J Plant Growth Regul (1995) 14:61–67

Journal of
Plant
Growth
Regulation

# Heavy Metal-Hormone Interactions in Rice Plants: Effects on Growth, Net Photosynthesis, and Carbohydrate Distribution

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Received October 7, 1994; accepted January 5, 1995

**Abstract.** The effect of external applications of gibberellins ($GA_3$) and abscisic acid (ABA) on the growth, carbohydrate content, and net photosynthesis of heavy metal–stressed rice plants (*Oryza sativa* cv. Bahía) was investigated. Treatment with cadmium (0.1 mM) and nickel (0.5 mM) inhibited rice growth and stimulated carbohydrate accumulation, especially in seeds from which seedlings were developing, stems, and first leaves. The addition of $GA_3$ (14 μM) to the rice culture solution together with Cd or Ni partially reversed the effects of heavy metals, stimulating growth as well as mobilization of carbohydrate reserves in seeds from which seedlings had developed. $GA_3$ increased the sugar content in roots and second and third leaves and also modified the carbohydrate distribution pattern compared with heavy metal–treated plants. In contrast to $GA_3$, ABA (19 μM) supplied to rice cultures potentiated the effect of heavy metals, inhibiting the growth of young leaves and the translocation of storage products from source to sink organs. In addition, sugars were accumulated in roots and second leaf but not in the third leaf, the extension in length of which was also inhibited by the treatment. Net photosynthesis rates recovered transitorily in Cd-treated plants after the addition of hormones. The possible relationship between growth and carbohydrate distribution, as well as the involvement of hormones, in the response of plant to heavy metal stress is discussed.

Rice plants accumulate high concentrations of heavy metals, such as Cd and Ni (Honma and Hirata 1984, Ros et al. 1992, Rubio et al. 1994), which are known to have various effects on plant metabolism (Foy et al. 1978, Clijsters and Van Assche 1985, Weigel 1985, Malik et al. 1992). Growth of plant organs is generally regarded as being controlled by a balance of endogenous hormones. Specifically in rice, the growth rate seems to be determined by the balance of gibberellin (GA), a growth promoter, and of abscisic acid (ABA), a growth inhibitor (Hoffmann-Benning and Kende 1992). On the other hand, both ABA and GA have also been implicated in the control of assimilate production and compartmentation in plants (Thomas 1986). Finally, the involvement of plant growth regulators, mainly ABA, in plant responses to different stresses has been postulated (Zeevaart and Creelman 1988). In this way, it has been shown that heavy metals alter hormone content in plants (Poschenrieder et al. 1989) and that the application of hormones to heavy metal–stressed plants reduced the uptake of these metals (Rubio et al. 1994).

Previously, we have demonstrated that Cd and Ni inhibit growth and also modify the carbohydrate distribution and content in rice seedlings (Moya et al. 1993). From these results, the next step is trying to answer the question if the external hormone applications might modify the alterations produced by heavy metals in rice plants. Our objective in this work was to study possible interactions between the heavy metals Cd and Ni and the plant hormones $GA_3$ and ABA that could reverse the negative effects caused by these heavy metals on the growth, carbohydrate distribution, and net photosynthesis in rice plants.

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**Abbreviations:** 5DT, 5 days after treatment; 10DT, 10 days after treatment; ABA, abscisic acid; $GA_3$, gibberellic acid; TMC, total metabolizable carbohydrates.

**Table 1.** Effect of 5DT or 10DT with Cd, Cd + $GA_3$, or Cd + ABA on the length (in millimeters) of rice organs[a]

| | 5DT | | | 10DT | | |
|---|---|---|---|---|---|---|
| | Cd | Cd + $GA_3$ | Cd + ABA | Cd | Cd + $GA_3$ | Cd + ABA |
| Root | 66 (72) | 80 (87) | 79 (86) | 72 (72) | 80 (80) | 89 (89) |
| Stem | 71 (73) | 98 (101)[b] | 72 (74) | 76 (64) | 118 (99)[b] | 71 (60) |
| Second leaf | 28 (97) | 29 (100) | 29 (100) | 28 (97) | 28 (97) | 28 (97) |
| Third leaf | 96 (66) | 137 (94)[b] | 43 (30)[b] | 111 (72) | 155 (101)[b] | 66 (43)[b] |

[a] Data in parentheses are the percentage with respect to nontreated plants.

