OLM 8.1. Growth-defence trade-off and its role in biological invasion

Consumers often substantially decrease the *pgr* of their resource populations, which means that variants of the latter deploying a successful defence strategy may spread. Plants have invented different methods to minimize grazing damage: they may accumulate toxic secondary metabolites (a strategy not exclusive to plants; Figure 8.1.1), increase their non-digestible tissue content (Figure 8.8) or excrete insoluble inorganic crystals like silicates, for example. All these defence methods have in common that they require resources to be effective. The resources invested into defence means less resource left for population growth (Figure 8.1.1), meaning that an adaptively optimal level of defence may exist.

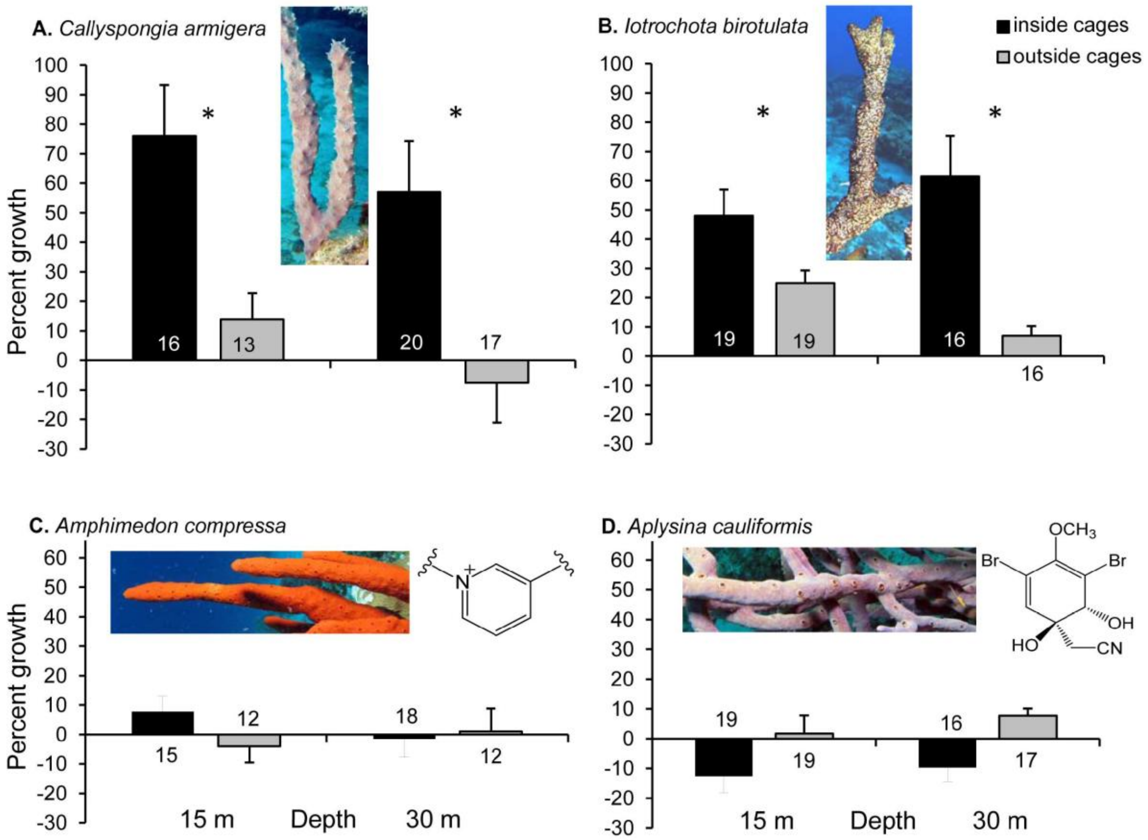

Figure 8.1.1: The growth-defence trade-off, which is a general feature of plants, can be shown to exist in sponges, too (Pawlik et al. 2013).

In an experiment with four Caribbean sponge species, those not using chemical defence (top row of panels) grew faster than toxin producing ones (bottom row) in the absence of consumer species (black columns). Excluding predation had a significant beneficial effect only on the non-defending species (* indicates a significant difference in the growth rates of individuals within and outside of the fenced area). In the presence of consumers the growth advantage of non-defenders is lost. The experiment has been carried out in two different depths differing also in plankton density.

