Intraspecific differences in physiological response of 20 wheat cultivars to enhanced ultraviolet-B radiation under field conditions

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Abstract

Field studies were conducted to determine the potential for alterations in physiology and the intraspecific variation in sensitivity of 20 wheat (Triticum aestivum) cultivars to enhanced ultraviolet-B (UV-B, 280–315 nm) radiation. The supplemental UV-B radiation was 5 kJ m⁻², simulating a depletion of 20% stratospheric ozone. Out of 20 wheat cultivars (from South China, North China and Mexico) tested, 13 showed significant changes in total chlorophyll content. In most of these sensitive species, chlorophyll a content was strongly reduced, and chlorophyll b content decreased in a lesser extent, leading to a decrease in chlorophyll a/b ratio. However, some species had an increased chlorophyll a/b ratio under enhanced UV-B. The effect of UV-B on flavonoid content also showed intraspecific differences, a significant increase for one cultivar, decreases in 12 cultivars and no effect on the other seven cultivars. Superoxide dismutase (SOD) activity of five cultivars was significantly increased, and that of six cultivars significantly decreased. Membrane permeability of 12 cultivars significantly increased, while only that of Dali 905 was significantly decreased. Malonaldehyde (MDA) contents of eight cultivars were increased significantly, while that of three cultivars was significantly decreased. Although large intraspecific differences were found for the different parameters measured, there was no clear correlation between them under UV-B radiation. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Chlorophyll; Flavonoid; Malonaldehyde; Membrane permeability; Superoxide dismutase; Triticum aestivum; UV-B radiation

1. Introduction

The rapid decline in stratospheric ozone concentrations has been confirmed by satellite measurements. The most pronounced thinning of the ozone layer has been measured over the Antarctic...
continent with up to 71% depletion during the Antarctic spring (Kerr, 1993). Recent mathematical models predict a further increase in solar UV-B irradiation in future years (Madronich et al., 1995). UV-B effects on plants have been the subjects of considerable research (Caldwell et al., 1995). An examination of more than 200 plant species reveals that roughly 20% are sensitive, 50% are mildly sensitive or tolerant and 30% are completely insensitive to UV-B radiation (Teramura, 1983). Whilst the impact of enhanced UV-B radiation on plant physiology, morphology, growth and biomass have been investigated extensively, little is known about intraspecific differences in physiological response to enhanced UV-B. Recently, intraspecific differences in flavonoid in cucumber (Murali and Teramura, 1986), soybean (Teramura and Murali, 1986; D’surney et al., 1993) and Arabidopsis thaliana (Li et al., 1993; Fiscus et al., 1999), flavonoid and chlorophyll in rice (Teramura et al., 1991) have been reported. Plant species and even genotypes within species can differ greatly in their responses to UV-B. In the recent experiment, the substantial growth suppression of A. thaliana flavonoid mutants suggests that the disruption of secondary metabolism at the chalcone isomerase site is affecting critical aspects of secondary metabolism. This may result in an impairment of the normal growth and differentiation process (Fiscus et al., 1999). Due to our lack of understanding of the role of intraspecific response differences to UV-B radiation, further studies on its importance should be undertaken.

On the other hand, most of the UV-B research in the past two decades has been conducted in growth chambers and greenhouses where the unnatural spectral balance of radiation can lead to unrealistic conclusions, which may have substantially changed plant sensitivity to UV-B. It is important in experiments to maintain a realistic balance between various spectral regions since both UV-A (315–400 nm) and visible (400–700 nm) radiation can have ameliorating effects on responses of plants to UV-B (Caldwell et al., 1995). In growth chamber and greenhouse experiments, the visible and UV-A radiation is usually much less than in sunlight, thus, even if realistic levels of UV-B are used in simulating ozone reduction, the plant response may be exaggerated relative to field conditions. Unfortunately, only 15% of the studies have been conducted under field conditions. While the laboratory and glasshouse studies provide information on mechanisms and processes of UV-B action, only field studies can provide realistic assessments of what will happen as the stratospheric ozone layer thins (Caldwell et al., 1995; Yue et al., 1998).

