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Four examples demonstrating the impact of Applied Botany on plant-based industrial processes

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Summary

Currently, many producers of plant-derived commodities indicate a scarcity of associates whose skills cover the entire field of plant biology and who bolster industrial research by linking it to basic plant biology. This scarcity is of particular concern to small and medium sized companies.
To illustrate the benefit of appropriate mediation between basic science and product-oriented research, four innovative examples of collaborative research are presented here. The examples cover a broad range of economically relevant issues, including green coffee processing, malting, production of spice and medicinal plants, and prevention of contamination with toxic natural products, such as nicotine or pyrrolizidine alkaloids. These examples illustrate that Applied Botany has the potential to improve even well-established production processes.
This article argues that innovative product-oriented research must focus on the relevant physiological processes occurring in the plants. In particular, the impact of cultivation and post-harvest processes on related metabolic processes should be considered, rather than placing continued focus on physical parameters or on economic aspects. In order to achieve practical and feasible solutions that also meet economic demands, interdisciplinary and cross-functional approaches between partners are essential.

Keywords: Applied Botany; physiological processes; product quality; interdisciplinary work, feasible solutions

Applied Botany: Modern plant biology in the context of industrial research

Physiological processes determine the material composition and the variability of living organisms. The material composition is of particular interest because it determines the product quality of crops and plant-derived commodities. This applies to physiological processes occurring during plant growth and development as well as during postharvest treatment and further processing. Thus, physiological processes are directly linked to product quality.
In principal, numerous publications exist dealing with the influence of physiological processes on the quality of plant-derived products. A well-known example of the deliberate utilization of physiological processes to enhance plant growth and development is the use of carbon dioxide (CO_2) to fertilize plants in greenhouse cultivation. It is widely understood that raising atmospheric CO_2 concentration increases the photosynthetic rate (e.g., SCHOPFER and BRENNICKE, 2010), which results in higher plant productivity and greater yields. Related experimental trials have been performed with various crops, such as tomatoes (*Solanum lycopersicum*; e.g., WITTWER and ROBB, 1964; ZHANG et al., 2014), cucumbers (*Cucumis sativus*; e.g., ITO, 1973) and sweet peppers (*Capsicum annuum*; e.g. NEDERHOFF, 1994). For a review of this topic, see PRIOR et al., 2012. Due to the highly beneficial effects of enhanced atmospheric CO_2 concentrations, it is commonplace in industrial greenhouse production to apply elevated CO_2 concentrations.
While the impact of various growth and cultivation conditions on the quality of crops has been relatively well analyzed, knowledge regarding the effects of postharvest procedures and processing techniques on plant material is scarce. This is especially true for deliberate manipulations of physiological processes through alteration of complex processing techniques. However, a prominent exception can be found in the postharvest physiology of several economically relevant fruits. A common method to influence fruit ripening is the deliberate application of the plant signal transducer ethylene or, depending on the desired purpose, the prevention of its biosynthesis. Ethylene is known to induce fruit ripening and senescence processes, so it is frequently administered after fruit storage in order to induce and synchronize fruit ripening (e.g., CORNELIUS and BARRY, 2007; BAPAT et al., 2010). On the other hand, if the retardation of ripening processes is desired during fruit storage, the synthesis of ethylene is deliberately prevented by inhibiting the activity of the key enzyme in its biosynthesis, namely the 1-aminocyclopropane-1-carboxylic acid (ACC) synthase. Since ACC synthase is inhibited by high CO_2 concentrations (e.g., DE WILD et al., 2005), increasing CO_2 concentration in the storage compartment or during transport can prolong the shelf life of various fruits, such as apples, pears, bananas and tomatoes, up to several months (for a review, see PAUL and PANDEY, 2014).
However, in many other areas the underlying plant physiological processes have not been adequately considered, despite their tremendous relevance to product quality. Related activities stand isolated and no systematic approaches are available to exploit the potential of physiological processes. This deficit is particularly clear in the development of alternative cultivation and postharvest processing techniques. One reason for overlooking basic plant physiological aspects may be that engineers involved in industrial research are primarily trained in technical subjects. Scientists exhibiting comprehensive experience in plant physiology as well as ample knowledge of metabolic processes are quite rare. Moreover, economic aspects often play a superior role. Producers are driven to optimize processing methods mainly due to economic considerations, while lower importance is placed on considerations of plant physiology. A further issue restraining industrial research is the limited availability and readiness of sophisticated plant biological laboratories to analyze fundamental and basic physiological processes. This is particularly restrictive for small and medium sized companies, which frequently are not capable of performing the necessary sophisticated and expensive molecular-biological, biochemical and phytochemical techniques. Moreover, in many cases even awareness of the relevance of physiological processes for product quality is lacking.
In addition, it is worth noting that the flow of knowledge between plant basic science and industrial applied research is very limited. The poor exchange between the sectors may be due to a lack of connection and communication platforms. In exaggerated terms, many plant scientists perch in a kind of ivory tower of basic science, while companies emphasize the protection of intellectual property rights and the thwarting of competitors. In this regard, a modern Applied Botany that is focused on plant physiology has the potential to act

