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Comment on Chemical Ecology in Wheat Plant–Pest Interactions. How the Use of Modern Techniques and a Multidisciplinary Approach Can Throw New Light on a Well-known Phenomenon: Allelopathy

Sir: Recently, Formsgaard, Macías et al., and Mathiassen et al. evaluated the usefulness of natural wheat (*Triticum aestivum* L.) allelochemicals as a tool to control weeds and other pests in agricultural fields (*1*−*3*). The preface by Formsgaard (*1*) also summarized the achievements of an international project, FATEALLCHEM, that was funded by the European Union. I realize that the results of the project may be the most significant recent advance in the science of allelopathy in agricultural ecosystems. Unfortunately, I must disagree with one of the major conclusions of FATEALLCHEM. I do not understand why Formsgaard (*1*) and Mathiassen et al. (*3*) conclude that future research should include the utilization and development of “varieties with maximum production of benzoxazinones”. I have several concerns that I divide into three categories.

First, Staman et al. (*4*) has found evidence that soil microorganisms may acclimate rapidly to metabolize allelochemicals that occur in soil at high concentrations. Thus, if large amounts of benzoxazinones are released continuously to the wheat rhizosphere, acclimated soil microbes may degrade a significant proportion of toxin molecules. This may override the benefits of maximum production of benzoxazinones in weed control. In addition, there is strong evidence that soil bacteria may adapt genetically to degrade xenobiotic toxins that suddenly become common and persist in growth substratum (*5*). I do not see any reason why this could not happen with natural allelochemicals if varieties with an extraordinarily high release capacity are cultivated. On the contrary, because varieties with maximum production of benzoxazinones are likely to contain and release benzoxazinones throughout the growing season, genetic adaptation may be faster than in case of synthetic herbicides that are added to agricultural fields infrequently (*6*, *7*). Therefore, I do not believe that current varieties can be utilized to estimate how efficiently a hypothetical, chemically aggressive wheat variety can inhibit weed growth.

Second, I do not understand why coevolution between cereals and their pests was not considered in the three papers mentioned above (*1*−*3*). Plants tend to adapt to novel allelochemicals if these are present in soil continuously (*8*−*10*). In the specific case of benzoxazinones, Schulz and Wieland (*11*) have proposed that many common weeds have coevolved with the meadowgrass family (Poaceae) to grow vigorously in the presence of benzoxazinones. This could have been taken into account by Mathiassen et al. (*2*) and Macías et al. (*3*), especially because “target effects” was one of the Work-packages in the FATEALLCHEM project (*1*). The authors could have studied the same target species as Schulz and Wieland (*11*) did, or they could have considered for how long their target species have lived in the same plant community with species containing benzoxazinones. Then, the coevolution hypothesis by Schulz and Wieland (*11*) could have been supported or disproved. If the hypothesis had been supported, maximum production of benzoxazinones might have appeared to be ineffective for controlling weed growth. Now, a conscientious reader may conclude that the whole possibility was neglected in FATEALLCHEM.

Third, because benzoxazinones and their derivatives contain nitrogen, wheat and other cereals may have a tradeoff between benzoxazinone production and growth. Whereas nitrogen is tightly bound in many benzoxazinone derivatives, 2-aminophenol contains an NH_2 group that may be separated from the rest of the molecule relatively easily. In fact, Takenaka et al. (*12*) have presented convincing evidence that *Pseudomonas* sp. AP-3 can metabolize 2-aminophenol to 3-aminophenol and further to pyruvic acid, which does not contain nitrogen. Pyruvic acid is needed in cellular metabolism in most organisms, including all animals and plants. 2-Aminophenol is also a precursor of 2-aminophenoxazin-3-one (APO) (*13*). APO is a very toxic benzoxazinone derivative studied by Macias et al. (*3*), but the authors excluded it as a practical herbicide model due to its high persistence in soil. If enhanced production of benzoxazinones has a genetic basis, the degradation of benzoxazinones may lead to higher and relatively constant levels of APO and other compounds that are not suitable for use as herbicides (*7*). In this respect, the use of species’ natural defense compounds may be a more complicated issue than the use of xenobiotic and transgenic pest management strategies (*14*). For all of these reasons, before cereal varieties with maximum production of benzoxazinones are developed, it is essential to study whether weeds or other pests are able to utilize benzoxazinone derivatives, and which degradation pathways are favored if benzoxazinone levels are enhanced.

Due to these concerns, I unfortunately have to cast doubt over the idea that maximum production of benzoxazinones is a

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proper way to fight pests. Instead, because certain simulations suggest that adaptation to toxins may be delayed if phytotoxin levels vary unexpectedly, I would search for varieties that can exude phytotoxins at irregular intervals (6, *10*, *15*). Although chaotic production and release of benzoxazinones may be an unrealistic research objective, certain commercially available chemicals could be applied to induce benzoxazinone production (*16*). A successful pest management strategy might also include the enhancement of temporal variation in benzoxazinone production. Such natural variation results from biotic attacks and changes in abiotic growth conditions (*17*).

To summarize, it is easy to agree with Formsgaard (*1*) that a framework for future assessments of allelopathic crops must include the development of validated analytical methods, considerations of relevant concentrations, and soil transformation studies. However, I emphasize that relevant concentrations should not be stable and that it is worthwhile to search for optimal strategies of production and release, not for maximum production and release. The ecological and evolutionary responses of soil biota to the altered release of phytotoxins must also be understood. Despite the concerns presented above, I confirm that the FATEALLCHEM project has been a necessary and highly successful step toward deeper understanding of allelopathy.

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