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Review

Breeding of ozone resistant rice: Relevance, approaches and challenges

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ABSTRACT

Tropospheric ozone concentrations have been rising across Asia, and will continue to rise during the 21st century. Ozone affects rice yields through reductions in spikelet number, spikelet fertility, and grain size. Moreover, ozone leads to changes in rice grain and straw quality. Therefore the breeding of ozone tolerant rice varieties is warranted. The mapping of quantitative trait loci (QTL) using bi-parental populations identified several tolerance QTL mitigating symptom formation, grain yield losses, or the degradation of straw quality. A genome-wide association study (GWAS) demonstrated substantial natural genotypic variation in ozone tolerance in rice, and revealed that the genetic architecture of ozone tolerance in rice is dominated by multiple medium and small effect loci. Transgenic approaches targeting tolerance mechanisms such as antioxidant capacity are also discussed. It is concluded that the breeding of ozone tolerant rice can contribute substantially to the global food security, and is feasible using different breeding approaches.

1. Introduction

Despite decades of international policy efforts to mitigate global change, world-wide combustion of fossil fuels is continuing at a high level, and will presumably continue to rise for decades, especially in transitional economies and developing countries (IPCC, 2014). This trend poses numerous problems to agricultural production, which faces the challenge of feeding a world population of more than nine billion people by the end of the 21st century, of which almost eight billion will live in less developed countries (United Nations, 2014). Anthropogenic climatic change is associated with various abiotic stresses negatively affecting crops, such as heat, drought, salinity, and submergence, which will occur at higher frequency and cause unpredictable crop yield losses (Battisti and Naylor, 2009; Brown and Funk, 2008; Wassmann et al., 2009). Moreover, the combustion of fossil fuels is a major source of air pollution, which affects both human health and plant growth. Tropospheric ozone constitutes the most widely recognized air pollutant affecting crop yields (Ashmore et al., 2006; The Royal Society, 2008; Van Dingenen et al., 2009). Ozone is formed in the troposphere from precursor pollutants such as nitrous oxides (NO_X), carbon monoxide (CO), and volatile organic compounds in photochemical reactions favored by high solar radiation and high temperatures (The Royal Society, 2008). Ozone concentrations below 40 ppb are usually not considered to affect crop yields, but this threshhold is often exceeded during warm and sunny days when sufficient ozone precursors are available (The Royal Society, 2008). Due to the rapid formation and decomposition of ozone in the atmosphere, its concentration often follows a diurnal pattern with a peak occurring in the early or late afternoon (Naja and Lal, 1996). It is taken up into the plant leaves during photosynthetic gas exchange and decomposes into reactive oxygen species (ROS) in the apoplastic space. This causes cell death (necrosis) due to direct oxidative damage, or due to programmed cell death processes stimulated by ozone (Kangasjarvi et al., 2005; Rao and Davis, 2001). Moreover, ozone hampers photosynthetic activity via stomata closure and loss of the activity of the photosynthetic enzyme Rubico (Wilkinson et al., 2012). Together, these effects lead to biomass losses in both natural vegetation and agricultural crops (Fiscus et al., 2005). Besides yield losses, changes in the quality of agricultural crops due to ozone exposure have been reported, such as increases in protein concentration of cereal grains (Frei et al., 2012a; Piikki et al., 2008b; Wang and Frei, 2011), and deterioration of the feed value of forage crops (Frei et al., 2011; Muntifering et al., 2006; Wang and Frei, 2011).

The most sustainable long-term strategy to alleviate the effects of tropospheric ozone on agricultural crops (and human health)

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would certainly be to reduce air pollution. Because transboundary and even intercontinental export of ozone and its precursors occurs (Lin et al., 2010), this would require internationally coordinated legislation to reduce emissions from diverse sectors such as industry, transportation, agriculture, private energy consumption, etc. (The Royal Society, 2008). In many developed countries (especially Europe, North America, and Japan), such policies have been adopted for several years, which has lead to stagnating or even reduced ozone precursor emissions (Oltmans et al., 2013). However, various emission scenarios suggest that precursor levels (especially methane and other VOC) may continue to rise in many parts of the world in the coming decades (The Royal Society, 2008; IPCC, 2014), leading to regional hotspots of ozone pollution (Jacob and Winner, 2009). Areas likely to experience rising ozone levels until 2050 include large parts of Asia, the Middle East, Africa, and South America (Lei et al., 2012; The Royal Society, 2008). Therefore, adaptation of crop production to rising levels of ozone is required as a mid-term strategy to avoid yield losses, and to ensure food security in those highly populated parts of the world. This could be done by shifting crop calendars to avoid major episodes of high ozone pollution, but a modeling study suggested that this measure had little effect on a global scale (Teixeira et al., 2011). A second option would be to breed crops, which are better adapted to high ozone levels.