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as a mediator for the transfer of botanical knowledge and analytical methods from basic plant science to industrial research, and *vice versa*.

As mentioned previously, further research is needed that focuses on the metabolic impacts of cultivation and postharvest production processes on the quality of plant-derived commodities. Improved understanding of plant physiological processes and their regulation is an important tool to improve product quality. Accordingly, the relevant processes should be analyzed thoroughly using modern plant biological methods such as genomic, proteomic and metabolomic approaches.

This, however, requires combining the expertise of plant physiologists and industrial researchers. Interdisciplinary and cross-functional project committees, consisting of plant biologists and industrial representatives, should be formed to define objectives, evaluate results and elaborate corresponding solution strategies. Continuous interdisciplinary exchange and collaboration promotes the development of solutions to ongoing problems and ensures rapid transfer into practice. In the next section, four innovative approaches in modern Applied Botany highlight how the application of basic plant physiology can improve traditional industrial production processes and the quality of the plant-derived commodities produced.

Exemplification of the ample capabilities of Applied Botany

As outlined above, the quality of plant-derived commodities can be modulated by altering either the conditions of plant growth (preharvest) or those of postharvest processing. However, in many cases no clear differentiation can be made. For example, malting of barley and processing of green coffee are frequently characterized as postharvest seed treatments; however, with respect to germination and seedling development, they in principle represent pre-harvest processes. In addition to these instances, whose denomination as pre- or post-harvest process seems to be problematic, two further examples are described that represent unambiguously pre-harvest processes. These are the impact of drought stress to increase the quality of medicinal and spice plants and the horizontal transfer of natural plant products as a source of contamination.

Drought stress: Optimizing the cultivation of medicinal and spice plants

It is well known that spice and medicinal plants grown in the Mediterranean region produce a more intense flavor than the same plants cultivated in Central Europe. It may be tempting to explain this phenomenon by the much higher light intensity in the Mediterranean area, but from the perspective of a plant physiologist, this deduction can be ruled out because even in Central Europe plants are generally exposed to an excess of light (Wilhelm and Selmar, 2011). However, another factor that differs markedly between Central and Southern Europe corresponds to the water supply. A comprehensive literature survey revealed that in many plant species drought stress causes enhanced concentrations of secondary metabolites, and that in many cases also their overall contents are increased (Selmar and Kleinwächter, 2013a). Until recently, a sound scientific rationale for this common phenomenon was lacking. Today the basic relation is understood: water shortage induces stomata closure, which strongly reduces CO_2-influx into the leaves. As result, far fewer reduction equivalents ($NADPH+H^+$) are consumed and re-oxidized via the Calvin cycle. Despite the fact that the various energy dissipating mechanisms are up-regulated, the reduction status of the chloroplasts increases significantly. In consequence, the ratio of $NADPH+H^+$ to $NADP^+$ is greatly increased, and, according to the law of mass action, all processes consuming $NADPH+H^+$ (e.g., the biosynthesis of highly reduced secondary plant products) will then be favoured even without any change in enzyme activity (Selmar and Kleinwächter, 2013a). These fundamental plant physiological considerations have been verified by ingenious drought stress experiments employing sage (*Salvia officinalis*) as a model plant (Nowak et al., 2010). The exogenous CO_2 concentration was varied to compensate for the stress-related decrease of endogenous CO_2 concentration. In consequence, the over-reduction related to drought stress was decreased, and accordingly, the stress-related increase in biosynthesis of secondary plant products (monoterpenes) was diminished.