Wheat is one of the major world food crops (Teramura, 1983), the effects of enhanced UV-B radiation on photosynthetic characteristics, growth, development, leaf quality, morphology, tiller number, crop structure, plant nutrients, decomposition, competition interaction between wheat and wild oat, intraspecific response differences, total biomass and yield have been studied (Li et al., 1998, 1999; Yue et al., 1998). Unfortunately, only few studies have been conducted under field conditions. In this study, we grew 20 wheat cultivars in field under ambient and supplemental levels of UV-B radiation with the objective to (1) determine, if UV-B radiation affects wheat physiology under field conditions; and (2) evaluate intraspecific differences in physiological response of 20 wheat cultivars to UV-B radiation in the field. We hypothesized that enhanced UV-B radiation will decrease chlorophyll content, and affect other physiological processes, i.e. insufficient protection by flavonoid will result in the production of oxygen radicals, and their insufficient removal by SOD will cause membrane damage which can be measured by membrane permeability and MDA content. These changes will result in intraspecific differences in physiological response under field conditions.

2. Materials and methods

2.1. Plant materials and growth conditions

The field experiment was conducted on a upland red soil at Yunnan Agricultural University, Kunming, China. No fertilization was necessary during the season. Seeds of 20 wheat (Triticum aestivum L.) cultivars, the most grown wheat
cultivars in China (19 cultivars) and Mexico (MY 94-9), were obtained from Lanzhou Agricultural Science Research Institute, Yunnan Academic of Agricultural Sciences, Gansu Academic of Agricultural Sciences and Henan Academic of Agricultural Sciences. They were sown in rows spaced 0.2 m apart at a density of 80 seeds m\(^{-1}\) in 120 plots of 2 × 1 m each on July 26, 1998. Five border rows were sown round each plot in order to minimize heterogeneity in microclimate. The overall experimental design was a randomized complete block with two UV-B treatments and three replications. At the three-leaf stage, plants were thinned to 60 m\(^{-1}\) for uniformity in growth. This planting density is within common sowing practice for the Kunming region.

2.2. UV-B radiation

Supplemental UV-B radiation was provided by filtered Gucun brand (Gucun Instrument Factory, Shanghai, China) 30 W sunlamps following the procedure outlined in Lydon et al. (1986). Lamps were suspended above and perpendicular to the planted rows (rows oriented in an east–west direction to minimize shading) and filtered with either 0.13 mm thick cellulose diacetate (transmission down to 290 nm) for supplemental UV-B radiation or 0.13 mm polyester plastic films (absorbs all radiation below 320 nm) as a control (Sullivan and Teramura, 1990). Cellulose diacetate filters were presolarized for 8 h and changed weekly to ensure uniformity of UV-B transmission. The spectral irradiance from the lamps was determined with an Optronic Model 742 (Optronic Laboratories Inc., Orlando, FL, USA) spectroradiometer. The spectral irradiance was weighted with the generalized plant response action spectrum (Caldwell, 1971) and normalized at 300 nm to obtain UV-B\(_{BE}\). Six lamps were installed above each plot. Plants were irradiated for 7 h daily from three-leaf stage to ripening stage, centered around solar noon. Plants under polyester-filtered lamps received only ambient levels of UV-B radiation (10 kJ m\(^{-2}\) UV-B\(_{BE}\) during clear sky conditions on the summer solstice). Plants beneath the cellulose diacetate filters received ambient plus supplemental levels of UV-B. The lamp height above the plants was adjusted weekly to maintain a distance of 0.45 m between the lamps and the top of the plants, and provided supplemental irradiances of five effective kJ m\(^{-2}\) UV-B\(_{BE}\). This supplemental level was similar to that which would be experienced at Kunming (25°N, 1950 m) with a 20% stratospheric ozone reduction during a clear day on the summer solstice (10 kJ m\(^{-2}\) UV-B\(_{BE}\)) according to a mathematical model of Madronich et al. (1995). Total daily photosynthetic photon fluence (PPF between 400 and 700 nm) under lamp fixtures was 90% of that above the lamps.

2.3. Measurements and statistical analyses

Physiological indicators of the first three fully expanded leaves of plants were tested in the stages of tillering and elongation of wheat. Two samples each of ten plants were taken from each plot. chlorophyll content was determined according to the method of Arnon (1949). Leaf discs of 100 mm\(^{2}\) were taken from leaves and extracted in 10-ml of acidified methanol (79:20:1 v/v, methanol:water:HCl) for flavonoid measurement, according to the procedure of Mirecki and Teramura (1984). Extract absorbance at 305 nm measured on a spectrophotometer was used as a measure of flavonoid. Superoxide dismutase (SOD) activity was determined according to the method of Giannopolitis and Ries (1977). Membrane permeability was determined according to the method of Fan and Blake (1994), and the conductivity of the bathing solutions was tested using a conductivity meter (DDS-IIC, Shanghai, China). Malonaldehyde (MDA) contents were determined according to the method of Heath and Packer (1968).