[b] Significantly different from the metal-treated plants: $P < 0.01$.

## Materials and Methods

### Plant Material

Rice (*Oryza sativa* L. cv. Bahía) seedlings were grown in 4l beakers containing an aerated culture solution as previously described (Ros et al. 1990). The cultures were kept in growth chambers at 30°C, 70% relative humidity (RH) (days) and 25°C, 90% RH (nights) with a 16-h photoperiod and a photosynthetically active radiation (PAR) irradiance of 95 $\mu$E $m^{-2}$ $s^{-1}$.

### Treatment with Xenobiotics and Phytohormones

Heavy metals or both heavy metals plus plant hormones (0.1 mM Cd or 0.5 mM Ni as chlorides; 14 $\mu$M $GA_3$ or 19 $\mu$M ABA) were added to the culture solution 6 days after sowing. Seeds (from which seedlings had developed), roots, stems, and leaves from treated and untreated plants were harvested 5 days (5DT) or 10 days (10DT) later, the height and photosynthesis were measured, and the carbohydrate content was determined as detailed below.

### Determination of Sugars

Samples were dried in a forced-air oven at 60°C and ground with a tissue grinder (Pulverissette, Fritch, Idar-Overstein, Germany). Hot 80% ethanol (8 $cm^3$) was added to 25 mg of the powdered material, and the mixture was boiled for 10 min. The procedure was repeated twice with the pellet obtained after centrifugation at 15,000 *g* for 10 min. Supernatants were combined and made up to 25 $cm^3$ with 80% ethanol. Aliquots of this extract were used for soluble sugars and sucrose analysis. For the determination of soluble sugars, an aliquot of the extract was transferred to a test tube, the ethanol was evaporated by immersion of the tube in a boiling water bath, and the aqueous residue was assayed with $H_2SO_4$-anthrone reagent as described by Fairbairn (1953), with glucose as standard. Sucrose was determined in another aliquot by the method of Roe (1934) after the elimination of free fructose from the extracts (Cardini et al. 1955).

The starch content was determined from the pellets obtained after centrifugation. These pellets were resuspended in 15 $cm^3$ of 35% $HClO_4$ and incubated overnight at room temperature. The volume was then made up to 25 $cm^3$ with distilled water. After filtration through filter paper, an aliquot was taken to quantify the glucose released by use of the method indicated above.

### Net Photosynthesis

Leaf photosynthesis was measured with a portable infrared gas analyzer (Licor Inc., Lincoln, NE), introducing both second and third leaves in the sample chamber. The leaf area was determined with an Image Analyzer (IBAS 2000, KONTRON, Everett MA).

### Statistical Treatment

All results are the mean of at least three independent experiments. Data were compared by analysis of variance and Newman-Keuls multiple-range test. The significance level was fixed at either $P < 0.05$ or $P < 0.01$.

## Results

### Hormone Effects on Rice Growth

The effect of $GA_3$ and ABA on the growth of Cd- and Ni-treated rice plants depended on plant organ. No significant effects of these hormones on the root length of heavy metal–treated plants were found (Tables 1 and 2). In the stems, ABA did not significantly affect the growth of Cd-treated plants but $GA_3$ stimulated it, reaching values similar to those of nontreated plants (Table 1). A similar trend to increase was observed after treatment with $GA_3$ (Table 2), although no significant effects were detected in Ni-treated plants.

