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INVITED REVIEW

EFFECTS OF UV-B RADIATION ON GROWTH AND DEVELOPMENT OF RICE CULTIVARS (*ORYZA SATIVA* L.).

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Abstract − Elevated near-UV radiation, containing a large amount of UV-B and a small amount of UV-C, inhibited the development of leaves and tillers, the increase in biomass production, the elongation of plant height, the photosynthetic rate and the chlorophyll content in rice plants in a phytotron. Elevated UV-B radiation filtered through cellulose diacetate film or UV-31 cut filter (transmission down to 290 nm) similarly suppressed each growth component above. Near-UV radiation-caused injuries were alleviated either by elevated CO_2 atmosphere or by exposure to high irradiance-visible radiation. On the basis of these findings, we examined cultivar differences in the resistance to UV radiation-caused injuries among 198 rice cultivars belonging to 5 Asian rice ecotypes (*aus*, *aman*, *boro*, *bulu* and *tjeleh*) from the Bengal region and Indonesia and to Japanese lowland and upland rice groups. It was shown that various cultivars having different sensitivities to the effects of near-UV radiation were involved in the same ecotype and the same group, and that the Japanese lowland rice group and the *boro* ecotype were more resistant. Among Japanese lowland rice cultivars, Sasanishiki (one of the leading varieties in Japan) exhibited more resistance to near-UV radiation, while Norin 1 showed less resistance, although these two cultivars are closely related. It was thus indicated that the resistance to the inhibitory effects of near-UV radiation of rice cultivars is not simply due to the difference in the geographical situation where rice cultivars are cultivated. From the genetic analysis of resistance to the inhibitory effects of UV radiation on growth of rice using F_2 plants generated by reciprocally crossing Sasanishiki and Norin 1 and F_3 lines generated by self-fertilizing F_2 plants, it was evident that the resistance to the inhibitory effects of elevated near-UV radiation in these rice plants was controlled by recessive polygenes.

INTRODUCTION

Recent research has established that chlorofluoromethanes and other gases associated with human activities cause a reduction in the stratospheric ozone concentration. Such reduction may lead to an increase in UV-B radiation reaching the Earth's surface. It is therefore urgent to determine how expansion of terrestrial UV-B radiation influences living matters. In order to study such an environmental change on growth and development of plant, investigations involving the whole plant and complete life cycle conducted in the phytotron or greenhouse are required. Especially, studies conducted in the field are invaluable, because they would be helpful in anticipating the potential changes in productivity of crops due to environmental changes. They will also be indispensable in the search for genetic food resources that may survive in or may adapt to the environmental changes. On the other hand, in spite of the global importance of cereals as staple food crops, a few studies have examined the effects of UV-B radiation on cereals. There is a noteworthy study on soybeans, in which Murali and Teramura[1] and Teramura *et al.*[2] examined the potential for alterations in the yield and seed quality of soybeans grown for 6 years in the field. They reported the necessity for multiple-year experiments and the need to increase the understanding of the interaction between UV-B radiation and other environmental stresses to assess the potential consequences of stratospheric ozone depletion. With respect to rice plants, Teramura *et al.*[3] found in greenhouses that, among 16 rice cultivars from 7 different geographical regions, Kurukaruppan (Sri Lanka), Himali (Nepal) and Tetep (Vietnam) cultivars were more tolerant to the effects of elevated UV-B radiation, and suggested that geographical location might influence sensitivity to UV-B radiation. Recently, Dai *et al.*[4] examined the effects of UV-B radiation on the growth of four lowland rice cultivars (IR line) in a phytotron to evaluate morphological and physiological parameters for identifying sensitive and less sensitive genotypes in future screening. They found that the distinct responses and relative ease in measurement of stomatal opening and ion leakage made these parameters suitable indices in selecting rice cultivars less sensitive to UV-B radiation after 2 weeks of UV-B treatment. Based on the relative change in total biomass production between UV-B irradiated and control plants, they also found that cv. IR 74 was the most sensitive and IR 64 was the least sensitive genotype.

