Bitter Melon (Momordica charantia L.) Rootstock Improves the Heat Tolerance of Cucumber by Regulating Photosynthetic and Antioxidant Defense Pathways

High temperature is considered a critical abiotic stressor that is increasing continuously, which is severely affecting plant growth and development. The use of heat-resistant rootstock grafting is a viable technique that is practiced globally to improve plant resistance towards abiotic stresses. In this experiment, we explored the efficacy of bitter melon rootstock and how it regulates photosynthesis and the antioxidant defense system to alleviate heat stress (42 °C/32 °C) in cucumber. Our results revealed that bitter-melon-grafted seedlings significantly relieved heat-induced growth inhibition and photoinhibition, maintained better photosynthesis activity, and accumulated a greater biomass than self-grafted seedlings. We measured the endogenous polyamine and hydrogen peroxide (H2O2) contents to determine the inherent mechanism responsible for these effects, and the results showed that heat stress induced a transient increase in polyamines and H2O2 in the inner courtyard of grafted seedlings. This increment was greater and more robust in bitter-melon-grafted seedlings. In addition, the use of polyamine synthesis inhibitors MGBG (methylglyoxal bis-guanylhydrazone) and D-Arg (D-arginine), further confirmed that the production of H2O2 under heat stress is mediated by the accumulation of endogenous polyamines. Moreover, compared with other treatments, the bittermelon-grafted seedlings maintained high levels of antioxidant enzyme activity under high temperature conditions. However, these activities were significantly inhibited by polyamine synthesis inhibitors and H2O2 scavengers (dimethylthiourea, DMTU), indicating that bitter melon rootstock not only maintained better photosynthetic activity under conditions of high temperature stress but also mediated the production of H2O2 through the regulation of the high level of endogenous polyamines, thereby boosting the antioxidant defense system and comprehensively improving the heat tolerance of cucumber seedlings. Taken together, these results indicate that grafting with a resistant cultivar is a promising alternative tool for reducing stress-induced damage.

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During their life cycle, plants face various environmental stimuli, including high temperature stress. In recent years, with the rise in global temperature, the greenhouse effect has continuously increased, and high temperatures have become a major environmental threat that adversely affects crop growth and productivity [1,2,3,4,5]. In China’s facility cultivation, especially in southern China, facility cultivation is frequently subjected to high-temperature stress [6], which leads to the suppression of crop growth and seriously inhibits the production and supply of vegetables [7]. Photosynthesis is one of the most heat-sensitive biological processes [8]. The activity of photosynthesis is directly associated with the amount of biomass production in plants [9]. It has been reported in several studies that heat stress can lead to the inhibition of plant photosynthesis and is the main reason for a reduction in crop yield [10,11,12]. The main reason for the reduction of photosynthesis is the inhibition of photosystem II (PSII) [13]. At the same time, PSII is considered to be a key part of high-temperature stress-induced photoinhibition [7].

Recently, a couple of studies showed that polyamines play a direct controlling role in regulating resistance against different types of plant stress, such as salt stress [14,15,16], heat stress [17], low temperature stress [18], drought stress [19], and flood stress [20,21]. Polyamines participate in complex signaling systems under abiotic stress which, in turn, regulates a series of defense responses in plants, thereby improving plant resistance against different environmental stressors [22]. There is a strong link between polyamines and different signaling molecules, such as H2O2, NO, and Ca2+, and these signaling molecules mediate the mitigation effect of polyamines on stress [23,24,25,26,27].

Grafting is a mature technical method that is used to enhance the stress tolerance of plants [28,29,30]. Grafting roots play a vital role in plants’ response to various stressors [31]. The tolerance of grafted rootstocks to adverse conditions directly affects the resistance of grafted seedlings [29]. Some previous studies have confirmed that resistant rootstock grafting can improve the stress tolerance of grafted plants by reducing photosynthesis inhibition [32], regulating osmotic substances [7], enhancing antioxidant defense [33], regulating hormone signaling [34], and mediating with microRNA transcription [35]. Moreover, rootstock grafting can improve the salt tolerance of cucumber seedlings by regulating endogenous polyamine metabolism. However, the specific role of endogenous polyamines and their regulatory networks in grafted plants under stressful conditions, particularly high temperature stress, has still not been fully elucidated.

Cucumber is an important facility horticultural crop with a high level of heat sensitivity. Bitter melon originated in India and is not cold-tolerant but is heat-resistant [6]. Therefore, we extensively studied the effect of heat-resistant bitter melon rootstock on the photosynthesis of grafted cucumber under conditions of high temperature stress and the physiological mechanism by which grafting alleviates the high temperature stress injury of cucumber plants. We also explored the regulatory mechanism of endogenous polyamines and H2O2 signaling molecules in grafted plants, and our results provide a theoretical basis for the cultivation of facility crops under a high-temperature regime.

In summary, our findings suggest that bitter melon rootstock improves the heat resistance of grafted seedlings by alleviating the photoinhibition induced
by heat stress and improving the antioxidant defense capacity of leaves by regulating the changes in endogenous polyamines and H$_2$O$_2$ in leaves under conditions of high temperature stress. However, further study is needed to determine how the contents of polyamines and hydrogen peroxide act on the antioxidant defense system.

**Keywords**

heat stress; grafting; cucumber; bitter-melon rootstock; polyamines; photosynthesis; Pla; abiotic stress; Momordica; high temperature; cucurbits

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