Statistical differences between mean of control and UV-B radiation treatment of any measured parameter were determined by T-test at the \(P < 0.05\) or \(P < 0.01\) level. Correlation analyses were applied to test correlation significance between two parameters.
3. Results

3.1. Chlorophyll contents

UV-B radiation had obvious effects on chlorophyll contents of the most of 20 wheat cultivars under field conditions (Table 1). Total chlorophyll contents of 13 cultivars were significantly reduced under UV-B radiation, mostly due to a strong reduction in chlorophyll a content and to a lesser extent reduction in chlorophyll b content. However, there were large intraspecific differences in chlorophyll a/b ratio with significant increases \((P < 0.05)\) in cultivars Longchun 16 and Huining 18 and significant decreases \((P < 0.05)\) for four cultivars, namely, Dali 905, Yunmai 39, Long 8425 and MY 94-9.

3.2. Flavonoid contents

The effect of UV-B on flavonoid content also showed intraspecific differences, a significant increase for Fengmai 24 \((P < 0.01)\); decreases in 12 cultivars \((P < 0.01\) or 0.05); and no effect on the other seven cultivars \((P > 0.05)\) (Table 2).

3.3. SOD activity

UV-B radiation had an obvious effect on SOD activity of most of the 20 wheat cultivars under field conditions (Table 2). SOD activity of five cultivars was significantly increased \((P < 0.01\) or 0.05), while that of six cultivars was significantly decreased \((P < 0.05)\).

3.4. Membrane permeability

Table 2 showed that UV-B radiation had obvious effects on membrane permeability of most of the 20 wheat cultivars under field conditions. Membrane permeability of 12 cultivars was significantly increased \((P < 0.01\) or 0.05), while membrane permeability of Dali 905 \((P < 0.01)\) only significantly decreased.

3.5. MDA contents

Effects of enhanced UV-B radiation on MDA contents were shown in Table 2. MDA contents of eight cultivars increased significantly \((P < 0.01\) or 0.05) by UV-B radiation, that of Huining 18 \((P < 0.01)\), Fengmai 24 \((P < 0.05)\), and Fan 19 \((P < 0.05)\) significantly decreased.

4. Discussion

This is the first report to suggest that intraspecific differences existed in physiological response of 20 wheat cultivars to enhanced ultraviolet-B radiation under field conditions. This is supported by the earlier findings of intraspecific differences in flavonoid metabolism in \textit{Cucumis sativus} (Murai and Teramura, 1986), soybean (D’sonrey et al., 1993) and \textit{A. thaliana} (Li et al., 1993; Fiscus et al., 1999), and in flavonoid content and chlorophyll content in rice (Teramura et al., 1991). Reductions in chlorophyll contents have often been used to assess the degrees of UV-B radiation sensitivity. UV-B radiation decreased chlorophyll contents in rice (Teramura et al., 1991) and soybean (Mirecki and Teramura, 1984) in a greenhouse experiment have been observed. In this study, chlorophyll contents were sensitive to enhanced UV-B radiation. So, they may be used as response indicator for assessing the degrees of UV-B radiation sensitivity. Correlation analyses showed that percentage change of chlorophyll a/b ratio was positively correlated with percentage change of contents of chlorophyll a \((r = 0.577, P < 0.01)\), and negatively correlated with percentage change of contents of chlorophyll b \((r = -0.076, P > 0.05)\). UV-B radiation significantly decreased chlorophyll contents, primarily because it destroyed the structure of chloroplasts, inhibited synthesis of new chlorophyll, and increased the degradation of chlorophyll (Sakaki et al., 1983). The mechanism of UV-B radiation decreasing chlorophyll contents is still not clear.