We have been studying the effects of UV-B radiation on growth and development of plant and microorganism, interaction between plant and microorganism and interaction between plant and plant. This paper shows the followings: (1) effects of elevated near-UV radiation, containing a large amount of UV-B and a small amount of UV-C, on growth and development of Japanese rice cultivars (*Oryza sativa* L.) in a phytotron and paddy field; (2) effects of elevated UV-B radiation on growth and development of rice cultivars; (3) cultivar differences in resistance to the inhibitory effects of near-UV radiation among Asian ecotypes and Japanese lowland and upland groups of rice; (4) recovery of near-UV radiation-caused injuries either by elevated visible radiation or by elevated CO_2 atmosphere and (5) genetic analysis of resistance to the inhibitory effects of near-UV radiation.

INHIBITORY EFFECTS OF ELEVATED NEAR-UV RADIATION ON GROWTH AND DEVELOPMENT OF JAPANESE RICE CULTIVARS (*ORYZA SATIVA* L.)

In our early experiments, unfiltered UV-B lamps were used instead of high quality UV-B radiation. We considered that cultivars showing resistance to the inhibitory effects of near-UV radiation, containing a large amount of UV-B with a small amount of UV-C, would exhibit higher tolerance to high quality UV-B radiation, too, because various biological phenomena having action peaks in the UV-C region also utilize the UV-A and UV-B regions of the spectrum to a lesser degree. For instance, an absolute action spectrum for cyclobutyl pyrimidine dimer induction in DNA in intact alfalfa seedlings peaks around 280 nm in a wave range as long as 365 nm.[5]

The effects of near-UV radiation on the increase in plant height of 4 Japanese rice cultivars (Norin 20, Zosan 1, Sasanishiki and Norin 1) were first examined in a phytotron.[6] When these cultivars were grown under irradiation with visible light supplemented with or without near-UV radiation, the increase in plant height of each rice cultivar was inhibited by supplementary near-UV radiation. Blazing appeared in Norin 20, Norin 1 and Zosan 13 days after the transfer of the plants to the near-UV irradiated conditions, and then browning gradually spread from older leaves to younger ones with the prolongation of the duration of cultivation. About 1.5 months later, Norin 1 became severely damaged: leaves and stems exhibited browning, drying and shrinking, and eventually died. It was observed that Sasanishiki was most resistant to the damaging effect of near-UV radiation, while Norin 1 was the least resistant. We further analyzed more precisely the mechanism whereby near-UV radiation affected biomass production and photosynthesis in Norin 1 and Sasanishiki. The experimental conditions were as follows: the photoperiod consisted of 12 h of light and 12 h of dark, and the temperature was maintained at 27°C during the day and 17°C at night. Fluence rate of photosynthetically active radiation (PAR) was about 115 μmol/m²/sec. The irradiance of near-UV radiation was varied at 4 different levels, "control", "low", "medium" and "high" levels. The fluence rate (W/m²) in UV region was 0.022 for the "control"; 0.133 for the "low" level; 0.294 for the "medium" level; and 0.573 for the "high" level. As shown in Figure 1, both the biomass production and photosynthetic activity in Norin 1 remarkably decreased with