Based on these findings, general cultivation practices for the production of medicinal and spice plants exhibiting enhanced contents of natural products have been elaborated (Selmar and Kleinwächter, 2013b; Paulsen et al., 2014; Bloem et al., 2014, Kleinwächter et al., 2015). By deliberately inducing drought stress, either by reducing irrigation or by enhancing drainage, the quality of spice and medicinal plants can be improved. Another approach, which is directly derived from this nexus and is very promising with respect to the "non-arid" conditions prevailing in Central Europe, concerns the application of methyl jasmonate (Me Ja). Analogous to drought, the application of this signal transducer should induce stress-related metabolic responses, including the increased content of secondary plant products. Similar approaches have already been successfully introduced for the cultivation of grapevines (*Vitis vinifera* L.). Vezulli et al. (2007) demonstrated that Me Ja treatment significantly increased the resveratrol content in cultivated grapes. These results have been verified by corresponding experiments employing nasturtium (*Tropaeolum majus* L.) in which the Me Ja application resulted in an increase in glucosinolate content of more than 70% (Bloem et al., 2014). Meanwhile, this approach was also successfully scaled-up to field conditions. Consequently, the next step would be the approval of a corresponding preparation for commercial use.

Horizontal natural product transfer: Contaminations of tea, spice and medicinal plants with nicotine and pyrrolizidine alkaloids

The contamination of plant-derived commodities, such as herbal teas, spices and phytopharmaceuticals, with toxic natural products, like nicotine and pyrrolizidine alkaloids (PAs), is a great challenge for producers and the processing industry (EFSA, 2011; BfR, 2013). In the case of PAs, one putative path of contamination has been identified, the mistaken co-harvesting of PA-containing weeds, but the source of nicotine contamination was fully unknown until recently. Similar to the well-known uptake of organic xenobiotics (e.g., Trapp and Legind, 2011), it was assumed that the alkaloidal contaminations could result from the uptake of these natural products from the soil. By applying cigarette tobacco to the soil of various experimental plants, this hypothesis was proven; all plants took up high amounts of the alkaloid leached out from the decaying tobacco (Selmar et al., 2015). In order to outline the relevance for practical application, this issue was also investigated under field conditions. It was illustrated that even one discarded cigarette butt per square meter is sufficient to generate nicotine concentrations in the acceptor plants ten times higher than the allowed maximum residue level (Selmar et al., 2018). In consequence, any discarding of cigarette butts in the fields has to be prevented, especially when extensive manual work is required in regions where smoking is common. Accordingly, this practice needs to be included in the code of Good Agricultural and Collection Practice (GACP).

Similar to the uptake of nicotine, plants also import PAs in significant amounts from the soil. Corresponding studies have revealed that the application of only 1 g of dried PA-containing plant material to the soil surface results in contaminations of up to 500 µg/kg dry weight in all plants grown in the vicinity. In consequence, these plants cannot be utilized as phytopharmaceuticals (Nowak et al., 2016). These findings have important implications for weed management. When PA-containing weeds (e.g., *Senecio vulgaris* L.) are killed with herbicides or hoed up, the plant material must be removed from the fields in order to prevent any PA transfer to the crop plants and thus entrance of PAs into the food chain. Based on these insights, the immediate removal of toxic weeds has already become common practice for producers of spice and medicinal plants. For instance, large firms such as the Martin Bauer Group and Waldland International instantly adopted this approach and now insist on the removal of PA-containing weeds from the fields.

Recent studies have revealed that the translocation of natural products from decaying plant materials into other plant species is a common occurrence that depends primarily on the physicochemical properties of the compounds, specifically membrane permeability and solubility (Selmar, Radwan and Nowak, 2015). In analogy to horizontal gene transfer, the interspecific transfer of natural products has been denoted as "horizontal natural product transfer." It is important to be aware that apart from nicotine and PAs many other natural products leached out from decomposing plant materials represent potential sources of further contaminations. In this regard, it is noteworthy that the European Food Safety Authority (EFSA) recently published a survey on the occurrence of tropane alkaloids in herbal teas (EFSA, 2018).

It is a well-known feature in chemical ecology that plants release allelochemicals in the soil, which can affect the germination and growth of competing plants in the vicinity (e.g., Bertin, Yang and West, 2003; Kalinova, Vrchotova and Triska, 2007). Accordingly, a direct transfer of allelochemicals between living plants has to be assumed. Despite this well-established knowledge, a corresponding transfer of natural products that do not have an allopathic effect, was not taken into consideration by industry as a potential contamination source. Meanwhile, it was demonstrated that not only rotting plant materials but also living plants can act as PA donors (Selmar et al., 2018). Accordingly, the concept of horizontal natural product transfer was extended.

