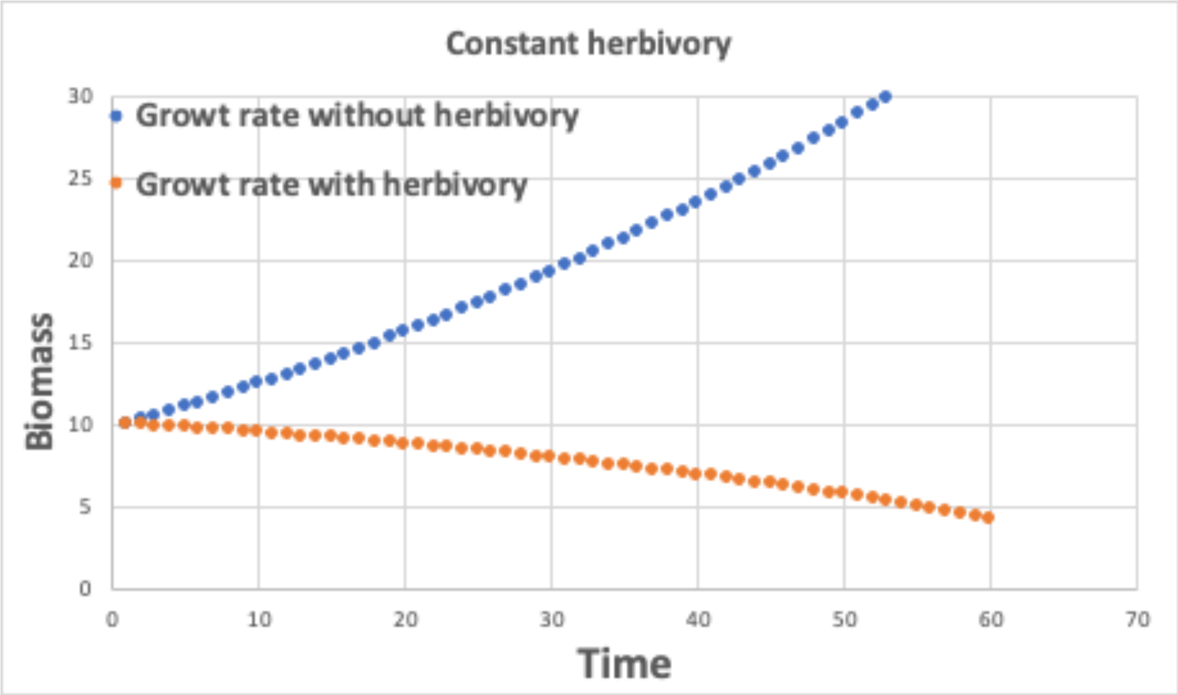


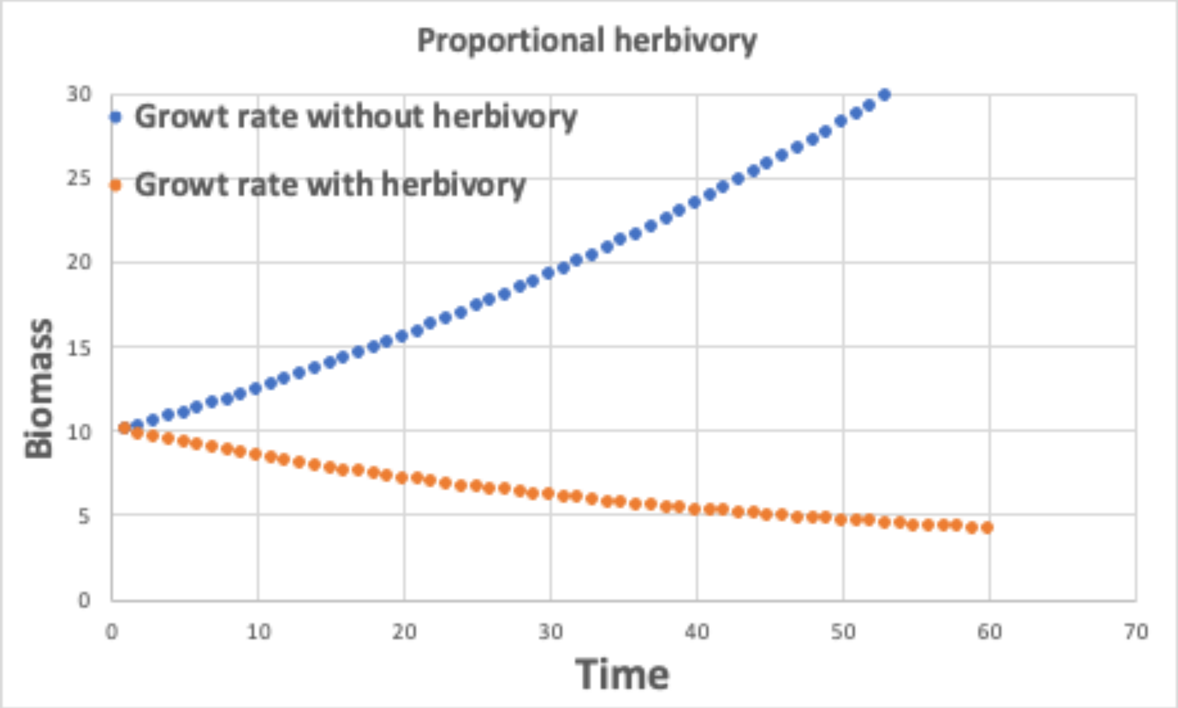
The cumulative damage curves are similar:

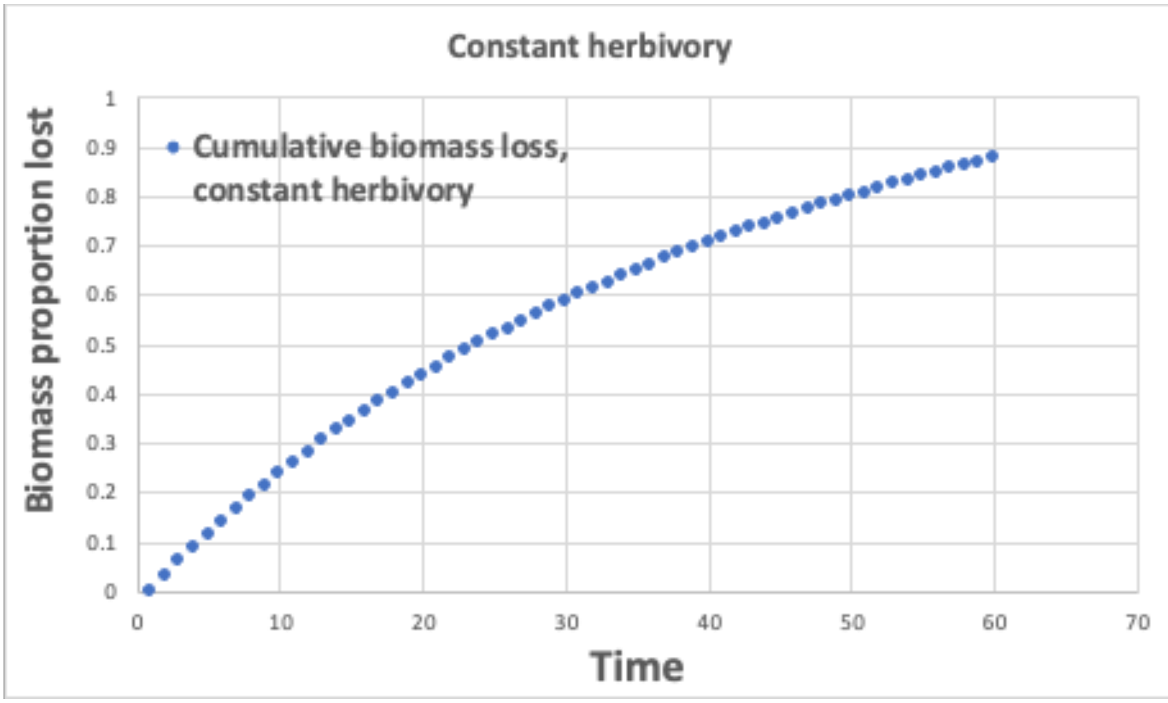


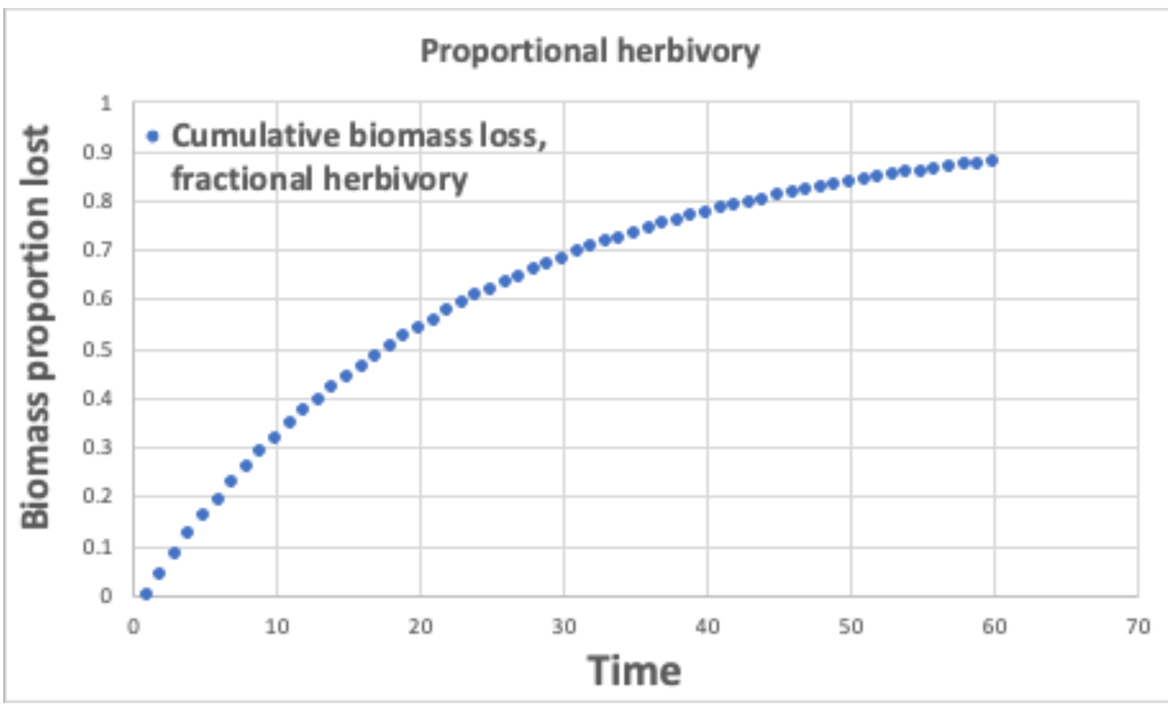


Also, it is possible to find similar curves for both kinds of herbivory when tissue removal produces high biomass loss (c = 0.3, z = 0.043):






Constant herbivory
Cumulative biomass loss, constant herbivory
Biomass proportion lost
Time
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
10
20
30
40
50
60
70


Proportional herbivory
Cumulative biomass loss, fractional herbivory
Biomass proportion lost
Time
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
10
20
30
40
50
60
70

We are not sure if predation curves can be used here as references, because the dynamics of tissue growth is not necessarily similar, to the dynamics of prey when the units are numbers of individuals but not biomass, but the above calculus showed that the general pattern of herbivory curve depends only slightly on the kind of tissue removal, but rather it depends on the relationship between growth rate and herbivory pressure. If this relationship is similar for both herbivory types, it means that the response to herbivory will be similar. So, even when the assumption of the constant herbivory is intrinsically contradictory with the existing knowledge, this assumption may produce similar results as proportional herbivory. In these calculi we assumed that the other investments are constant. For our model, the relationship between biomass loss and time are important. As the results of our study do not depend qualitatively on the type of herbivory rate, we propose that the causes of some differences between the Coley's model and our model are: (1) The definition of the goal function (growth rate in the Coley's model, and lifetime reproductive success in our model), (2) The optimization technique, (3) Constant damage rate produced relatively small damage in fast-growing plants, because more time is needed to attain the same tissue consumption comparing to proportional herbivory, and this constant damage produces large damage in slowly growing plants in shorter time interval: that is why the results of Coley's model are qualitatively similar to our model, but quantitively different (large differences in Coley's model, small differences in our model).

1. Coley, P.D.; Bryant, J.P.; Chapin III, F.S. Resource availability and plant antiherbivore defense. *Science* **1985**, *230*, 895-899, doi:10.1126/science.230.4728.895.