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Review

Plant metabolite profiles and the buffering capacities of ecosystems

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ABSTRACT

In spite of some inherent challenges, metabolite profiling is becoming increasingly popular under field conditions. It has been used successfully to address topics like species interactions, connections between growth and chemical stoichiometry or the plant's stress response. Stress exerts a particularly clear impact on plant metabolomes and has become a central topic in many metabolite profiling experiments in the fields. In contrast to phytochambers, however, external stress is often at least partially absorbed by the environment when measuring under field conditions. Such stress-buffering capacities of (agro)-ecosystems are of crucial interest given the ever-increasing anthropogenic impact on ecosystems and this review promotes the idea of using plant metabolite profiles for respective measurements. More specifically I propose to use parameters of the response of key plant species to a given stress treatment as proxies for measuring and comparing stress-buffering capacities of ecosystems. Stress response parameters accessible by metabolite profiling comprise for example the intensity or duration of the impact of stress or the ability of the plant organism to recover from this impact after a given time. Analyses of ecosystem stress-buffering capacities may improve our understanding of how ecosystems cope with stress and may improve our abilities to predict ecosystem changes.

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1. Introduction

Despite a number of caveats listed further below, ecological questions have successfully been studied using metabolomic techniques for quite some time. Ecometabolomics, as this approach has been named (Penuelas and Sardans, 2009), has most often been applied to specific organisms sampled from a given environment. Recently also "meta-metabolomic" analyses targeting for example decomposed leaf (Wallenstein et al., 2010) or soil samples (Jones et al., 2014) have been reported. As pointed out further below, the impact of stress on a particular compartment or organism has received particular attention in ecometabolomics. When studying plant reactions to stress under environmental conditions, it is important to note, however, that the environment itself may constitute a strong buffer for stress (Folke et al., 2004). The impact of drought on a given plant for example is strongly depending on soil water reserves (Peterman et al., 2013), which in turn depend

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on soil pore structure (Perrier et al., 1996). Furthermore, the impact of drought, as of many other stress factors, may be modified by the presence of symbiotic microorganisms, as for example by mycorrhizal fungi (Miransari, 2010; Bothe et al., 2010).

In my eyes there are several reasons, why this ability of ecosystem to alleviate the impact of stress should be regarded as a prime target for ecometabolomic experiments: (i) given the anthropogenic impact in general and the impact of climate change in particular, the importance of stress in natural and agricultural ecosystems is continuously increasing (Steffen et al., 2011). (ii) There are strong indications that the ability of ecosystems to cope with stress is negatively affected by the consequences of human activities, as for example by a general decrease in biodiversity (Elmqvist et al., 2003) or by soil compaction and deterioration experienced in agricultural systems (Batey, 2009). (iii) The stress-buffering capacities of ecosystems may be important parameters for predicting catastrophic shifts in ecosystem properties, this way possibly serving as early warning signals prior to irreversible ecosystem collapse (Scheffer et al., 2009).

Given the importance of ecosystem buffering capacities, this review tries to point out how to use ecometabolomics for assessing such capacities. In short I propose to use aboveground plant metabolite profiles as proxies for measuring how a given stress treatment is affecting key plant species in various ecosystems. This review will focus mainly on primary metabolites, since the connections of plant secondary metabolites and stress have extensively been covered elsewhere (Yang et al., 2012; Patra et al., 2013). After a close summary of caveats resulting from the complex regulation of metabolite levels, results from recent metabolomic field experiments will be shortly summarized. Subsequently the prominent role of stress in ecometabolomics will be pointed out and approaches will be outlined how to use ecometabolomics for the analysis of ecosystem buffering capacities.

2. Complex regulation of metabolite steady state levels and resulting challenges for field experiments

Technical challenges connected to metabolite profiling are due to the enormous chemical diversity of metabolites and to their large range of concentrations. Because of this, no analytical approach has been established so far, capable of providing a complete, unbiased picture of all metabolites from a given organism (Allwood et al., 2011). Furthermore, a lack of comprehensive compound databases and of software tools translating shifts in metabolite steady state levels into shifts in metabolic fluxes constitute severe hurdles when it comes to the interpretation of metabolite profiles. Since there are many excellent reviews covering details of the most important analytical approaches (GC–MS, LC–MS, NMR; Allwood et al., 2011; Lei et al., 2011; Okazaki and Saito, 2012), respective technical issues and limitations will not be covered here.

