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Responses of soil enzymatic activities to transgenic *Bacillus thuringiensis* (Bt) crops - A global meta-analysis

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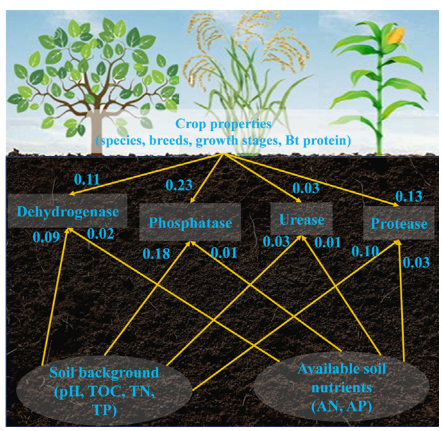
HIGHLIGHTS

- The dehydrogenase and urease generally positively responded to Bt crops.
- Residue incorporations following Bt crop harvest elicited stronger response ratios.
- The significant responses usually appeared under Bt cotton or in middle growth stages.
- The enzymatic responses ascribed more to Bt crop properties than to soil properties.

GRAPHICAL ABSTRACT



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ABSTRACT

Transgenic *Bacillus thuringiensis* (Bt) crops have been widely planted, and the resulting environmental risks have attracted extensive attention. To foresee the impacts of Bt crops on soil quality, it is essential to understand how Bt crops alter the soil enzymatic activities and what the important influencing factors are. We compiled data from 41 published papers that studied soil enzymatic activities with Bt crops and their non-Bt counterparts. The results showed that dehydrogenase and urease significantly increased, but neutral phosphatase significantly decreased under Bt crop cultivations without Bt residues incorporation. The activities of dehydrogenase, β-glucosidase, urease, nitrate reductase, alkaline phosphatase, and aryl sulfatase significantly increased under Bt crop cultivation with Bt residues incorporation. The response ratios of other enzymes were not significantly changed. Generally, the response ratios of soil enzymes were greater with Bt residues incorporation than those of Bt crop cultivations without Bt residues incorporation. Further, the response ratios of soil enzymes varied with Bt crop types and growth periods. It was the strongest under Bt cotton among Bt crops, and the significant responses usually

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Growth stages
Dehydrogenase

appeared in the middle growth stages. The responses of soil enzymes ascribed more to the properties of Bt crops than to soil properties across sites. Given - significant responses of some soil enzymes to Bt crops, we recommended that soil environmental risks should be carefully evaluated over the transgenic crops.

1. Introduction

Transgenic *Bacillus thuringiensis* (Bt) crops refer to crops that have been genetically modified to express the insecticidal protein to guard against the feeding from target pests. Since their appearance in the 1990s, Bt crops have been widely planted over the last two decades due to their benefits for agriculture, such as the reduction of pesticide usage (Huang et al., 2010; Qaim and Zilberman, 2003) and management labor (Huang et al., 2005), as well as the increases in grain production (Pray et al., 2001; Xia et al., 2011). The Bt crops account for a considerable proportion of total crops, 80% for cotton and 32% for maize (James, 2017). The total area of Bt crops has amounted to 2.3 billion hectares (James, 2017), which is mostly located in the United States, Brazil, Argentina, India, Canada, and China. The area is anticipated to increase in future (Parisi et al., 2016), as many Bt rice breeds are in the pipeline for commercialization. However, the resultant environmental risks have aroused increasing concerns (Andow and Zwahlen, 2006; Dale et al., 2002; Wolfenbarger and Phifer, 2000; Romeis et al., 2008), particularly on soil quality (Mendelsohn et al., 2003; Saxena et al., 1999; Saxena and Stotzky, 2001).

The enzymes catalyze the biogeochemical processes in soil, such as the urease and phosphatase participate in nitrogen and phosphorus cycles, respectively, and the dehydrogenase could mirror the metabolic activity of soil microbes. The changes in activities of soil enzymes are crucial for soil quality (Karlen et al., 2001; Bastida et al., 2008). Moreover, alterations in the soil enzymatic activities are considered as early warning indicators of soil quality (Bergstrom et al., 1998; Garcia-Ruiz et al., 2008) due to their high sensitivity to environmental changes (Dick, 1994; Geisseler and Horwath, 2009; Roldan et al., 2005). Over the last two decades, a significant number of studies have examined the influences of Bt crops on soil enzymatic activities (Mina et al., 2011; Shen et al., 2006; Singh et al., 2013; Velmourougane and Sahu, 2013). For instance, Bt crops increased the activities of soil enzymes, e.g., dehydrogenase (Mina et al., 2011); however, they have no effect on nitrate reductase activities (Philippot et al., 2006), which implies different responses of soil enzymes to Bt crops. Further, the activities of phosphatase (Sarkar et al., 2009) increase in response to Bt cotton, but they are not changed by Bt rice (Fang et al., 2012), which implies that the responses of soil enzymes might vary with Bt crop types. However, we have a very limited understanding of the general response patterns of soil enzymes to Bt crops, which impede an accurate assessment of the environmental risks that they pose.

