Ingestion rate affects mass and nutrient balance and allocation

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Introduction

Elements cycles in ecosystems are impacted by animal communities in various ways. One is the consumption of a resource, its use for growth and maintenance, and the release of wastes, a process which might accelerate or slow down the dynamics depending on the demographic and physiologic characteristics of communities (De Mazancourt et al. 1998). The quantity and quality of the consumed resource affect growth, maintenance, and the release of wastes in both quality and quantity in a process that depends on individuals and species level traits (e.g. digestive physiology). Although the effect of resource quality on organismal and wastes chemical composition has been thoroughly investigated, and in various taxa (e.g. Kagata et al. 2012, Zhang et al. 2014, Südekum et al. 2016), the influence of food limitation on this elemental mass-balance has been poorly documented.

Yet, there are strong grounds to hypothesize a link between food limitation and elemental mass balance at the individual level. Digestion and assimilation of food are required for both maintenance, growth and can vary in efficiency and cost energy. From an evolutionary standpoint, frequent food limitation cycles might favor individuals which have higher assimilation and/or growth efficiency to compensate for food limitation (Pfeiffer et al. 2001, Roller & Schmidt 2015). When energy and/or biomass intake rates are below maintenance level, the individual has an advantage to increase assimilation and/or growth efficiency or to reduce maintenance and growth requirements (Glazier 2002, Hou et al. 2015). However, whether such an improvement in assimilation efficiency is possible depends on the energetic costs associated with this improvement if there is any, and if the energy intake covers it while being low. If energy intake is sufficient, the individual could invest more energy in digestion, decreasing the amount of wastes produced, something that could be observed in several species (Ali et al. 2021, Windell 1978, Clauss 2013). But if energy intake is too low, the digestion function could be impaired, leading to low assimilation efficiency. Thus, food limitation might trigger higher assimilation efficiency, up to the point where the cost of

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assimilation can not be met anymore because of low intake. There were contrasted results on this topic

This reasoning can be broadened to specific elements which, like energy, are necessary for growth and maintenance. For example, nitrogen (N) and sulfur (S) compose protein, phosphorus (P) is central to metabolic reaction and nucleic acids, potassium (K), sodium (Na), calcium (Ca) and magnesium (Mg) are important for osmoregulation and signaling. Food limitation might change the elemental composition of the animal and of the wastes that it produces (ref). Indeed, there could be element-specific increase in assimilation efficiency in food limitation conditions which might however depend on the content of this element in the resource. A resource rich in N, although provided in low amounts to an individual, might be sufficient to support its requirement in N, leading to no investment in additional N-digestion efficiency. The contrary is true for resource low in N, and the same reasoning might apply to the other elements. In turn, these dynamic elemental modifications of the animal's body and waste composition might alter the conditions in which its resource is living, in a way that might change both its quality and productivity.

These individual level processes can also scale up to population level processes. The functional response links resource density to per capita intake rate. If there is an additional link between per capita intake rate and assimilation efficiency, then the resource density and the assimilation efficiency could be constrained to a certain relationship. In environments where resource levels vary, for example seasonally, this link between resource density and waste nutrient fluxes could affect the temporal dynamics of nutrient cycling. Insects and arthropods represent the major parts of terrestrial animal biomass (Bar-on et al. 2018). The boom bust cycles that insects often show could be the conditions where these processes would occur.

Here we investigate the link between food limitation and elemental mass balance experimentally in a polyphagous insect larvae (Spodoptera littoralis) fed an artificial diet at discrete and restrictive levels. We investigated total mass balance, as well as P, Na, Ca, Mg, K and S mass balance.

Materials and methods

In order to investigate the link between food limitation and the elemental mass balance, we tested submitted 7th instar Spodoptera littoralis larvae to contrasted levels of food limitations, and measured intake, growth, and egestion rates as well as the chemical composition of the food, the larvae and the frass.

Study system

We chose to work with the cotton leafworm Spodoptera littoralis, a polyphagous lepidopteran that is easily reared on artificial food, which makes it a suitable model to study the effect of food limitation. The frass represents the total digestive and excretory wastes which make the nutritional balance easier. Moreover, the exuviates being consumed, there was no need to account for the exuviates chemical composition. This species has six to seven larval instars depending on environmental conditions (Baker & Miller, 1974). Individuals from a

laboratory strain were reared on a semi-artificial diet at 23 °C, 60–70 % relative humidity, and a 16:8 light/dark cycle. Individuals were isolated at their 7th and last instar moult before pupation and subsequently submitted to various levels of food. This stage has the advantage of producing enough frass to enable individual frass chemical analysis.
We choose to distribute a homogen artificial diet that the insect can not sort. The diet was a hydrogel with composition detailed in table 1.

Experiments

6 th instar larvae were isolated in individual 15mL circular polyethylene boxes and provided with ad libitum food until molt completion. The 7th instar larvae were reared individually in the same boxes. Individuals were weighed at the beginning of their 7th instar and three days later, at the end of the experiment.

Each of the 400 individuals was randomly assigned to one of the 5 food provision levels (120, 240, 360, 480 and 900 mg of fresh weight). From their 7th instar molt, individuals were given this fixed amount of food every day, for three days, except when prepuping occurred. Leftovers and frass were collected everyday, stored at -20°C until pooling with other samples from the same individual, dried for 72 hours at 60°C in an oven, and their dry mass was measured. At the end of the experiment, 50% of individuals from each treatment were sacrificed at -20°C, dried for 72 hours at 60°C in an oven, and their dry mass measured. The other half of individuals were used to investigate the effect of food treatment on mortality, emergence proportion and mass at emergence. For logistics reasons, to complete the experiment for the 400 individuals, 40 individuals were taken every week for 10 weeks with 8 individuals for each of the 5 food provision levels.

Chemical analysis

Food subsamples were collected for chemical analysis. Food leftovers, caterpillars, and individual frass samples were dried for 72 hours at 60°C in an oven, and ground to a fine powder using a ball grinder. C and N were measured using an elemental analyzer.

Samples were microwave-digested (Milestone 1200 Mega,Milestone Inc., USA) in Teflon bombs using a mixture of HNO3 and HCl and subsequently measured for P, K, Mg ,Ca , S and Na using ICP-OES.

Growth and mass balance metrics

From the weight and elemental content of food and frass, and individual body masses, we were able to compute the growth and net and mass-specific ingestion and egestion rates (total and by element), the digestibilities of food and of elements (% of food or element that were assimilated), and the growth efficiency (% of food that resulted in growth). Computation and units are given in table 2.

Results

Discussion

References