Indeed, up to now, the exact mechanism of transfer is still unknown. However, co-culture experiments with ragwort (*Senecio jacobaea*) and parsley (*Petroselinum crispum*) clearly demonstrated that the alkaloids are transferred via the soil, either due to an active exudation or as a result of minor injuries to the roots. With respect to the prevention of contamination, these results indicate that current weed management needs to be improved: instead of hoeing PA-containing weeds, they should be extracted entirely, including the roots, and removed from the site. The corresponding transfer into practical application is currently on the way.

In addition to the relevance for contamination of plant-derived commodities, the phenomenon of horizontal transfer of natural products may have significance for basic plant biology and agricultural production in general. With respect to agricultural practices, it may improve understanding of various hitherto unexplained effects in agricultural practice, such as the benefits of crop rotation and co-cultivation.

Germination and stress: Metabolic changes in coffee seeds during green coffee processing

Just like oil, wheat or soybeans, coffee represents one of the top ten commodities in global trade. In the past, green coffee, the tradable seeds of the coffee tree (*Coffea arabica* L.), had always been regarded as inanimate plant material. In the coffee processing industry, only the basic chemical and physical parameters had been considered in the approaches developed to increase product quality. This perspective applied to all aspects of green coffee processing, including postharvest treatments like depulping and drying. In contrast, the perspective of plant biologists is quite different, and the various metabolic reactions of green coffee are in the center of focus. With respect to germination physiology, one has to be aware that the seeds of tropical plants are not dormant (e.g. Pammenter and Berjak, 2000; Chin, 1978). Accordingly, as soon as they are exposed to favorable conditions, they will germinate. Moreover, any decrease in the water content of vital cells (e.g., during drying) induces various metabolic stress responses (Radwan et al., 2014). Substantial research on this topic was triggered by the elucidation of well-known quality differences between wet and dry processed green coffees. Since the conditions affecting metabolic responses are quite different in each type of processing, the underlying metabolic bases were intensively studied. It was revealed that in the first phases of raw coffee processing, especially in the course of wet processing, the seeds do indeed germinate (Selmar and Bytof, 2006). Subsequently, depending on the speed of the drying, drought stress induced metabolic responses are dominant and substantially change the composition of the coffee beans (Knopp et al., 2006; Kleinwächter and Selmar, 2010; Kramer et al., 2010). As consequence of these plant physiological insights, a paradigm change in the coffee producing industry was initiated (Selmar, Bytof and Kleinwächter, 2014). Nowadays, it is common knowledge that raw coffee seeds are living organisms with an active metabolism, offering great potential for quality improvement (Selmar and Bytof, 2006; Kleinwächter and Selmar, 2010). It is intriguing to realize that by understanding and considering the plant's physiology, it became possible to deliberately change composition of green coffee by altering the processing conditions. Thus, plant physiology was the key for improvement of green coffee quality by altering conditions impacting the most relevant aroma precursors (Kleinwächter, Bytof and Selmar, 2014). Meanwhile, such approaches led to physiologically based optimizations of various steps in coffee processing in order to improve the aroma potential of raw coffees (Kleinwächter, Bytof and Selmar, 2014). A relevant example for the successful implementation of plant physiological knowledge into green coffee processing practice concerns the modification of the so-called BECOLSUB process. This type of green coffee processing falls in between the classic dry and wet processing. Similar to wet processing, the coffee cherries are depulped; however, the fermentation step, which is responsible for the degradation of residues of the fruit flesh, is substituted by mechanical removal of the sticky pulp. Because of its economic advantages, coffee producers immediately favored this procedure. Unfortunately, the quality of the corresponding coffees was far lower than that of the wet fermented ones. Based on this research, it was possible to predict that additional storage of the mechanically cleaned beans could solve this problem. Today, such interim storage is implemented worldwide by coffee producers.