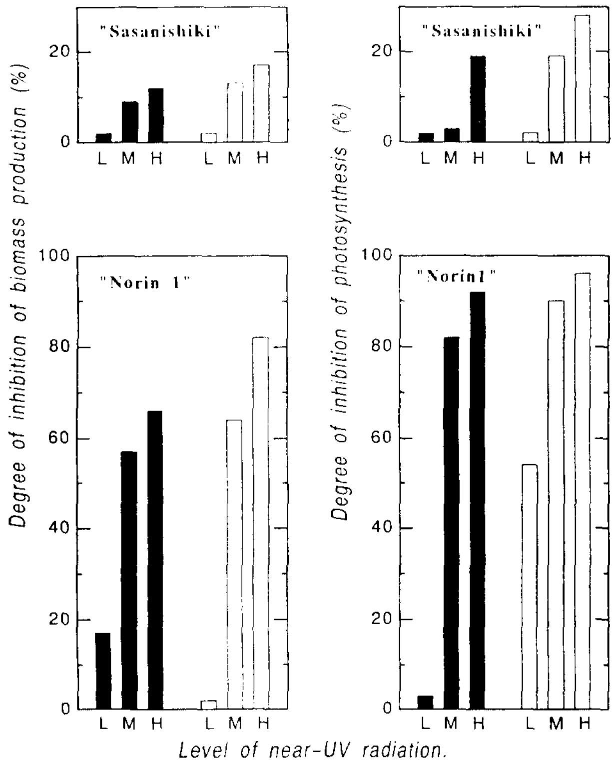

Figure 1. Inhibition of biomass production and photosynthesis in Sasanishiki and Norin 1 by the increase in near-UV radiation supplemented to visible radiation. See experimental conditions in the text.[6]

the increase in the irradiance of near-UV radiation: the degree of inhibition of biomass production in the plants grown for 2 weeks under the "medium" and "high" irrradiance level of near-UV radiation was 58 and 64%, respectively. The degree of inhibition of photosynthesis determined in the 5th leaf of the plants grown for 2 weeks under the "high" irradiance level of near-UV radiation was about 90%. A remarkable reduction was observed in particular in the biomass production and photosynthesis determined in the 7th leaf of plants grown for 4 weeks under the "high" irradiance level of near-UV radiation: the degree of inhibition of biomass production amounted to almost 80% and that of photosynthesis exceeded 90%. The extent of biomass production and photosynthesis in Sasanishiki also decreased with the increase in the irradiance of near-UV radiation. However, the degree of inhibition of biomass production and photosynthesis in this cultivar was much lower than that of Norin 1.

According to the data base of Hokuriku Agricultural Experiment Station in Japan.[7] Norin 20 is an early maturing variety requiring approximately 79 days for ear emergence, while the others require about 110 days. The plant height of this cultivar is as short as 70 cm; it has a large number of ears per plant but a small number of grains per ear. Zosan 1 is a variety with a tall plant height (102 cm) with long ears, a small number of ears per plant but a large number of grains per ear. The plant height of Sasanishiki, a leading variety in Miyagi prefecture of Japan is 77 cm; the size of the ear and number of grains are intermediate between those of Norin 20 and Zosan 1. The plant height of Norin 1 is 89 cm, and its ears and grains are similar to those of Sasanishiki. Hence, the results described above indicated that the degree of resistance to UV radiation was independent of the plant shape.

We have been studying the effects of near-UV radiation on growth of Sasanishiki and Norin 1 in the paddy field since four years ago (unpublished data). According to 1992's data, the development of tiller in Norin 1 was markedly inhibited by elevated near-UV radiation in the early stage of growth compared with that of Sasanishiki. This was not the case concerning the increase in plant height. With lengthening the duration of growth, the degree of reduction in tiller formation was gradually recovered. Number of sterile seeds increased in both cultivars grown under elevated near-UV radiation: percentage of sterility was about 10% higher than that of non-elevated near-UV irradiated control. Grain size became a little smaller. About 35% yield reduction was observed. Protein content of grain increased by *ca.*10%, indicating the lowering of rice quality. It was totally evaluated that Norin 1 was less resistant to elevated near-UV radiation than Sasanishiki in 1992. The summer in 1993 in Japan was cold and rainy. Mainly due to a lack of sunshine, the difference in growth between Sasanishiki and Norin 1 was clear, although grain yield of both cultivars was lowered. In 1994, we examined the effects of high quality UV-B radiation instead of near-UV radiation. Unfortunately, the weather in 1994 was so sunny and a little drier that neither growth injuries nor the difference in growth between those two cultivars were confirmed. In this way, the effects of UV-B radiation was so much influenced by the other environmental conditions that requirement for multiple-year experiments should be emphasized. We are thinking of continuing field studies for more a couple of years.

