RICE ALLELOPATHY AND MOMILACTONE

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ABSTRACT

Rice has been extensively studied with respect to its allelopathy as part of a strategy for sustainable weed management options. All available information indicates that rice plants possibly release unknown allelochemicals into the neighbouring environments. A large number of compounds, such as phenolic acids, fatty acids, indoles and terpenes, were identified in rice root exudates and decomposing rice residues as putative allelochemicals. Among them, momilactone B may play an important role in rice defence mechanism in the rhizosphere for the competition with invading root systems of neighbouring plants.

Keywords: Allelopathy, Allelochemical, Momilactone, Root exudates, Sustainable weed management.

INTRODUCTIONw

Weeds cause reductions in rice yield and quality and remain one of the biggest problems in rice production. The negative impacts of commercial herbicide use on the environment make it desirable to diversity weed management options. Allelopathy is one of the options (Rimando and Duke, 2003, Macías *et al*., 2007; Kong, 2008; Tesio and Ferrero, 2010).

Allelopathy is the direct influence of an organic chemical released from one living plant on the growth and development of other plants (Inderjit and Duke, 2003; Belz, 2007; Macías *et al*., 2007). Allelochemicals are such organic chemicals involved in the allelopathy (Rice, 1984; Putnam and Tang, 1986; Inderjit, 1996). Allelochemicals can provide a competitive advantage for host-plants through suppression of soil microorganism and inhibition of the growth of competing plant species because of their antibacterial, antifungal, and growth inhibitory activities (McCully, 1999; Hawes *et al*., 2000; Bais *et al*., 2004).

Rice has also been extensively studied with respect to its allelopathy as part of a strategy for sustainable weed management options. A large number of rice varieties were found to inhibit the growth of several plant species when these rice varieties were grown together with these plants under the field or/and laboratory conditions (Dilday *et al*., 1994; 1998; Kim *et al*., 1999; Olofsdotter *et al*., 1999;

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Azmi *et al*., 2000; Gealy *et al*., 2003; Seal *et al*., 2004a; Kim *et al*., 2005). These findings suggest that rice may produce and release allelochemicals into neighbouring environment, thus encouraging the exploration of allelochemicals in rice.

Many secondary compounds, such as phenolic acids, fatty acids, indoles and terpenes, were identified in rice root exudates and decomposing rice residues as putative allelochemicals (Takeuchi *et al*., 2001, Rimando and Duke, 2003, Khanh *et al*., 2007). However, these compounds are almost ubiquitous in plants and rice allelopathy can not be explained by these compounds (Olofsdotter *et al*., 2002b; Seal *et al*., 2004b). Diterpen, known as momilactone B, which are unique to rice, have been isolated (Kato-Noguchi *et al*., 2002). Momilactone B inhibits the growth of typical rice weeds like *Echinochloa crus-galli* and *E. colonum* at concentrations greater than 1 μM (Kato-Noguchi *et al*., 2008a). Rice plants secrete momilactone B from the roots into the rhizosphere over their entire life cycle (Kato-Noguchi *et al*., 2003b). These observations suggest that rice plants may inhibit the growth of the neighbouring plants through the secretion of momilactone B into their rhizosphere.

Rediscovery of Momilactone

About 5,000 rice seedlings, cv. Koshihikari, were hydroponically grown for 14 days in order to screen for any allelochemicals in rice root exudates. Keeping track of the biological activity, the culture solution was purified by several chromatographic fractionations and finally 2.1 mg of putative compound causing the inhibitory effect of the rice seedlings was isolated (Kato-Noguchi *et al*., 2002; Kato-Noguchi and Ino, 2003a). The chemical structure of the inhibitor was determined from high-resolution MS, and ^{1}H- and ^{13}C-NMR spectral data as momilactone B. Momilactone B was later found in root exudes of other allelopathic rice cultivars, PI312777, with 5,7,4′-trihydroxy-3′,5′-dimethoxyflavone and 3-isopropyl-5-acetoxycyclohexene-2-one-1 (Kong *et al*., 2004). In addition, another potential allelochemical momilactone A was found in rice root exudates of cv. Koshihikari (Kato-Noguchi *et al*. 2008b).

Momilactone A and B were first isolated from rice husks as growth inhibitors (Kato *et al*., 1973; Takahashi *et al*., 1976). Momilactone A and B were later found in rice leaves and straw as phytoalexins (Cartwright *et al*., 1977; 1981; Kodama *et al*., 1988; Lee *et al*., 1999). Thereafter, the function of momilactone A as a phytoalexin has been extensively studied and several lines of evidence indicate that momilactone A has an important role in rice defense system against pathogen attacks (Nojiri *et al*., 1996; Araki and Kurahashi, 1999; Takahashi *et al*., 1999; Tamogami and Kodama, 2000; Agrawal *et al*., 2002). Although the growth inhibitory activity of momilactone B was much greater than that of momilactone A (Takahashi *et al*., 1976; Kato *et al*., 1977), the efforts to find the function of momilactone B were limited.