The optimal level of defence is dependent on the decrease in *pgr* due to herbivory, which depends on herbivore density in turn. Invasive plant species occupying new area are usually under reduced grazing pressure, because their specialized consumers are rarely introduced to the new area with them. It is from this fact and the assumption of a growth-defence trade-off that Blossey & Nötzold (1995) formulated their „evolution of increased competitive ability (EICA)" hypothesis. This states that the level of defence decreases (sometimes completely vanishes) in the invaded area, and the plants invest the extra resource thus released into growth and gain an edge in the competition for light. They have tested their hypothesis on purple loosestrife (*Lythrum salicaria*), a native European species that has become a dangerous invader in the USA. The specialized herbivore of this plant is *Hylobius transversovittatus*, a weevil species the imago of which consumes the leaves and whose larvae feed on the roots. The beetle does not occur in the USA (even though it had been introduced for pest control, it was missing from the studied area). The mortality of the larvae was very high (81.9%) on plants from Europe, whereas it was only 37.3% on plants from America, indicating a significant decrease of defence in the latter. Cultivating the two plant variants in a common garden with the herbivore excluded the American version has grown significantly taller (Figure 8.1.2).

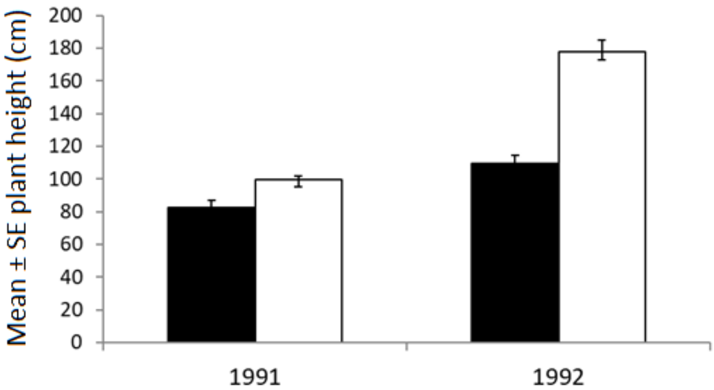

Figure 8.1.2 Greenhouse experiment

Cultivating native European (black columns) and alien (white columns) populations of purple loosestrife (*Lythrum salicaria*) the latter grows taller (data from Blossey & Nötzold, 1995).

In order to test the hypothesis further, many other invasive plant species have been studied, but only some of them supported the prediction. One of the possible reasons for the failures may be that at an abundance of resources and with the plant species capable of fast regeneration after grazing, the alternative fast regeneration strategy may be superior to defence. A typical example for this is the study on *Alternanthera philoxeroides* (alligatorweed) briefly discussed in the textbook (Ch8Tradeoff, p. 147). There are two different variants of this South American invasive seaweed species in its native area: the slow-growing *A. p. var. acutifolia* and the faster *A. p. var. obtusifolia*. The specialized herbivore of this plant species is *Agasicles hygrophila* (alligator weed flea beetle). Both the larva and the imago of the beetle feed on the plant, and the larvae pupate inside cavities they munch in the stem of the plant. The slow-growing variant has higher stem tissue density which makes it less favourable for the beetle to feed on it, but it also makes the plant slower to grow (Figure 8.8), which is a typical example for defence-growth trade-off. The fast-growing variant compensates for the damage due to herbivory by fast regeneration instead of avoiding the damage in the first place. Both variants have been introduced to North America, but only the slow-growing variant invaded China. Pan et al. (2012) have compared the growth of the native strains with that of the invasive ones in common garden experiments. The invasive individuals of the slow-growing variant have grown faster and taller than the native ones (Figure 8.1.3.a,b) as expected, but the fast-growing variant has not shown any difference between invasive and native strains. Given free choice for the larvae of the beetle they always consumed most from the fast-growing variant and least from the slow-growing native one (Figure 8.1.3.c). The proportion of successful pupation in 4 weeks has shown the same trend in larvae fed on different variants of the plant (Figure 8.1.3.d). The averages of the five groups studied show a strong correlation between defence and growth: the slower the plant grows the worse resource it is for the herbivore (Figure 8.8, p.148). In the invasive populations of the native variant growing slower but defending itself more efficiently the ability of defence has decreased while their growth has increased as predicted by the EICA hypothesis. The fast-growing variant did not show such a change, however, probably because it has already maximized its growth to its physiological limit.