EFFECTS OF ELEVATED HIGH QUALITY UV-B RADIATION ON GROWTH AND DEVELOPMENT OF RICE CULTIVARS

Effects of high quality UV-B (containing no UV-region below 290 nm) on growth and development of rice was examined in a phytotron. The radiation emitted from Toshiba 20 SE fluorescent lamps (emitting a large amount of UV-B and a small amount of UV-C) was filtered through either cellulose diacetate film or glass cut-filter UV 31 so that the radiation below 290 nm was eliminated. The development of tiller, the increase in fresh weight and dry weight, the chlorophyll content and the total leaf nitrogen were decreased by elevated UV-B radiation, while accumulation of UV-absorbing compound (flavonoids) in leaf was increased (unpublished data).

CULTIVAR DIFFERENCES IN RESISTANCE TO THE INHIBITORY EFFECTS OF NEAR-UV RADIATION AMONG ASIAN ECOTYPES AND JAPANESE LOWLAND AND UPLAND CULTIVARS OF RICE

As described above, a possibility that the rice cultivars having more resistance to near-UV radiation could be screened by examining the effects of various irradiance levels of near-UV radiation supplemented to visible radiation in a phytotron was indicated. We[7] therefore examined cultivar differences in resistance to the inhibitory effects of near-UV radiation among 5 Asian rice ecotypes (*aus, aman, boro, bulu, tjereh*) and the Japanese lowland (*j.l.r.*) and upland rice groups (*j.u.r.*; *Oryza sativa* L.). The *aus, aman, boro* ecotypes, from Bengal region, and the *tjereh* ecotype, from Indonesia, belong to *indica*. The *bulu* ecotype, from Indonesia, belongs to the tropical *japonica,* and

Japanese lowland and upland rice groups belong to the temperate *japonica*. When experimental plants were grown under the "low" irradiance level, a wide range in the frequency distribution was observed in every ecotype and group, but remarkable differences among ecotypes and groups were observed neither in the pattern of the distribution nor in the mean of the ratio of FW of sample/control (open columns in Fig.2). Different sensitivities to the effects of near-UV radiation were involved in the same ecotype and in the same group: one type was promoted by near-UV radiation i.e. "resistance", while the other type