Germination and stress: The impact of malting on the physiology of barley seedlings

Archeological findings indicate that malting and beer brewing was practiced in ancient Egypt. Thus, the malting process surely is one of the oldest techniques invented for food processing. One of the basic ingredients of beer apart from yeast and hope is malt. Malt is produced by germination of cereal seeds, like barley (*Hordeum vulgare* L.). The malting process can be divided into three steps; the steeping, the germination and the kilning. In the first step, the seeds are imbibed for several hours in water in order to induce seed germination. Then, the germination process induces the mobilization of starch and the breakdown of cellular structures. In the final malting step, the germination process is terminated by drying the seedlings in kiln ovens. The high temperatures in kilning are responsible for the generation of the typical color and flavor compounds of malts (for detailed information on malting, refer to Kunze, 2010; Narziss, 1999).

As previously noted, the malting process is among the earliest food processing techniques established by man. Despite its long history, many unanswered questions remain if one starts to analyze the processing through the eyes of a plant physiologist. With respect to malting physiology, the most intriguing issue concerns the role and impact of CO_2. Plant physiologists consider CO_2 an inert gas that is the limiting factor of the photosynthesis. In contrast, in the malting business CO_2 is considered a toxic compound that has to be efficiently removed from the seedling by excessive aeration. In order to explore this contradiction and to elucidate the actual impact of CO_2 during malting, the relevant physiological processes occurring in the barley seeds in the steep tanks were analyzed. As expected, it was demonstrated that CO_2 does not exhibit any toxic effects. However, high concentrations of this gas severely inhibit the biosynthesis of germination-related enzymes, although the seeds are still viable even after being incubated under extremely high CO_2 concentrations (Kleinwächter, Meyer and Selmar, 2012). Indeed, up to now, the exact mode of action is still unknown, but there are some indications of possible competitive interactions between oxygen and CO_2 (Kleinwächter, Meyer and Selmar, 2012).

Another important problem in industrial-scale malting comes from biochemical heterogeneities in the malt. These variations result in asynchronous degradation of carbohydrates. In consequence, insufficient hydrolysis of galactomannans located in the cell wall causes severe problems in the brewing process by blocking filters during lautering (Palmer, 2000; de Sá and Palmer, 2004). Based on comprehensive analyses of the physiological processes occurring in the barley seeds during malting, the biochemical background of these heterogeneities was unveiled. The combination of high layers of malt beds (3-4 m) and inhomogeneous aeration in the steeping tanks causes significant spatial differences in the partial pressures of oxygen and carbon dioxide (Kleinwächter et al., 2014). As consequence, the progression of germination differs, creating large biochemical heterogeneities. In conclusion, the primary cause of insufficient hydrolysis of galactomannans, and thus the blockage of filters during lautering, is related to asynchronous germination depending on position in the steep tank. Accordingly, simple modifications in the process control (changes in the extent of aeration and enhancement of the steeping temperatures) enable the production of malts exhibiting enhanced homogeneity (Kleinwächter et al., 2014; Müller et al., 2013). This example clearly demonstrates that even well-established processes can be optimized by transferring basic plant physiology knowledge into industrial research. In this sense, it may be worth revisiting other well-established production processes through the eyes of a plant physiologist.

Conclusions

These four examples highlight that plant physiological processes play a key role in the quality of plant-derived products. Consequently, an increased understanding of the relevant processes enables deliberate improvement of product quality. Yet, it is not sufficient to focus solely on physiological process. Rather, the greatest improvements can be made by comprehensively considering plant metabolism and its complexity in a systemic manner, especially in interaction with the environment.

In addition, these examples demonstrate that the transfer of basic plant science knowledge into industrial research could initiate strong impulses for product-related research. This even accounts for traditional and well-established processes, as has been clearly illustrated for the malting process. Continuous interdisciplinary work and collaboration in project committees can enable the development of feasible and economically acceptable solutions that are directly transferable into practice.

Apart from the basic scientific approaches, a great challenge is the implementation of new concepts and ideas into product-related research. One future goal is to optimize knowledge transfer. Thus, modern Applied Botany should seek to act as a mediator between basic plant science and industrial product-related research.

In order to support sophisticated applied botanical approaches in Germany, reconsideration of research funding practices and of the evaluation of scientific performance is required. Indeed, the Deutsche Forschungsgemeinschaft (DFG) offers a variety of research programs that unfortunately are not available for applied research. Moreover, when scientific performance is evaluated on the basis of funding raised, DFG projects are frequently rated two times better than projects funded by other sources. In this regard, a new approach is required to achieve the same support for basic and applied research.

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