The responses of soil enzymes to Bt crops may be contingent on the amount of Bt protein and the quality and/or quantity of enzymatic substrates. First, under Bt crop cultivation, the residues on the soil surface may or may not be incorporated into the soil, which results in different amounts of Bt protein and substrate inputs. This suggests that there might be different responses in soil enzymatic activities with or without residues incorporation. Second, the amount of Bt protein is generally more in cotton (up to 56.1 ng g^{-1} dry soil; Yang et al., 2012) than in other crops (e.g., 1.5 ng g^{-1} dry soil for rice; Wang et al., 2013); suggesting the response of soil enzymes may vary with different Bt crops. Third, the contents of soil Bt protein are greater during the middle growth stages in contrast to the early growth stages (Olsen et al., 2005; Xiao, 2013). There are also relatively more substrates from root exudation during the middle growth stages (Aulakh et al., 2001). These suggest that the responses of soil enzymes may change in different growth stages. Based on these characteristics, we hypothesized: (1) the effects of Bt crop cultivation with Bt residues incorporation on soil enzymes would be greater than those without Bt residues incorporation; (2) the effects of Bt cotton on soil enzymes would be stronger than those of other Bt crops; (3) the significant responses of soil enzymes are more likely to be observed in middle growth stages in comparison with other growth stages.

Aside from Bt crops, the response ratios of soil enzymatic activity may also strongly correlate to the soil physical-chemical properties (Garcia-Ruiz et al., 2009; Haynes, 1999). The activities of acid phosphatase and glucosidase increased with higher soil nitrogen content, while alkaline phosphatase, amidase, and urease decreased with higher soil nitrogen (Dick et al., 1988). Higher soil organic matter content could stimulate the activities of urease, alkaline phosphatase (Goyal et al., 1999), and aryl sulfatase (Dick et al., 1988). However, the relative importance of soil properties and Bt crop properties to the response ratios of enzymatic activities has not yet been quantified. We hypothesized that soil properties may play a less important role than do Bt crop properties on the changes in soil enzymatic activities.

To test the above hypotheses, we conducted a meta-analysis to comprehensively examine the responses of soil enzymatic activity to Bt crops. Specifically, we initially quantified the responses of soil enzymatic activity to Bt crop cultivations with or without Bt residues incorporation. Subsequently, we explored how the responses of soil enzymatic activity varied across Bt crops or in different growth periods. Finally, by analyzing the relationship of the response ratios of soil enzymatic activity with Bt crops and soil physical-chemical properties we unraveled the relative contributions on the responses.

2. Materials and methods

2.1. Database compilation

Data were compiled by retrieving all published scientific literatures that investigated the effects of transgenic crops on soil enzymatic activities using the Web of Science (http://apps.webofknowledge.com) and China National Knowledge Infrastructure Database (http://www.cnki.net/) prior to July 1, 2017. The treatments are Bt crop cultivations and non-Bt crop cultivations. The criteria for selecting the appropriate observations to construct our database were:

(1) studies were conducted to detect the effects of Bt crops on soil enzymatic activities including intracellular enzymes (dehydrogenase, catalase, nitrate reductase, and nitrite reductase) and extracellular enzymes (β-glucosidase, invertase, polyphenol oxidase, urease, protease, acid phosphatase, alkaline phosphatase, neutral phosphatase, phosphomonoesterase, phosphodiesterase, and aryl sulfatase) either in the field or greenhouse;
(2) the management in treatments were the same except for crop breeds (Bt crop vs. non-Bt counterpart);
(3) experiments with the duration being more than one growing season;
(4) mean enzymatic activities, standard deviations (or standard errors), and sample sizes were provided in the text, tables, and/or figures.

Using these criteria, we obtained 41 published papers that encompassed cotton, maize, and rice. The following variables, if available, were also obtained from original literatures: locations, soil texture, pH, total organic carbon (TOC), total nitrogen (TN), total phosphorus