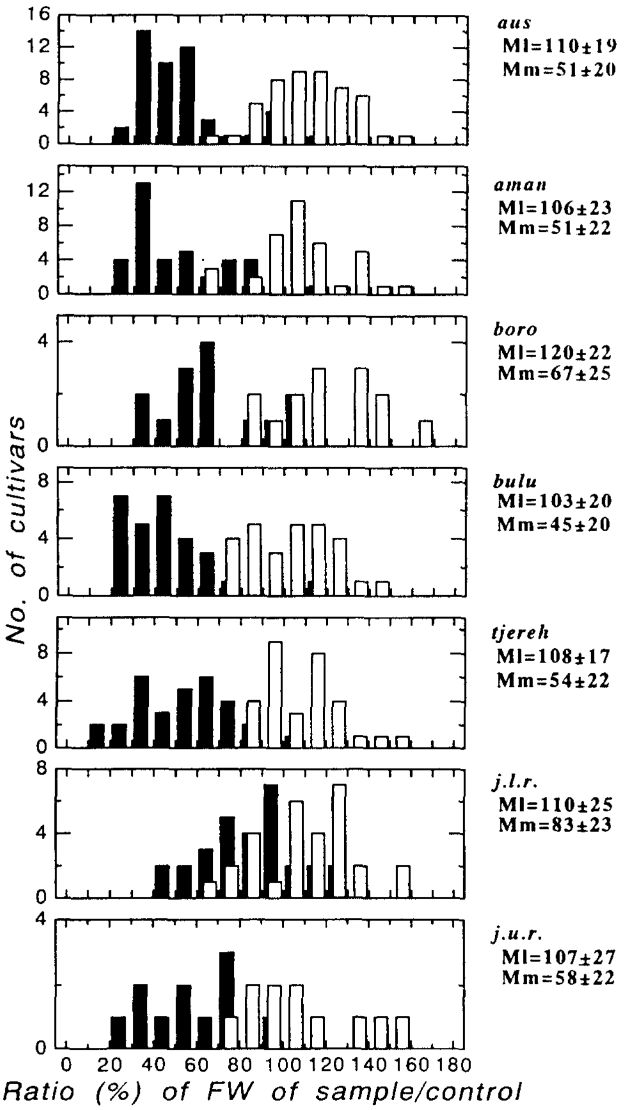

Figure 2. Frequency distribution of the ratio (%) of fresh weight of the sample to that of the control. Open and black columns show the results of plants grown under the "low"- and "medium" irradiance levels of supplemental near-UV radiation, respectively. Ml and Mm are mean + SD of ratio of fresh weight in plants grown under the "low"- and "medium" near-UV radiation, respectively.[7]

was inhibited by near-UV radiation i.e. "sensitive". The proportion of cultivars resistant to the "low" irradiance level in individual ecotypes or groups differed: 79% for the *boro*; 69% for the *aus*; 68% for the *aman*; 57% for the *bulu* and 58% for the *tjereh*, respectively. As for the Japanese rice cultivars, 75% of the *j.l.r.* and 54% of the *j.u.r.* were resistant, respectively. With an increase in the irradiance level of near-UV light to the "medium" level, the pattern of the frequency distribution of the ratio of FW of sample/control significantly shifted towards the lower values and the mean decreased markedly (closed columns in Fig. 2). However, it should be noted that *j.l.r.* maintained a mean of 83%, which was the highest value, and the *boro* ecotype showed 67%, while that the others showed a mean below 58%. Furthermore, the proportion of cultivars resistant to the "medium" irradiance level was 21% for the *j.l.r.* and 14% for the *boro* ecotype, respectively, while that of others was below 4%. With an increase in the irradiance level of near-UV light to the "high" level, the pattern of the frequency distribution of the ratio of FW of sample/control in all ecotypes and groups was similar to that as seen in plants grown under the "medium" irradiance level, except that the mean of each ecotype somewhat decreased. Even in cultivars grown under the "high" irradiance level, 2 cultivars of *j.l.r.* and 1 cultivar of each of *boro, bulu* and *tjereh* exhibited resistance to the near-UV radiation. Similar results were observed concerning the effects of elevated near-UV radiation on the increase in plant height and chlorophyll content in the 3rd leaf. Overall, it was clear that the *j.l.r.* group and the *boro* ecotype were more resistant to the inhibitory effects of near-UV radiation: Sasanishiki belonged to the most resistant group while Norin 1 did to the less resistant one. The data suggested that the differences in resistance to near-UV radiation was not related to the geographical origins of the rice cultivars examined.

Figure 3 shows the relationship between the ratio of the fresh weight under the "low" irradiance level and the ratio of the fresh weight under the "medium" irradiance level for the *boro* and *bulu* ecotypes and the *j.l.r.* group. It is clear that cultivars which showed stronger resistance to the "low" irradiance level did not necessarily show stronger resistance to the "medium" irradiance level. On the contrary, some cultivars showed stronger resistance to the "medium" irradiance level than to the "low" irradiance level. These findings indicate that rice plants might have different types of response to different irradiance levels of near-UV radiation: one was for the "low" irradiance level, the other being for the "medium" irradiance level. It was further