Biological Activity of Momilactone

Momilactone A and B, respectively, inhibited the growth of *Amaranthus lividus, Digitaria sanginalis* and *Poa annua* at concentrations greater than 20 ppm (ca. 60 μM) and 4 ppm (ca. 12 μM) (Chung *et al*., 2005). Momilactone A and B were also reported to inhibit the growth of *Echinochloa crus-galli* and *E. colonum,* which are the most noxious weeds in rice fields, at concentrations greater than 10 and 1 μM, respectively. Thus, effectiveness of momilatone B on growth inhibition is much greater than that of momilactone A. The growth inhibitory activities of momilactome B are also greater than those of momilactone A under other bioassay systems, (Takahashi *et al*., 1976; Kato *et al*., 1977; Fukuta *et al*., 2007; Toyomasu *et al*., 2008).

Momilactone A and B, respectively, inhibited root and shoot growth of rice seedlings at concentrations greater than 100 and 300 μM. IC_{50} values of momilactone A and B on rice root and shoot were not obtained because of their weak inhibitory activities against rice. The inhibitory activities of momilactone A and B, respectively, on the root and shoot growth of rice seedlings were 1 - 2 % and 0.6 - 2 % of those on the root and shoot growth of *E. crus-galli* and *E. colonum*. Thus, the effectiveness of momilactone A and B on the growth of rice seedlings was much less than that on the growth of *E. crus-galli* and *E. colonum.* These results suggest that the toxicities of momilactone A and B to rice seedlings are much less than those to the two weed species (Kato-Noguchi *et al*., 2008a).

Momilactone in Rice Life Cycle

Momilactone A and B were secreted from rice plants into the rhizopsphere throughout all life cycle stage of rice (Kato-Noguchi *et al*., 2003b; 2008a). The secretion level of momilactone A and B increased until flowering initiation, and decreased thereafter. The level of momilactone A and B at day 80 (around flowering) was 1.1 and 2.3 μg/plant/day, which was 55- and 58-fold greater than that at day 30. Although concentration of momilactone A in rice was greater than that of momilactone B, secretion level of momilactone B was greater than that of momilactone A, which suggests that momilactone B may be selectively secreted into the rhizophere than momilactone A.

Considering the growth inhibitory activity and concentrations found in the bioassay medium, momilactone A may cause only 0.8 - 2.2% of the observed growth inhibition of *E. crus-galli* roots and shoots by rice. However, momilactone B in the medium was estimated to cause 59 - 82% of the observed growth inhibition of *E. crus-galli* roots and shoots by the rice seedlings. In addition, the concentrations of momilactone B in the medium reflected the observed differences in the growth inhibition of *E. crus-galli* by the eight rice cultivars investigated (Kato-Noguchi *et al*., 2010). This suggests that the allelopathic activity of rice may be primarily depend on the secretion level of momilactone B. Therefore, momilactone B may play a very important role in rice allelopathy.

Rice Allelopathy and Allelochemicals

Since the first observation of allelopathy in rice by Dilday *et al*. (1989), more than 16,000 rice accessions from 99 countries in the USDA-ARS germplasm collection have been screened. Of these, 412 accessions inhibited the growth of *Heteranthera limosa* and 145 accessions inhibited the growth of *Ammannia coccinea* (Dilday *et al*., 1994; 1998). Similar attempts have been conducted in some other countries, and a large number of rice varieties were found to inhibit the growth of several plant species when these rice varieties were grown together with these plants under field and/or laboratory conditions (Kim *et al*., 1999; Olofsdotter *et al*., 1999; Azmi *et al*., 2000; Gealy *et al*., 2003; Seal *et al*., 2004a; Kim *et al*., 2005). These findings suggest that rice may produce and secrete allelochemicals into its neighboring environments.

Although mechanisms of the exudation are not well understood, it is suggested that plants are able to secrete a wide variety of compounds from root cells by plasmalemma-derived exudation, endoplasmic-derived exudation, and proton-pumping mechanisms (Hawes *et al*., 2000; Bais *et al*., 2004). Through the root exudation of compounds, plants are able to regulate the soil microbial community in their immediate vicinity, change the chemical and physical properties of the soil, and inhibit the growth of competing plant species (MuCully, 1999; Hawes *et al*., 2000; Bais *et al*., 2004). Momilactone B was secreted from rice plants into the rhizopsphere throughout all life cycle stage of rice (Kato-Noguchi *et al*., 2003b; 2008a). Considering the inhibitory activity and the secretion level, momilactone B may play a very important role in rice defense mechanism in the rhizosphere as an allelochemical.

The use of allelopathic rice cultivars and allelochemicals can definitely reduce the ecological impact, particularly by reducing the amount of herbicide used. Allelopathic rice cultivars combined with cultural management options is, therefore, an interesting and potential technique, contributing to alternative chemical control of weeds in paddy ecosystems (Weston, 1996; Olofsdotter, 2001; Olofsdotter *et al*., 2002a). Such an allelopathy-based technique for paddy weed control is the most easily transferable to the low-input management systems prevailing in most Asian rice farming systems (Kong, 2008).

Therefore, the rice allelopathy may be one of the options in the sustainable weed management strategies.

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