The growth of the second leaf was already completed when treatments started, and this may be the reason why neither heavy metals alone nor hormones and heavy metals caused effects (Tables 1 and 2). In the third leaf, however, especially in Cd-treated plants, ABA potentiated the inhibition of growth produced by heavy metals whereas $GA_3$ reestablished the values found in nontreated plants. As with the stems, the growth recovery resulting from $GA_3$ treatment was higher for Cd-treated plants than for Ni-treated plants. In the latter, a

**Table 2.** Effect of 5DT or 10DT with Ni, Ni + GA$_3$, or Ni + ABA on the length (in millimeters) of rice organs[a]

| | 5DT | | | 10DT | | |
|---|---|---|---|---|---|---|
| | Ni | Ni + GA$_3$ | Ni + ABA | Ni | Ni + GA$_3$ | Ni + ABA |
| Root | 51 (55) | 68 (74) | 72 (78) | 53 (53) | 61 (61) | 70 (70) |
| Stem | 68 (70) | 86 (89) | 75 (77) | 70 (59) | 85 (71) | 69 (58) |
| Second leaf | 26 (90) | 27 (93) | 27 (93) | 28 (97) | 28 (97) | 27 (93) |
| Third leaf | 52 (36) | 58 (40) | 37 (26) | 54 (35) | 76 (49)[b] | 49 (32) |

[a] Data in parentheses are the percentage with respect to nontreated plants.

[b] Significantly different from the metal-treated plants: $P < 0.05$.

significant recovery of leaf growth was only observed after 10DT (Table 2).

### *Hormone Effects on Carbohydrate Levels and Photosynthesis*

The effect of Cd or Ni treatment on the carbohydrate content of rice plants found in this work confirms previous results (Moya et al. 1993), showing an increase in stem, second leaf, and seed from which the seedling had developed but a decrease in roots and third leaf compared with nontreated rice plants. Supplying ABA or GA$_3$ to the nutrient solution, together with heavy metals, resulted in various changes in the starch, soluble sugar, and sucrose content, depending on the organ (Tables 3 and 4). The starch content in seeds tends to either decrease or increase in the presence of GA$_3$ or ABA, respectively. The soluble sugar content was also diminished by GA$_3$, especially in Cd 5DT.

In roots, higher levels of all of the sugars determined were observed in the presence of both ABA and GA$_3$ (Tables 3 and 4). The stimulating effect on carbohydrate accumulation caused by ABA in Ni-treated plants was higher than that of GA$_3$; both hormones had similar effects on Cd-treated plants.

In stems, no significant changes were produced by GA$_3$ in the carbohydrate levels of Cd-treated plants at either 5DT or 10DT (Table 3). However, because Cd treatment alone increases the sugar content of stems, the carbohydrate levels observed in this organ were higher than those in nontreated-plants. ABA transiently stimulated a further accumulation of sugars, especially soluble sugars and sucrose, potentiating the effect produced by Cd in 5DT. In Ni-treated plants, no effects of ABA or GA$_3$ on the stem carbohydrate content were observed in 5DT, but in 10DT, both GA$_3$ and ABA produced a trend to a reduction of the starch content and an accumulation of soluble sugars and sucrose (Table 4).

The greatest effect of hormones on carbohydrate content was observed in leaves (Tables 3 and 4). In the second leaf, supply of ABA or GA$_3$ together with Cd increased the content of all sugars after 5DT and the effect remained for the starch fraction at 10DT (Table 3). Although GA$_3$ and ABA had effects on Ni-treated plants similar to those observed for Cd-treated ones, only a significant increase in starch after 5DT could be observed (Table 4).

In the third leaf of Cd-treated plants, GA$_3$ increased the starch, soluble sugar, and sucrose content of Cd-treated plants after 5DT and the starch content after 10DT, stimulating accumulation to even higher values than those found in nontreated plants (Table 3). The opposite occurred with ABA treatment because this hormone potentiated the effect of Cd and thus caused a reduction of sugars determined after 5DT and of starch at both sampling times. As observed in the second leaf, the effect of hormones on the third leaf sugar content was less evident in Ni-treated plants (Table 4). GA$_3$ increased the soluble sugar content in 5DT and starch in 10DT; ABA lowered significantly the sucrose content after 5DT but had no effect after 10DT.