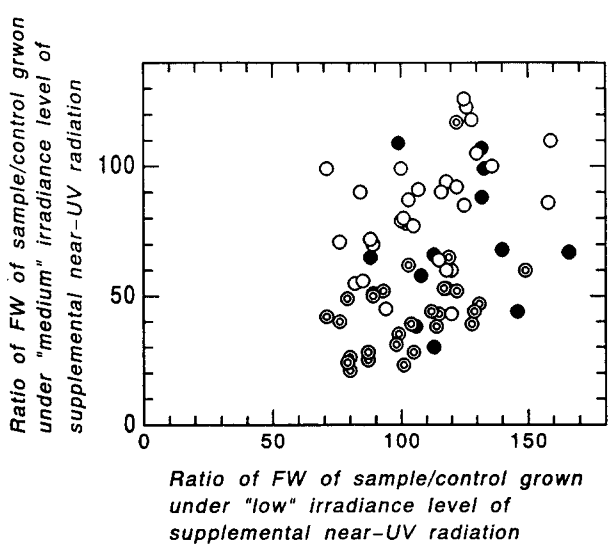

Figure 3. Relationship between the ratio of fresh weight of the sample/control grown under the "low" irradiance level of near-UVradaition and the ratio of the sample/control grown under the "medium" irradince level. The result of the *j.l.r.* group, *boro* and *bulu* ecotype was shown as (○), (●) and (◎), respectively.

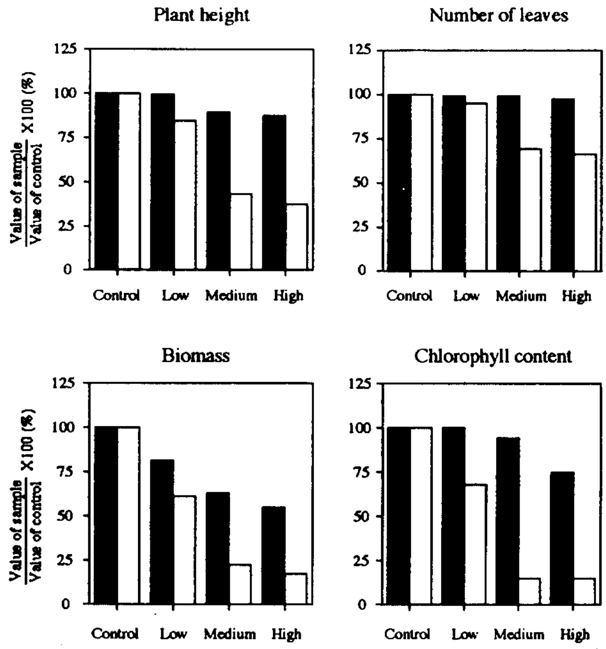

Figure 4. Effects of near-UV radiation supplemented to "low"- or "high" irradiance level of visible radiation on the growth of Sasanishiki. Tested plants were grown for 4 weeks under a "low" (open column) - or "high" (black column) irradiance level of visible radiation supplemented with various levels of near-UV radiation.

suggested that the differences in resistance to the inhibitory effects of near-UV radiation among rice plants could relate to the difference between degrees of those two responses.

RECOVERY OF NEAR-UV RADIATION CAUSED-INJURIES BY ELEVATED VISIBLE RADIATION OR ELEVATXD CO_2 ENVIRONMENT

Experimental plants were grown for 4 weeks under two different levels of visible radiation, i.e. "low" and "high" irradiance levels. The irradiance of the "high" level was about 2 times higher than that of the "low" level. The irradiance of near-UV radiation was varied at 4 different levels as described previously. The growth components such as plant height, leaf formation, fresh weight (FW) and dry weight (DW) of biomass and total chlorophyll content in Norin 1 and Sasanishiki grown under the "low" irradiance level of visible radiation also decreased with the increase in the irradiance of near-UV radiation (Fig.4; ref. 6). When both cultivars were grown under the "high" irradiance level of visible radiation, the increase of the irradiance of near-UV radiation resulted in the reduction of each growth component as well. However, the degree of reduction of all the parameters decreased as compared with the "low" irradiance level of visible radiation. It was thus indicated that the parameters in both cultivars grown under "low" irradiance level of visible radiation were more inhibited by near-UV radiation than those of the cultivars grown under the "high" irradiance level of visible radiation. The degree of inhibition in all the parameters of Norin 1 was higher than that of Sasanishiki irrespective of the amount of visible radiation applied (data not shown). It should be noted that the degree of inhibition of each growth component caused by near-UV radiation was alternated by the increase of the amount of visible radiation, and that such reductions in inhibition in Sasanishiki were more pronounced than those of Norin 1. These results suggested that the capacity to recover from the inhibitory effects of near-UV radiation through the exposure to visible radiation was greater in Sasanishiki than Norin 1. It is therefore considered that the difference in the resistance to near-UV radiation between Norin 1 and Sasanishiki may be attributed either to the sensitivity to near-UV radiation or to the capacity to recover from the injury caused by near-UV radiation through the exposure to visible radiation.