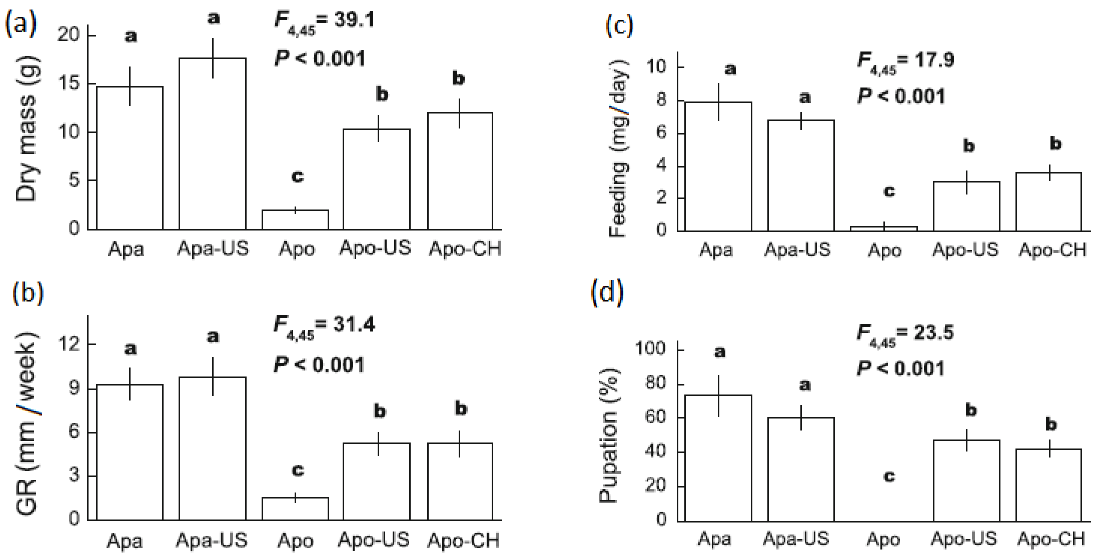

Figure 8.1.3. Common garden experiment with two variants of alligatorweed, *Alternanthera philoxeroides* (Pan et al. 2012).

a) plant mass after 8 weeks of growth; b) elongation rate of shoots (GR); c) quantity consumed by an *Agasicles hygrophila* larva upon free choice of plant variant; d) fraction of successfully pupated *Agasicles hygrophila* larvae feeding on each variant. Different letters above the columns denote significant difference. Apa = A. p. *var. acutifolia*, fast-growing, Apo = A. p. *var. obtusifolia,* slow-growing native Argentinian (no label) and invasive (US= USA, CH= China) individuals.

The distribution of chemical defence may not be even within the plant individuals: defending young leaves may yield a higher increase in *pgr* (MacCall & Fordyce 2010). On one hand, these feature less dense tissue and they are more efficient metabolically accordingly, but they have not yet covered the resource investment into producing them (negative carbon gain). On the other hand, they are more attractive targets to herbivores because of their higher nitrogen content, the very feature making them more efficient in photosynthesis. An elevated concentration of chemical defence substances is therefore expected in younger leaves. Alba et al. (2012) have found an increased iridoid glycoside concentrations in the young leaves of common mullein (*Verbascum thapsus*,

Figure 8.1.4).

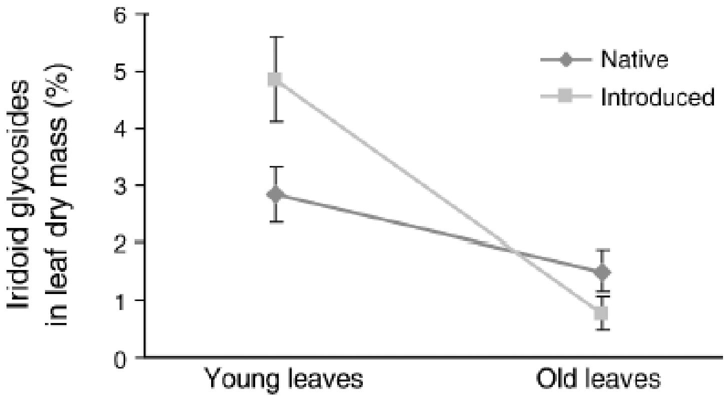

Figure 8.1.4. Concentrations of iridoid glycosides in young and old leaves of native and invasive individuals of *Verbascum thapsus* (Alba et al. 2012).