As a result of all of these changes in the carbohydrate levels, the relative distribution of total sugars between the plant organs was also modified (Fig. 1). GA$_3$ caused an increase in the relative distribution of sugars in roots and leaves and a decrease in seeds compared with heavy metal–treated plants. ABA also changed the relative distribution of sugars, particularly, the distribution between the second and third leaves after 5DT. Thus, in Cd+ABA–treated plants, the second-to-third-leaf sugar ratio was increased almost three times compared with that in Cd-treated plants. It is also worth noting the higher percentage of total sugars in roots found after all ABA treatments.

Net photosynthesis was transitorily affected by hormones. Whereas after 10DT, no differences were observed with respect to heavy metal–treated plants, at 5DT, both hormones respectively increased or lowered the photosynthetic activity of Cd- or Ni-treated plants (Fig. 2).

**Table 3.** Content of starch, soluble sugars, and sucrose (micrograms per plant) in seeds, roots, stems, and leaves from plants treated with Cd, Cd + $GA_3$, or Cd + ABA for 5DT or 10DT.[a]

| | 5DT | | | 10DT | | |
|---|---|---|---|---|---|---|
| | Cd | Cd + $GA_3$ | Cd + ABA | Cd | Cd + $GA_3$ | Cd + ABA |
| Seed | | | | | | |
| Starch | 914 (197) | 363 (78) | 1,242 (268) | 286 (129) | 142 (64) | 311 (141) |
| Soluble sugars | 1,330 (190) | 905 (129)[b] | 1,263 (180) | 263 (286) | 184 (200) | 377 (410) |
| Sucrose | 464 (194) | 319 (133) | 386 (162) | 132 (203) | 100 (153) | 170 (262) |
| TMC | 2,244 (193) | 1,268 (109) | 2,505 (215) | 549 (175) | 326 (104) | 688 (220) |
| Root | | | | | | |
| Starch | 195 (78) | 245 (98)[b] | 235 (94)[b] | 219 (104) | 313 (148)[b] | 296 (140)[b] |
| Soluble sugars | 34 (121) | 60 (214) | 73 (261) | 29 (100) | 57 (197)[c] | 57 (197)[c] |
| Sucrose | 31 (148) | 40 (190) | 59 (281) | 26 (144) | 44 (244) | 43 (239) |
| TMC | 229 (82) | 305 (110)[c] | 308 (111)[c] | 248 (103) | 370 (154)[b] | 353 (147)[b] |
| Stem | | | | | | |
| Starch | 582 (129) | 608 (135) | 720 (160) | 647 (124) | 671 (129) | 731 (140) |
| Soluble sugars | 295 (215) | 271 (198) | 526 (384)[c] | 230 (147) | 240 (154) | 328 (210) |
| Sucrose | 220 (297) | 155 (209) | 463 (626)[c] | 138 (182) | 122 (161) | 226 (297) |
| TMC | 877 (149) | 879 (149) | 1,246 (212)[c] | 877 (130) | 911 (135) | 1,059 (156) |
| Second leaf | | | | | | |
| Starch | 37 (103) | 46 (128)[c] | 52 (144)[b] | 37 (106) | 51 (146)[c] | 58 (166)[b] |
| Soluble sugars | 46 (139) | 59 (179)[c] | 74 (224)[b] | 48 (145) | 62 (188) | 58 (176) |
| Sucrose | 34 (148) | 49 (213)[c] | 65 (283)[b] | 33 (236) | 50 (357) | 50 (357) |
| TMC | 83 (120) | 105 (152)[b] | 126 (183)[b] | 85 (125) | 113 (166)[c] | 116 (174)[c] |
| Third leaf | | | | | | |
| Starch | 155 (78) | 241 (122)[b] | 91 (46)[b] | 212 (106) | 295 (148)[b] | 160 (80)[b] |
| Soluble sugars | 181 (92) | 240 (122)[c] | 109 (55)[c] | 202 (102) | 224 (113) | 151 (76) |
| Sucrose | 161 (116) | 204 (147)[c] | 97 (70)[b] | 159 (121) | 183 (140) | 123 (94) |
| TMC | 336 (85) | 481 (122)[b] | 200 (51)[b] | 414 (104) | 519 (130)[c] | 311 (78)[c] |

[a] Data in parentheses are the percentage with respect to nontreated plants.