Apart from technical problems, however, the complexity of the regulation of metabolite levels is a major challenge when working with metabolite profiles. In general, metabolites can be rapidly interconverted in enzymatic reactions, and individual metabolites often are the products and educts of several of such reactions (Fig. 1). This complex form of metabolic interconnections complicates recording and evaluation of metabolite profiles. An increased flux through a given metabolic pathway, for example, is not necessarily reflected by increased levels of respective intermediates. Increased levels of such intermediates do not necessarily indicate an increased flux through the pathway. Furthermore, each of the reactions producing or degrading a given metabolite may be regulated in a different way. Such regulatory processes may serve to adapt metabolism to outside conditions (e.g., to stress) or to intrinsic features of the plant (e.g., to the plant genotype or to the plant developmental status). Alternatively they may tend to maintain concentrations of metabolites within certain margins (homeostasis). One example for this latter kind of regulation would be feedback-inhibition, which can be observed for many biosynthetic pathways. The velocity of enzymatic reactions and of regulatory processes is responsible for the very dynamic behavior of metabolite profiles (“metabolic snapshots”, Okazaki and Saito, 2012).

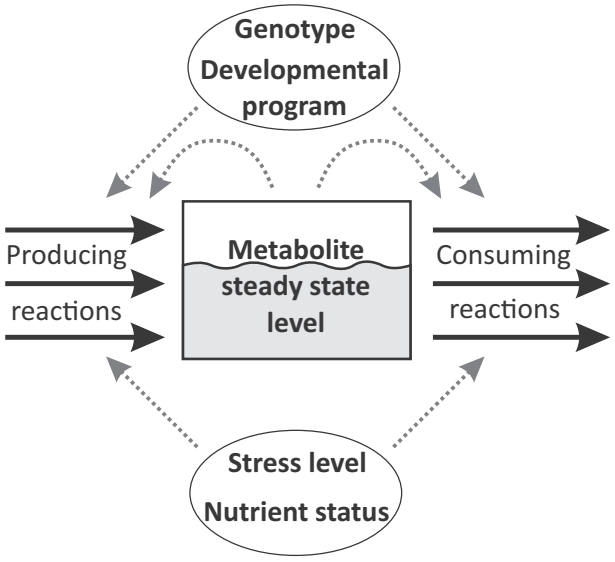

Fig. 1. Regulation of metabolite steady state levels: metabolites may be the products and educts of several enzymatic reactions (black arrows) differing in regulatory properties. Regulation (grey arrows) aims at maintaining metabolite levels within a certain range (regulation by metabolite levels) or to allow reactions of the organisms to endogenous (developmental program, genotype) or exogenous (stress, nutrient status) factors.

In summary, metabolite levels may be influenced by numerous exogenous or endogenous factors different from the one under study or they may be indifferent to the factor under study due to homeostasis. The very short time scale of metabolic reactions may work in favor of short-term, random factors and to the disadvantage of experimental treatments which usually are effective on a longer time scale. The implications of these four issues (exogenous, endogenous factors, homeostasis and time scale) for metabolite profiling experiments under field conditions will be discussed below.

2.1. Exogenous factors

As already outlined, levels of individual metabolites may be influenced by a large number of external factors like soil parameters or weather conditions. Even without this external variability, experiments using *Arabidopsis thaliana* under phytochamber conditions have demonstrated a relatively high variability in metabolite levels of about 40% when comparing individual plantlets (Fiehn et al., 2000). In field experiments Ossipov et al. (2008) observed a similar degree of variability when analyzing individual genotypes (between 10% and 50%) for most metabolites. Some metabolites, however, showed higher variability in this experiment (30 metabolites ranged between 50% and 90%, 5 ranged between 90% and 140%.) Particularly high variability was observed for some secondary metabolites known to respond to biotic or abiotic stress. Apparently, this factor had not been controlled completely in the experiments.

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