However, specialized herbivores may adapt to the toxins produced by their host plants (sometimes by accumulating the toxins in their own bodies, applying them as chemical defence themselves). Often they use the toxins as chemical traces in finding the food plant (Figure 8.1.5). This makes maintaining too high a toxin concentration often unproductive. Plants invading new area often get rid of their specialized herbivores and thus also of the disadvantage related to high toxin concentrations. In North American invasive populations of the common mullein the iridoid glycoside concentrations have been much higher in the young leaves than in the native European strains exposed to their specialized herbivores (Figure 8.1.4). In this case it may be the trade-off between avoiding generalist herbivores and specialized ones that drives the evolution of secondary metabolite production.

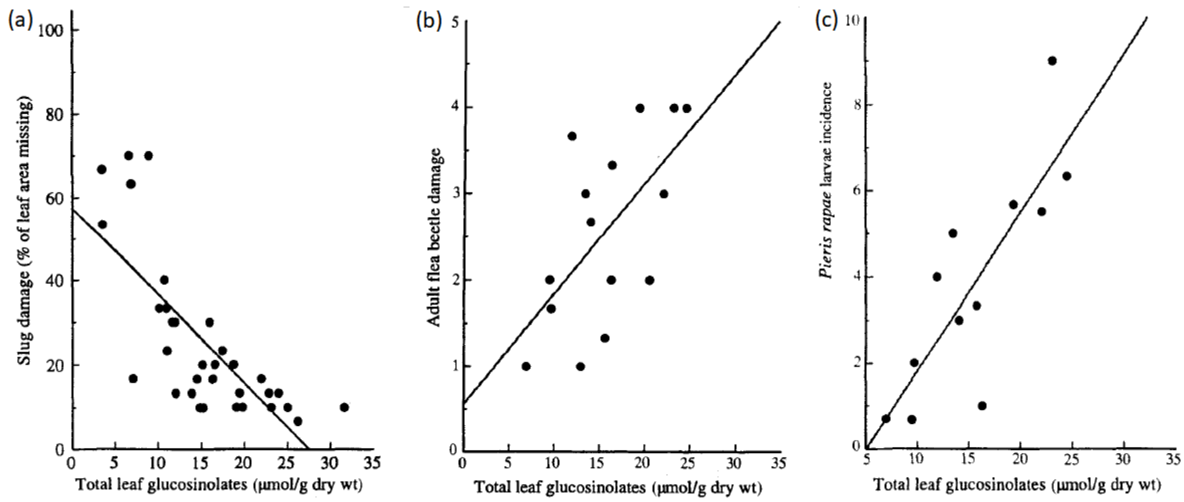

Figure 8.1.5 Indications for a trade-off between avoiding generalist herbivores and specialized ones (Giamoustratis & Mithen 1995).

The glycoseinolate concentrations in different variants of the oilseed rape (*Brassica napus ssp. oleifera*) are different. These are toxic compounds in general, but some herbivores specialized in feeding on Brassicaceae are adapted to them. a) A higher concentration of the toxin reduces grazing by generalist herbivores like slugs, but b) increases that by specialized ones like leafhoppers and c) caterpillars of small whites (*Pieris rapae*), probably because the specialists use the toxin as a chemical clue to find the plants.

These examples show that even if the defence-growth trade-off may be present in all plants capable of producing secondary metabolites to avoid herbivory, its effect may not always be observed. A more complete picture can be obtained by considering other possible trade-off relations like the one between herbivore tolerance vs. herbivore defence, or avoiding generalist vs. specialized herbivores. Therefore, we may conclude that reduced defence and the consequential increase in competitive ability is a frequent but not exclusive explanation to the success of invasive plant species.

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