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Review

Thermal stress impacts reproductive development and grain yield in rice

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ABSTRACT

Rice is highly sensitive to temperature stress (cold and heat), particularly during the reproductive and grain-filling stages. In this review, we discuss the effects of low- and high-temperature sensitivity in rice at various reproductive stages (from meiosis to grain development) and propose strategies for improving the tolerance of rice to terminal thermal stress. Cold stress impacts reproductive development through (i) delayed heading, due to its effect on anther respiration, which increases sucrose accumulation, protein denaturation and asparagine levels, and decreases proline accumulation, (ii) pollen sterility owing to tapetal hypertrophy and related nutrient imbalances, (iii) reduced activity of cell wall bound invertase in the tapetum of rice anthers, (iv) impaired fertilization due to inhibited anther dehiscence, stigma receptivity and ability of the pollen tube to germinate through the style towards the ovary, and (v) floret sterility, which increases grain abortion, restricts grain size, and thus reduces grain yield. Heat stress affects grain formation and development through (i) poor anther dehiscence due to restricted closure of the locules, leading to reduced pollen dispersal and fewer pollen on the stigma, (ii) changes in pollen proteins resulting in significant reductions in pollen viability and pollen tube growth, leading to spikelet sterility, (iii) delay in heading, (iv) reduced starch biosynthesis in developing grain, which reduces starch accumulation, (v) increased chalkiness of grain with irregular and round-shaped starch granules, and (vi) a shortened grain-filling period resulting in low grain weight. However, physiological and biotechnological tools, along with integrated management and adaptation options, as well as conventional breeding, can help to develop new rice genotypes possessing better grain yield under thermal stress during reproductive and grain-filling phases.

Contents

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1. Introduction

Rice (*Oryza sativa* L.) is a most important staple cereal crop with about half of the world population depending on it for their dietary requirements. Worldwide, rice is grown in 114 countries on 161 million hectares (M ha) to produce >650 million tons (FAO, 2012). In the Asia-Pacific region, rice is grown from the flood plains of Bangladesh to the Himalayan foothills of Nepal, and from the rainforests of Indonesia to the desert plains of Australia. Over 90% of the global rice, is produced and consumed in Asia, on an area of 143 M ha to produce 612 million tons (FAO, 2012).

The productivity of rice in the tropics, subtropics and temperate areas is threatened due to frequent episodes of low (cold stress) and high (heat stress) temperatures (Table 1). A recent report projected that the occurrence of extreme temperature stress will increase in the future (IPCC, 2014).

All plant species have an optimum temperature range for efficient physiological functions such as growth, development and reproduction. Temperatures above or below that range will have a negative impact on plant performance leading to a loss in economic yield. Chilling and freezing stresses are collectively known as low-temperature stress or cold stress. Chilling stress is induced when temperatures are below optimum and low enough to cause injury without producing ice crystals within the soft tissues of the plants; freezing stress arises when crystals of ice come into existence inside the soft tissues. Tolerance capabilities vary among different plants for chilling (0–15 °C) and freezing (<0 °C) temperatures. Rice originated from the tropical and subtropical regions, that's why it is highly sensitive to cold stress as well as its production is also severely affected in temperate regions leading to complete crop failure in extreme cases (Xie et al., 2012). The incidence of cold stress is common in many Asian countries (Koike et al., 1990; Zhang et al., 2014a,b). In other regions, such as West and East Africa, United States, Europe, and South America, rice crops must be cold tolerant as the frequent occurrence of chilling stress threatens its productivity. The southernmost state of Brazil (Rio Grande do Sul), produces >60% of the total rice production in South America and is prone to low temperatures. This region, along with Argentina and Uruguay, is prevalent for the cultivation of indica rice in South America. The physiological causes of yield losses in rice from cold stress vary between vegetative and reproductive stage. During the vegetative stage, source build-up can be a severe constraint whereas in the reproductive stages cold stress affects the sink formation through e.g., floral abscission, sterile pollen production, pollen tube burst, aborted ovules, as well as abridged seed development (Kuroki et al., 2007; Oliver et al., 2007).

Temperatures above the optimum range for plant growth and development, defined as heat stress, can equally injure or permanently damage both vegetative and generative organs of rice. The impact of heat stress on plant performance primarily depends on the intensity, duration, and timing (relative to plant development) of the stress, but is more detrimental during the reproductive and grain-filling stages (Cao et al., 2008; Tenorio et al., 2013). Yield losses due to heat stress, induced by temperatures >33 °C, are common in several parts of the world (Table 1).

IPCC projects a mean annual temperature increase of 0.7–0.9 °C per decade in Southeast Asia (IPCC, 2014) which equates to 4.8 °C by 2100 (ADB, 2009). Every 1 °C rise in to minimum seasonal growing temperature may reduce grain yield by about 10% (Peng et al., 2004, Table 1).

Recent reviews on the impact of cold (Zhang et al., 2014b), and heat stress on rice (Mitsui et al., 2013), focused primarily on vegetative processes and grain yield. These reviews illustrated limited facts about the consequences of cold and heat stress on the reproductive processes—the most sensitive to adverse thermal environments—including panicle formation, flowering,