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7. October 2008

Review of the PhD-Thesis submitted by Vit Latzel
“Tolerance and resistance of plants to disturbance“

In his PhD-Thesis, Vit Latzel explores the functional significance of clonal plant traits in relation to disturbance. Specifically, he considers the bud bank as a mechanism of tolerance to disturbance and the spread of induced resistance through lateral rhizomes as a mechanism of resistance. I would like to stress that clonal traits are strongly underrepresented in current work on functional traits and progress in this field is highly appreciated. Therefore, I consider the thesis a very timely endeavour.

Vit Latzel's work relies on three carefully designed experiments that make up the main chapters of his thesis. The thesis starts with a short introduction that mainly serves as an outlook to the next chapters. This is unfortunate because the introduction would be the place to explain the context of this work, especially the disturbance concept in plant ecology and the tolerance and resistance concept. For instance, tolerance and resistance as plant strategies are placed in a template of disturbance severity, predictability and frequency in Table 1 (apparently, there is a mistake in the last two rows). Predictability is often cited in the context of seed bank studies but it is hardly ever explained how plants can “predict” future disturbances. Altogether, at this place, I would have



welcomed a more thorough introduction to the traits and as well as to disturbance as an environmental regime for plants.

The second chapter gives a perspective on overlooked traits in response to grazing, especially shoot cyclicity. This is an important subject because many studies published so far deal with a very limited trait set that can be hardly seen as sufficient to understand the diversity of plant responses to grazing. Vit Latzel rightly criticises the use of plant height as a single predictor for a plant's response to grazing and emphasises the value of clonal traits associated with resprouting. He also emphasises consideration of trade-offs between traits which is however not well elaborated in this article.

The first two chapters have set the scene for the experimental part of the work. The third chapter describes the outcome of an experiment designed to evaluate the role of the bud bank in comparison to seed traits in an urban environment. Disturbance was simulated by tilling, and the role of the bud bank by adding a treatment where plants were killed with herbicides. The study showed that the bud bank played an important role in plant regeneration following disturbance. Regeneration from buds can be faster and thus competitively superior to regeneration from seeds.

The fourth chapter reports another experiment that deals with the fitness of seeders versus resprouters under different nutrient regimes. The experiment with *Plantago media* and *Plantago lanceolata* investigated the question whether a species with a predominant resprouting strategy would be more successful on nutrient-poor sites than species with a predominant seeding strategy. Although resprouting was affected by nutrient availability, the experiment did not clearly confirm this hypothesis. This experiment showed that hypotheses found in the literature are often rather simplistic and processes found in one ecosystem (in this case fire-prone systems) cannot be easily transferred to other ecosystems (e.g. meadows).

I consider the fifth chapter the most innovative one of the thesis. It deals with systemic induced resistance to herbivory in *Trifolium repens*. The organism feeding on *Trifolium* was a caterpillar. This study provided evidence that maternal ramets gave parental support to young offspring ramets that reduced the risk of damage by herbivory. On the other hand, in the absence of herbivory, uninduced phenotypes were superior to induced phenotypes. This experiment was particularly carefully designed. I have learned a lot from this chapter.

The sixth chapter is a short summary of the previous chapter and does not provide much more insight than what is said previously.

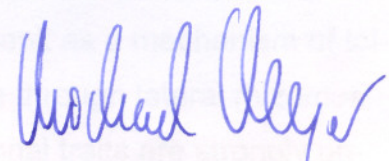
Aspects that I consider positive

- A very timely research that sheds light on overlooked, though important topics in functional ecology
- Three carefully planned experiments that cover different aspects of clonal traits in response to disturbance
- Published articles

Aspects that I consider negative

- Rather short introduction that gives less information on the background of the research than desirable.
- A final section that is too short to give a well elaborated synthesis of the importance of clonal traits for the regeneration of plants following disturbance, especially in comparison with seed traits.

This thesis fulfils the necessary requirements for a PhD-Thesis and I take the liberty to recommend defence.



Prof. Dr. Michael Kleyer

Vít Latzel: Tolerance and resistance of plants to disturbance: a review

The thesis is composed of four papers (one of them more of a review-type) and a short introduction and a summary; the candidate is the first author of two of them. As the individual papers are rather disparate, I will discuss each of them separately.

Paper 2

This is an essayistic/review paper. It addresses primarily consistency of functional trait response to grazing, discusses several candidate traits correlated with grazing, and proposes using some other traits (clonal growth/bud bank traits) that can potentially be used. It also addresses correlations between the traits.