Flavonoids have been proposed by some investigators to act as optical filters, by absorbing UV-B radiation in the upper tissue layer and thus preventing damage to sensitive targets. Recent
<table>
<thead>
<tr>
<th>Cultivar name</th>
<th>Chlorophyll a (Control)</th>
<th>+ UV-B</th>
<th>Change (%)</th>
<th>Chlorophyll b (Control)</th>
<th>+ UV-B</th>
<th>Change (%)</th>
<th>Chlorophyll (a + b) (Control)</th>
<th>+ UV-B</th>
<th>Change (%)</th>
<th>Chlorophyll (a, b) (Control)</th>
<th>+ UV-B</th>
<th>Change (%)</th>
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<td>Bi 90-5</td>
<td>0.88 ± 0.09</td>
<td>0.58 ± 0.08</td>
<td>−34.1**</td>
<td>0.61 ± 0.08</td>
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<td>−21.3</td>
<td>1.50 ± 0.12</td>
<td>1.06 ± 0.07</td>
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<td>1.21 ± 0.11</td>
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<td>Fengmai 24</td>
<td>1.02 ± 0.10</td>
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<td>−42.2**</td>
<td>0.77 ± 0.06</td>
<td>0.52 ± 0.02</td>
<td>−32.5**</td>
<td>1.78 ± 0.13</td>
<td>1.10 ± 0.08</td>
<td>−38.2**</td>
<td>1.32 ± 0.12</td>
<td>1.14 ± 0.09</td>
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<td>0.71 ± 0.04</td>
<td>−1.9</td>
<td>1.70 ± 0.08</td>
<td>1.56 ± 0.07</td>
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<td>1.36 ± 0.17</td>
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<td>Fan 19</td>
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<td>−28.8**</td>
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<td>−30.3**</td>
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<td>3.39</td>
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<td>1.89 ± 0.12</td>
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<td>1.48 ± 0.06</td>
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<td>Yunnan 39</td>
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<td>−54.7*</td>
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* Mean ± S.D., n = 6; * and **, significant difference between control and UV-B radiation at P<0.01 or P<0.05, according to T-test.
<table>
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<tr>
<th>Cultivar name</th>
<th>Flavonoid content (absorption 305 nm)</th>
<th>SOD activity (U mg FW(^{-1}))</th>
<th>Membrane permeability (10(^3) μm cm(^{-1}))</th>
<th>MDA contents (μM g FW(^{-1}))</th>
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<td></td>
<td>Control</td>
<td>+ UV-B</td>
<td>Change (%)</td>
<td>Control</td>
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<td>Bi 90-5</td>
<td>0.74 ± 0.05</td>
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<td>-20.3*</td>
<td>0.65 ± 0.02</td>
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<td>Fengmai 24</td>
<td>0.37 ± 0.02</td>
<td>0.43 ± 0.02</td>
<td>16.2*</td>
<td>0.75 ± 0.03</td>
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<td>YV 97.31</td>
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<td>Fan 9</td>
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<tr>
<td>Yunnai 39</td>
<td>0.68 ± 0.03</td>
<td>0.56 ± 0.03</td>
<td>-17.6*</td>
<td>0.80 ± 0.04</td>
</tr>
<tr>
<td>Minxian 26</td>
<td>0.61 ± 0.03</td>
<td>0.52 ± 0.02</td>
<td>-14.8*</td>
<td>0.80 ± 0.02</td>
</tr>
<tr>
<td>Wenmai 5</td>
<td>0.59 ± 0.04</td>
<td>0.53 ± 0.05</td>
<td>-10.2</td>
<td>0.76 ± 0.03</td>
</tr>
<tr>
<td>Liaoqun 4</td>
<td>0.47 ± 0.03</td>
<td>0.39 ± 0.02</td>
<td>-17.0*</td>
<td>0.86 ± 0.02</td>
</tr>
<tr>
<td>Lanzhou 30101</td>
<td>0.59 ± 0.04</td>
<td>0.52 ± 0.04</td>
<td>-11.9</td>
<td>0.93 ± 0.04</td>
</tr>
<tr>
<td>Long 8425</td>
<td>0.63 ± 0.03</td>
<td>0.38 ± 0.03</td>
<td>-39.7**</td>
<td>0.89 ± 0.02</td>
</tr>
<tr>
<td>Longchun 8139</td>
<td>0.70 ± 0.04</td>
<td>0.56 ± 0.03</td>
<td>-20.0*</td>
<td>0.92 ± 0.06</td>
</tr>
<tr>
<td>Longchun 16</td>
<td>0.63 ± 0.03</td>
<td>0.52 ± 0.02</td>
<td>-17.5**</td>
<td>0.73 ± 0.02</td>
</tr>
<tr>
<td>MY 94-9</td>
<td>0.53 ± 0.04</td>
<td>0.38 ± 0.05</td>
<td>-28.3*</td>
<td>0.78 ± 0.05</td>
</tr>
<tr>
<td>Longchun 15</td>
<td>0.57 ± 0.02</td>
<td>0.47 ± 0.03</td>
<td>-17.5*</td>
<td>0.81 ± 0.03</td>
</tr>
<tr>
<td>Huining 18</td>
<td>0.68 ± 0.05</td>
<td>0.51 ± 0.02</td>
<td>-25.0*</td>
<td>0.69 ± 0.05</td>
</tr>
</tbody>
</table>