Cultivars Sasanishiki and Norin 1, *japonica*, and Marith-bati and Surjamkhi, *indica*, were grown in 12 h light (27 °C) and 12 h dark (17 °C). Cvs. Sasanishiki and Marith-bati have more resistance to near-UV radiation, while the other two have less resistance. CO_2 concentration in the growth cabinet

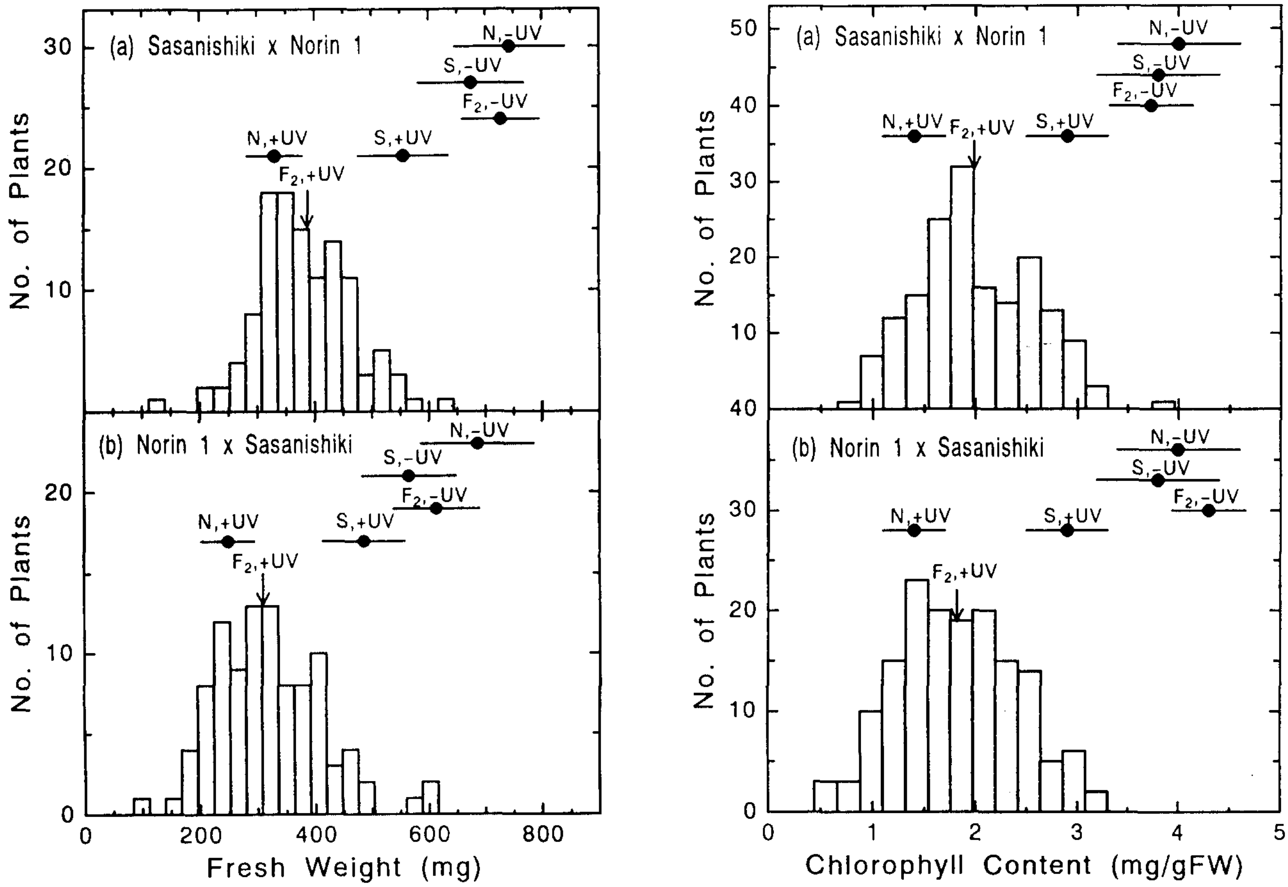

Figure 5. Frequency distribution of fresh weight per plant (left) and chlorophyll content per unit fresh weight (right). Symbols in the figures: N, -UV, N, +UV, S, -UV, S, +UV, F_2, -UV, F_2, +UV are Norin 1 (N), Sasanishiki (S) and F_2 plants of cross between Norin 1 and Sasanishiki grown without or with supplemental near-UV radiation. The bars indicate the mean + SD.[8]

was adjusted to about 350 ppm all day for the ambient CO_2 environment. In elevated CO_2 environment, CO_2 concentration was kept at 700 ppm during the day alone, and returned to about 350 ppm at night. Growth components such as fresh weight, tiller number and plant height were significantly increased by elevating CO_2 concentration in the two types of cultivars. Elevation of CO_2 concentration alleviated the inhibitory effect of near-UV radiation. However, there was no specific correlation between the degree of enhancement of growth by elevating CO_2concentration and the degree of reduction in inhibitory effects of near-UV radiation by elevating CO_2 concentration (unpublished data).

GENETIC ANALYSIS OF RESISTANCE TO THE INHIBITORY EFFECTS OF NEAR-UV RADIATION.

Some experimental plants were grown in visible radiation supplemented with near-UV radiation, while others were grown without near-UV radiation. The degree of resistance to near-UV radiation was estimated in terms of the degree of reduction caused by supplemental near-UV radiation in the fresh weight of the aboveground plant parts and the chlorophyll content per unit fresh weight. Fresh weight and chlorophyll content in F_2 plants generated by reciprocally crossing cv. Sasanishiki, a cultivar more resistant to near-UV radiation, and Norin 1, a cultivar less resistant to such radiation, exhibited a normal frequency distribution. The heritabilities of these two properties in F_2 plants were low under conditions of non-supplemental near-UV radiation. Under elevated near-UV radiation, the F_2 population shifted to the lower range of fresh weight and chlorophyll content, and the means were close to those of Norin 1 (Fig. 5).