[b] Significantly different from the metal-treated plants: $P < 0.01$.

[c] Significantly different from the metal-treated plants: $P < 0.05$.

## Discussion

The exogenous supply of $GA_3$ to rice seedlings treated with Cd or Ni stimulated stem and leaf growth in such a way that, in Cd-treated plants, it mimicked the growth of nontreated plants (Tables 1 and 2). The recovery of stem and third leaf length was complete in the treatments with Cd+$GA_3$. In addition, $GA_3$ stimulated the mobilization of carbohydrate reserves from seeds and their translocation to the growing organs, i.e., the third leaf, in which the carbohydrate levels were even higher than in nontreated plants (Table 3).

It has been reported that ABA decreases heavy metal absorption in rice plants (Rubio et al. 1994). However, ABA treatment did not reverse the inhibition of growth caused by heavy metals in stems and third leaf (Tables 1 and 2). Higher levels of sugars were found in ABA plus heavy metal–treated plants, especially after 5DT (Tables 3 and 4). This increase is a consequence of a decreased utilization of carbohydrate for growth rather than an increase in synthesis from assimilated carbon, because the daily increase in dry weight in Cd+ABA–treated plants is approximately 50% higher than the one estimated by photosynthesis. ABA also appears to affect the sugar translocation and distribution in the plant because an increase in the carbohydrate content in the second leaf and a decrease in the third leaf were observed. However, ABA did not affect or even potentiate the inhibition induced by heavy metal treatment on sugar translocation from seeds to other plant organs. As a result, carbohydrates were accumulated in sources (second leaf and seeds) or storage sink (roots), probably as the result of the inhibition of their translocation to expanding leaves.

ABA would, therefore, potentiate the effects of heavy metals by accumulating carbohydrates and inhibiting growth, whereas $GA_3$ tends to reverse these effects by increasing growth and stimulating sugar mobilization. The effects of hormones were more obvious in Cd- than in Ni-treated plants, perhaps because the concentration used for Ni caused more drastic effects on rice plants, reducing any

**Table 4.** Content of starch, soluble sugars, and sucrose (micrograms per plant) in seeds, roots, stems, and leaves from plants treated with Ni, Ni + $GA_3$, or Ni + ABA for 5DT or 10DT.[a]

| | 5DT | | | 10DT | | |
|---|---|---|---|---|---|---|
| | Ni | Ni + $GA_3$ | Ni + ABA | Ni | Ni + $GA_3$ | Ni + ABA |
| Seed | | | | | | |
| Starch | 1,848 (398) | 1,583 (341) | 2,426 (523) | 485 (219) | 353 (160) | 608 (275) |
| Soluble sugars | 2,101 (300) | 1,914 (273) | 1,969 (281) | 625 (679) | 576 (626) | 738 (802) |
| Sucrose | 679 (284) | 538 (225) | 552 (231) | 334 (514) | 255 (392) | 294 (452) |
| TMC | 3,949 (339) | 3,497 (300) | 4,395 (378) | 1,110 (355) | 929 (297) | 1,346 (430) |
| Root | | | | | | |
| Starch | 136 (54) | 164 (66)[b] | 175 (70)[c] | 144 (68) | 154 (73) | 184 (87)[b] |
| Soluble sugars | 33 (118) | 53 (189) | 75 (268)[c] | 22 (76) | 34 (117) | 52 (179)[b] |
| Sucrose | 30 (143) | 42 (200) | 68 (324)[b] | 19 (105) | 24 (133) | 41 (228) |
| TMC | 169 (61) | 217 (78)[b] | 250 (90)[c] | 166 (69) | 188 (78) | 236 (98)[b] |
| Stem | | | | | | |
| Starch | 1,091 (242) | 938 (208) | 989 (219) | 1,800 (345) | 1,227 (236) | 1,281 (246) |
| Soluble sugars | 779 (569) | 831 (607) | 866 (632) | 675 (433) | 720 (462) | 765 (490) |
| Sucrose | 708 (957) | 708 (957) | 711 (961) | 454 (597) | 599 (788) | 672 (884) |
| TMC | 1,870 (318) | 1,769 (301) | 1,855 (315) | 2,475 (367) | 1,947 (288) | 2,046 (302) |
| Second leaf | | | | | | |
| Starch | 42 (117) | 57 (158)[b] | 57 (158)[b] | 45 (129) | 58 (166) | 59 (169) |
| Soluble sugars | 103 (312) | 129 (391) | 121 (367) | 115 (348) | 91 (276) | 107 (324) |
| Sucrose | 89 (387) | 122 (530) | 114 (496) | 86 (614) | 74 (529) | 94 (671) |
| TMC | 145 (210) | 186 (270) | 178 (257) | 160 (235) | 149 (219) | 166 (244) |
| Third leaf | | | | | | |
| Starch | 109 (55) | 109 (55) | 71 (36) | 110 (55) | 152 (76)[b] | 115 (58) |
| Soluble sugars | 150 (76) | 190 (96)[b] | 122 (62) | 152 (76) | 168 (84) | 184 (92) |
| Sucrose | 143 (103) | 158 (114) | 105 (76)[b] | 128 (98) | 138 (105) | 158 (121) |
| TMC | 259 (66) | 299 (76)[b] | 193 (49)[c] | 262 (66) | 320 (80) | 299 (75) |