This review outlines the relevance, approaches and challenges in adapting rice – arguably the world's most important food crop – to rising tropospheric ozone levels by breeding of adapted varieties. In this context, rice is a particularly relevant crop species because among the countries projected to experience excessively high ozone levels in the coming decades are Asia's largest rice producers with billions of consumers depending on rice as their daily staple food.

2. Tropospheric ozone in Asian rice producing countries

In the past decades, large parts of Asia have experienced both rapid economic and population growth. As a result, Asia has been the continent with the fastest growth in fossil fuel consumption and consequently soaring emissions of greenhouse gases and ozone precursors (IPCC, 2014). Recent patterns of tropospheric ozone mixing ratio in Asia derived from satellite-based measurements (Ziemke et al., 2006) are shown in Fig. 1 for the year 2013 and in Supplementary Fig. S1 for the year 2012. These figures suggest that tropospheric ozone concentrations are relatively low from November to January in most parts of Asia, but increasing pollution is observed during the rest of the year with some regional differences. Generally the ozone pollution patterns in Asian countries can be classed into three regional catagories as detailed below, and severe damage to rice production can be expected when peak ozone episodes overlap with critical growth stages of the rice crop.

2.1. South Asia

On the Indian subcontinent (including Myanmar) the pollution level is generally severe. The highest values are observed during March to May, while the onset of the monsoon leads to climatic conditions, which are less conducive to ozone formation (Engardt, 2008) (Fig. 1). Surface measurements in urban, semi-urban and rural sites in western India confirmed that the onset of the monsoon led to general decreases in tropospheric ozone levels and an almost complete offset of diurnal ozone patterns, while the highest pollution levels were seen in late winter and spring, *i.e.* February to April (Beig et al., 2007; Debaje et al., 2010; Naja and Lal, 1996). Ship-based measurement over the Bay of Bengal indicated sudden increases of ozone concentrations in the post-monsoon period from October to November (Mallik et al., 2013). The highest concentrations in that study were observed in the northern Bay

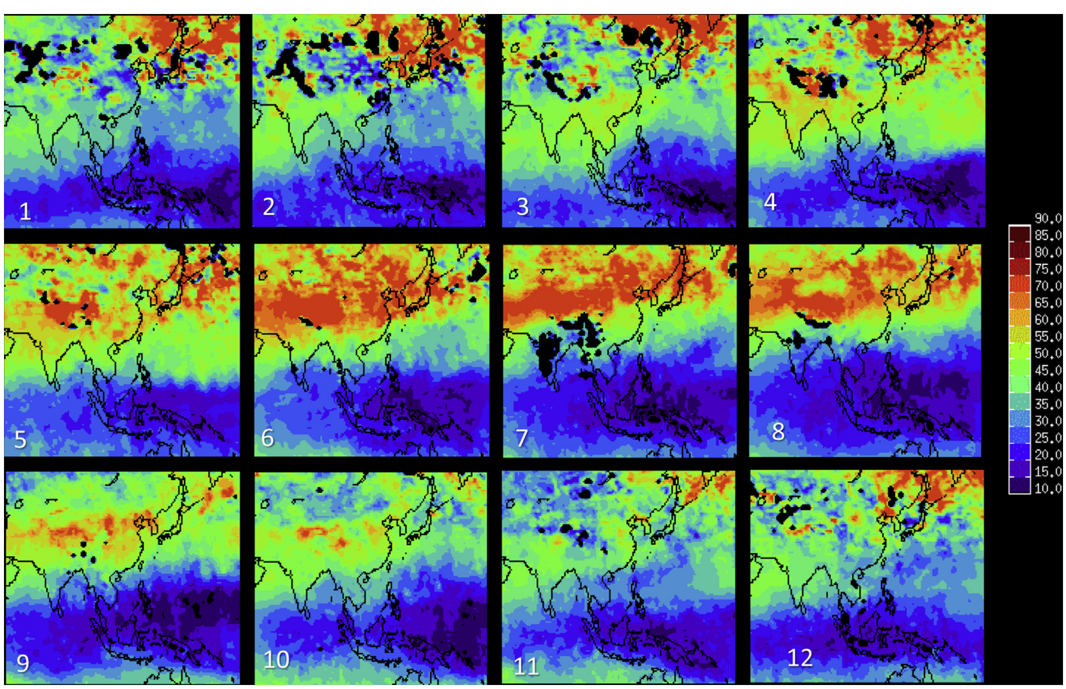

Fig. 1. Monthly average tropospheric ozone volume mixing ratio in Asia in the year 2013. The color scale indicates the density of ozone divided by the density of all constituents in a unit volume of air (ppbv) in the total tropospheric column. The monthly average values were derived from satellite-based daily measurements made each day at about 1:30 pm local time - monthly mean maps were then derived by averaging these daily maps over each month (Ziemke et al., 2006). Numbers on the maps indicate the respective month in the course of the year starting with January. Maps were compiled and modified in June 2014 from http://acd-ext.gsfc.nasa.gov/Data_services/cloud_slice/. Corresponding maps for the year 2012 are shown in Supplementary Fig. S1.