* Mean ± S.D., n = 6; * and **, significant difference between control and UV-B radiation at P < 0.01 or P < 0.05, according to T-test.
results from studies with cucumber suggest that intraspecific responses could be at least partly due to inherent intraspecific differences in the accumulation of leaf flavonoids (Teramura and Murali, 1986). The study by Reuber et al. (1996) suggested that a flavonoid mutant of barley (*Hordeum vulgare*) exhibited increased sensitivity to UV-B radiation especially in the primary leaf. The content of flavonoid in barley mutant was only 7% as compared with the mother variety in the primary leaf. Differences in UV-absorption characteristics between the mutant and the mother line were clear from the spectrophotometric analysis (Reuber et al. 1996).

For barley cv. Atlas, L-phenylalanine ammonia-lyase (PAL) was assumed to play a key role in the UV-B acclimatization by a synthesis of flavonoids (Liu and McClure, 1995). In primary leaves of barley cv. Gerbel, the UV-mediated increased accumulation of flavonoid was closely correlated with increased activity and amount of immunologically detectable chalcone synthase (CHS). In leaves of several plant species, including rye (*Secale cereale*), CHS was found to play a major role in UV regulation of the flavonoid pathway (Reuber et al., 1996). In another experiment, the substantial suppression of growth of *A. thaliana* flavonoid mutants by UV-B radiation suggests that the disruption of secondary metabolism at the chalcone isomerase site caused an impairment of the normal growth and differentiation process (Fiscus et al., 1999).

A considerable amount of data demonstrated how UV radiation altered membrane structure or function: inhibited K⁺-ATPase and peroxidized lipids in *T. aestivum* (Wright et al., 1981), and decreased membrane resistance in *Chara corallina* (Doughty and Hope, 1973). The damage to non-photosynthetic membranes that was detected by electron microscopy generally required high fluence or occurred only after a long lag time following irradiation. In the latter case, the effect of UV-B can be regarded as an acceleration of normal senescence processes (Skokut et al., 1977). Damage to components of isolated plant membranes can also be determined chemically, lipid damage required high fluence; inactivation of ATPases occurred at lower fluence. The physiological effects of UV-B stimulated membrane changes are uncertain. There is little evidence that the UV damage to membranes is responsible for cell death. UV-stimulated membrane changes may play a role in the UV-induced synthesis of anthocyanins (Murphy, 1983).

Intraspecific differences in physiological responses of crop cultivars to enhanced UV-B radiation under field conditions were complex as observed in most of the 20 wheat cultivars in this paper. However, out of 20 wheat cultivars, the ranking of every indicator was different (Table 3). Correlations between the indicators were not observed (*P* > 0.05). In a flavonoid mutant of barley (*H. vulgare*), the low flavonoid content in leaves was correlated with a decline in apparent quantum yield and the less robust appearance of the mutant plants as compared with the mother variety (Reuber et al., 1996). The responses of SOD activity and MDA contents to enhanced UV-B radiation were not well known. UV-B radiation may induce the production of peroxo free radical, such as O₂⁻, H₂O₂, resulting in membrane lipid peroxidation, which lead to changes in membrane structure, and alter membrane permeability finally (Murphy, 1990).

In this study, the response index was an integration of the effect on plant height, LAI, tiller number, shoot biomass and grain yield of 20 wheat cultivars, which could reflect the overall sensitivity of wheat cultivars to enhanced UV-B radiation (Li et al., 2000). Correlation analysis showed that the response index did not correlate with chlorophyll contents, flavonoid contents, membrane permeability, SOD activity and MDA contents, respectively (*P* > 0.05). However, Tevini et al. (1990) had demonstrated that in rye the dose-dependent increase in flavonoid production is sufficient to fully protect the photosynthetic machinery from UV-induced damage. Preliminary results suggest that intraspecific differences in UV-B sensitivity in wheat may also be related to difference in the concentration of UV absorbing compounds in leaves (Murali and Teramura, 1986). In soybean, the effect of UV-B on total plant biomass was dependent on the concentration of UV-B absorbing compounds (D’surney
et al., 1993). In spinach and bean, however, such a relationship was not found, suggesting that intraspecific differences in UV-B sensitivity may arise through a complex of specific responses rather than a generalized response (Murali and Teramura, 1986).

There are clearly important intraspecific differences in response of the measured physiological parameters to enhanced UV-B radiation. Since no correlation between these effects and the response index was found, other parameters may determine the sensitivity to UV-B.

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References