[a] Data in parentheses are the percentage with respect to nontreated plants.
[b] Significantly different from the metal-treated plants: $P < 0.05$.
[c] Significantly different from the metal-treated plants: $P < 0.01$.

observable recovery or potentiation by hormone application.

The increase in dry weight measured in plants 6 to 16 days old is 50 to 60% higher than that estimated from current photosynthesis. Therefore, during this period, the seeds represent the main supply of carbohydrates to the plants. So, ABA and $GA_3$ may mainly affect the distribution and translocation of seed reserves. Although there is an activation of photosynthesis by $GA_3$ after 5DT coinciding with the greatest effect of hormones on carbohydrate content, this activation was not maintained over the whole period of treatment and it was only observed in Cd-treated plants. A higher level of photoassimilates may explain the stronger response of Cd-treated plants to hormones after 5DT but not all of the changes in carbohydrate content and partitioning.

The stimulation of growth provoked by $GA_3$ is related, at least in part, to a higher rate of assimilate translocation from seeds; this is in accordance with the suggestion that GAs are involved in initiating source activities as well as in activating translocation and loading at the source tissue (Patrick 1987, Aloni et al. 1986). There would also appear to be a relationship between the inhibition of growth caused by ABA and lower rates of assimilate translocation from sources (seeds and second leaf) to expanding leaves (third leaf); this agrees with previous observations of the inhibition of phloem loading by ABA (Thomas 1986, Vreugdenhil 1983), which could account for the accumulation of assimilates in source and thus the inhibition of the third leaf growth.

The inhibition of rice growth and the accumulation of storage products that result from heavy metal treatment could be an adaptation mechanism by which plants could maintain a greater viability in this adverse condition and eventually recover if the toxin is removed. In this way, Thompson and Couture (1990) found that, in populations of *Selenastrum capricornutum* exposed to Cd, the synthesis of storage products was increased, leading to energy levels (cellular ATP) sufficient to allow the survival of the population while being too low to sustain growth. An increase in the number of lipid and