The heritabilities of these two properties were the same in the reciprocal crosses, indicating that maternal inheritance was not involved. Inheritance of chlorophyll content per unit fresh weight was further determined in F_3 lines generated by self-fertilizing F_2 plants of Sasanishiki and Norin 1. The results showed that the F_3 population was segregated into three genotypes, namely, resistant homozygotes, segregated heterozygotes and sensitive homozygotes, with a ratio of 1:65:16. These values did not fit with the segregation ratio of 1:2:1 (x^2 NS 1:2:1=33.58; difference significant with $p < 0.01$).

It was thus evident that the resistance to the inhibitory effects of elevated near-UV radiation in these rice plants was controlled by recessive polygenes. It was also indicated that cv. Sasanishiki, which was bred to be resistant to cool summer damage, must have acquired resistance from some progenitor during the breeding. However, it is still obscure why Sasanishiki has strong resistance to near-UV radiation and it might be impossible to trace back the process of breeding. Consequently, it is indispensable that the relationship between the genetic mechanism and physiological mechanism of the resistance to the inhibitory effects of near-UV radiation should be solved.[8]

CONCLUSION

This report introduced fundamentally physiological and genetic aspects of the effects of UV-B radiation on growth and development of rice and of resistance to the inhibitory effects of UV-B radiation on growth of rice. We are now progressing biochemical and molecular biological studies regarding the mechanism of resistance to the inhibitory effects of UV radiation on growth and development of rice. I am hoping to have a chance again to introduce our further studies in the near future.

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