Questions

- the paper shows well that there is no set of traits that would be consistently favoured under grazing. Why do you think this is the case? Is it indeed only the confounding effect of moisture – i.e. do you think that if the moisture gradient is accounted for, the set of traits favoured by grazing will become more consistent?
- When assessing trait correlations (Fig. 2), did you in any way take into account relationship of the plants to grazing (apart from using plant height)?

Comments

- Cluster analysis of traits (Fig. 2): it is not clear to me whether this is taken from some other paper, or whether this is published for the first time here. In any case, the description of what it shows, how the data were collected, and the classification performed should be more clear. If it is an already published figure, reference to the original paper should be there.
- How the height was assessed and divided into two categories? Why did you use cluster analysis to address correlations of trait syndromes to height?

Paper 3

This is a well-performed study of seeder vs. resprouter plants to disturbance, but I do not find the results very informative or unexpected. Prevalence of seed regeneration at herbicide-treated plots is hardly surprising, just as larger vegetative regeneration in the tilled treatment.

Questions

- how were multistate traits dealt with in the stepwise variable selection? The table seems to indicate that variables representing individual states were selected independently of each other (which is a disputable technique at least). What were the reasons for this approach?
- Why did you expect invasive plants would be doing better than native plants? (I agree that a combination of strategies is useful, but nowhere in the intro you present evidence that invasive plants are better on this point.)

- Why an indirect measure of species response to the treatment (species position on the first canonical axis of a multivariate analysis) was used as a measure of the species' response to the treatment instead of a more direct (univariate) one?
- The full factorial treatment would require also "kill seeds-retain resprouts" treatment. Have you considered also such treatment?

Comments

- I do not understand the difference between cover and abundance. Both terms are used in the results and discussion, but only cover is defined in the methods. Does abundance refer to number of species, cover of one species, frequency of one species over all treatment plots or something else? There is no clue to this in the methods section.
- the description of how trait values were assigned to species is by far too short. I also found no mention of "guild" in the methods. Although the aim of the study is to examine bud-bank traits, most of the trait listed in the Table 1 are not bud bank traits.
- The full list of the traits tested in the paper does not seem to be available – only significant traits are shown in the results.
- Why the fruit type was chosen as one of the tested traits – is there any hypothesis on this trait? This variable has a strong taxonomic bias – it is strongly correlated to the "legume" variable (see Tab. 1).
- p. 43: *Tanacetum vulgare*, *Cirsium vulgare* and *C. arvense* are not invasive species by the common usage of the term.
- Information on number of degrees of freedom is often missing. This is necessary to understand the data structure underlying the analyses in the tables.

Paper 4

This is a well-performed and interesting study, but the generality of the findings (and thus the potential space for interpretation) is limited by the fact that only two species (i.e. essentially one data point) are compared.

Questions

- An difficulty in this paper is the simple size effect that may (allometrically) determine the outcome (allocation and fitness) and, even worse, this effect may differ between resprouters and seeders. Differences in allocation may thus be due simply to the fact that seeders were bigger (which is a contingent effect of the experimental design). What approach would you propose to handle this potentially allometric effect?
- I doubt that main effects (resprouters/seeders, fertilization or not) can be reasonably interpreted here as their effects depend too much on contingencies of the experiment. For example, if the resprouters were grown for one season more before the testing proper started, their yield would be much larger. In my opinion only interactions can sensibly be examined. Could you comment on this?
- You state (p. 60) that the species from richer habitat invested more into competitive ability if fertilized, whereas the species of poor habitats invested more into seed production. I do not understand why this fact is surprising. What would be your prediction?

Comments

- In most tables, information on number of degrees of freedom is missing. This is necessary to understand the data structure underlying the analyses in the tables.
- I do not understand the comment (p. 53) that ten years of cultivation in a common garden has excluded "undesirable environmental effects", in particular if the plants in the experiment started from seeds. Do you have any information of the pollination/fertilization patterns in the commercial seed supplier's garden?
- root/shoot ratio: the analysis was based on non-transformed data? A better approach would be to analyse root biomass and use shoot biomass as a covariate.

Paper 5

This is a well-designed but rather unrelated study of induced resistance to herbivores along fragments of a clonal plant.

Questions

- the outcome of the cost-benefit analysis of the system will strongly depend on the overall density of the predator in the field. Have you (i) collected data on mean herbivore pressure in the field and its variance, and (ii) considered this effect in the analysis?
- I would appreciate more comments on how the framework of this paper can be linked to the other papers that deal with resprouting.

The core of the thesis is the set of the three experimental papers (papers 3, 4, and 5). These are good studies, but they work with different model systems, address (rather) unrelated questions and refer to different contexts. They do not make an attempt to put the findings into any common framework. This is fine with the individual papers, but I sorely miss such an attempt with the thesis as such, where both the introduction and the general discussion repeat major findings of individual papers, but provide little more than a trivial summary in addition to that. (Both parts are very short and thus can hardly contain sufficient substance.) I would also appreciate a wider discussion of different roles of tolerance and resistance to disturbance (keywords from the title) and a more accurate discussion of these terms.