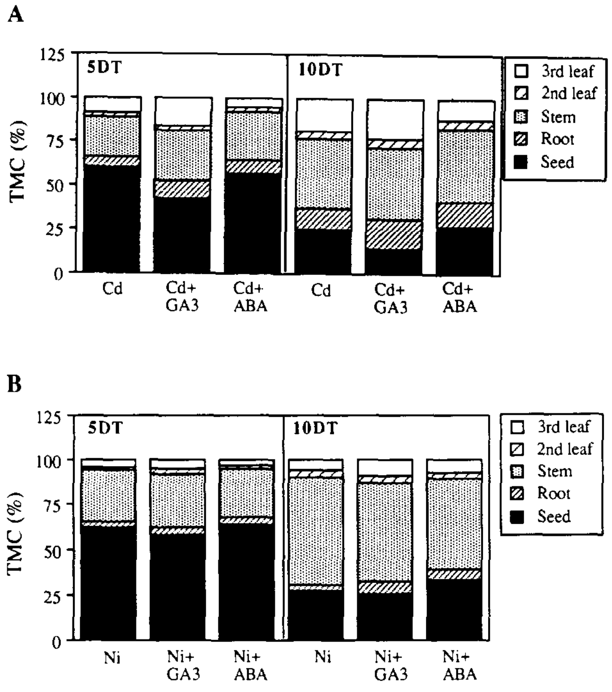

**Fig. 1.** Relative distribution of total sugars between the different organs in plants treated for 5DT or 10DT with (A) Cd, Cd + $GA_3$, or Cd + ABA or (B) Ni, Ni + $GA_3$, or Ni + ABA.

starch vesicles has also been reported in algae exposed to Cd (Rachlin et al. 1984, Prévot and Soyer-Gobillard 1986). Because hormones are implicated in the regulation of assimilate metabolism and growth (Thomas 1986, Dijkstra et al. 1990), it may be possible that they play a role in the response of plants to heavy metal stress. In fact, there is strong evidence that ABA is involved in the adaptation of plants to stresses such as cold or salt (Zeevaart and Creelman 1988, Walton 1980). In this way, Munns (1993) has related the growth inhibition produced by salt stress with the fall in assimilate or hormone supply to the growing regions. Additionally, in deepwater rice, the capacity of plants to elongate rapidly in order to avoid drowning when they become submerged is thought to be related to the GA to ABA ratio (Hoffmann-Benning and Kende 1992), which could govern the growth responses in this plant.

In conclusion, our results show that $GA_3$ reverses the inhibition of growth and assimilate translocation produced by heavy metals, whereas ABA potentiates the metals' effects. The mechanism by which this occurs and whether or not plant growth regulators are implicated in the response of rice plants to heavy metal stress await further study.

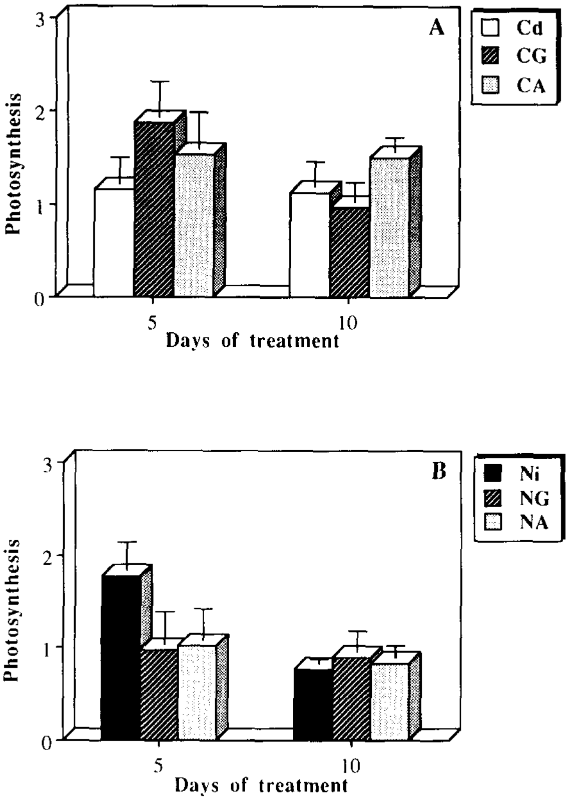

**Fig. 2.** Effect of 5DT or 10DT with either Cd, Cd + $GA_3$ (CG), and Cd + ABA (CA) (A) or Ni, Ni + $GA_3$ (NG), and Ni + ABA (NA) (B) on net photosynthesis (micromoles of $CO_2$ per square meter per second) of rice plants.

*Acknowledgments.* This work was supported by the Spanish Dirección General de Investigación Científica y Técnica (DGICYT PB91-0645) and by a bursary to J.L. Moya López from the Conselleria de Educació i Ciència de la Generalitat Valenciana. Rice seeds were the kind gift of Dr. Juan Castell (Cooperativa de semillas de arroz, Sueca).

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