Some of the papers do not seem to be edited well and definitely leave space for further work (even some published ones!). Some sentences are not complete (e.g. missing verbs), there are quite a few typing and spelling errors (the typeset is also far from perfect – see e.g. Table 1 on p. 39). I also miss a statement on the candidate's contribution to the multi-authored papers.

However, the thesis has demonstrated that the candidate is able to do research of his own, and process the results to produce potentially publishable papers. Therefore I recommend the thesis for defence. Still I reserve further questions concerning this work for the defense.



Tomáš Herben
3rd November, 2008

Review of Dissertation by Vit Latzel

“Tolerance and Resistance of Plants to Disturbance”

Keith Edwards

The dissertation by Vit Latzel investigates both theoretical and applied aspects of plant responses to disturbance. In particular, he studied the role of reproductive traits in how well grassland plants respond to mowing. The published articles and in-review manuscript which comprise the dissertation show clarity of thought and grasp of the theoretical principles involved that clearly meet the requirements for a doctorate.

Tolerance to disturbance was examined by studying the ability of various plant species to resprout from axillary or adventitious buds when subjected to mowing. Such information is useful for providing further insight into the functioning of plants, from the scale of individuals to that of a plant community. In addition to this theoretical aspect of the work, the results can also be useful for better managing pasture habitats.

The first paper (Chapter 2) provides a good overview of the concept of plant functional traits. Resprouting ability and other clonal traits, heretofore often overlooked and thus understudied, may provide better predictive ability in terms of plant response to a disturbance in pasture areas than the more traditionally measured traits, such as plant height. This is an interesting and informative summary of the current state of this theoretical concept and shows that this concept has serious limitations as currently espoused. My only problems with this chapter were

the sometimes poor English and several mistakes with citations (for example, there is no Lepik et al. 2004 citation in the Reference section).

Chapter 3 is a paper published in *Applied Vegetation Science* dealing with the role of bud banks and resprouting ability in plants after mowing and cutting disturbances. This study was an imaginative manipulative experiment and clearly shows the ability of Vít Latzel to develop and conduct good scientific studies. One can always question the realism of the selected treatments, but in this case they seem to be in the realm of the possible. I found it interesting that the invasive species in the study sites were negatively affected by the disturbance, a result opposite to what is normally found. The given rationale for this seems quite logical. It also points out that the area may have been subjected to a different disturbance regime prior to the application of the treatments and that the invasive species found in these sites at the start of the experiment were better adapted to the original disturbance regime. This is also interesting in that it shows how species composition in a community can change when the disturbance regime changes and the suitability of using reproductive traits to predict such compositional changes. I found Figure 1 to have too many arrows, making it hard to understand the information that the authors wanted the reader to get. However, since the paper is already published, there is little that can be done about it now.

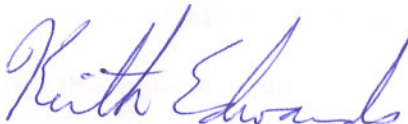
Chapter 4 is a good small study of the effect of nutrients on the fitness of two closely related *Plantago* species, growing naturally in different nutrient conditions. In addition, the plants were manipulated to investigate the interaction of nutrient

conditions with regeneration ability (sprouters vs seeders). This was a well-developed and conducted experiment. I have no further comments about this particular paper.

The last paper (Chapter 5) investigated the costs and benefits of induced resistance in clonal plants to disturbance. This study is a good addition to the numerous past studies investigating the evolutionary aspects of plant-herbivore interactions. The experiment was well-conceived and conducted. It was nice to see that the researchers took care in avoiding pseudoreplication in their analyses. I found it interesting that total plant biomass did not differ between the induced and control plants. It is possible that differences in total plant biomass may occur in the future, but that would require a longer time scale in which the experiment is run. It would also be useful to perform similar experiments under more natural field conditions, to determine how changing environmental conditions may affect these responses.

Overall, the work encompassed in this dissertation is of high quality and shows Vít Latzel to have the requisite knowledge and skills for having a successful scientific career. His proposed future research topics follow from his doctoral studies and indicate a good level of curiosity and intellectual rigor needed for being a top scientist. Therefore, in my opinion, Vít Latzel has fully earned his doctorate degree.

I will reserve any questions I have concerning this work for the defense.

A handwritten signature in blue ink that reads "Keith Edwards". The signature is written in a cursive style with a large initial "K".