J Plant Growth Regul (1997) 16:35–41

Journal of
Plant
Growth
Regulation

Growth Responses and Allocation of Assimilates of Rice Seedlings by Paclobutrazol and Gibberellin Treatment

K.-O. Yim,[1] Y. W. Kwon,[2] and D. E. Bayer[1,]*

[1]Section of Plant Biology, University of California, Davis, California 95616 USA; and the [2]Department of Agronomy, College of Agricultural and Life Science, Seoul National University, Suwon, Gyunggi-do, Republic of Korea

Received May 30, 1996; accepted December 10, 1996

Abstract. Paclobutrazol [(2*RS*,3*RS*)-1-(4-chlorophenyl)methyl-4,4-dimethyl-2-(1h-1,2,4-trizol-1-yl)penten-3-ol] effectively decreased vegetative growth of rice (*Oryza sativa* L.) seedlings and increased the chlorophyll content. The number of veins in a leaf, the calculated number of stomata per leaf, and the length of guard cells were not altered by the paclobutrazol treatment, suggesting an effect on cell elongation. The allocation pattern of carbohydrates was changed by either gibberellin (GA) or paclobutrazol treatment. GA_3 induced more shoot growth and less accumulation of starch than the control and paclobutrazol-treated seedlings. Photosynthetic ability was not affected by either paclobutrazol or GA_3 treatment. Paclobutrazol-treated plants allocated a smaller amount of photosynthates for vegetative shoot growth and stored more as starch in the crowns than the control and GA_3-treated plants. The same starch degrading activity in the crown tissue of paclobutrazol-treated seedlings as in control plants suggests that the accumulated starch is utilized in a normal activity for growth including leaf emergence, tiller formation, and root production, resulting in improved seedling quality.

Key Words. Paclobutrazol—Gibberellin—Rice seedling growth—Rice seedling morphology—Carbohydrate allocation—Seedling quality

Specific regulation of plant growth by the application of plant growth regulators has been studied extensively to improve growth behavior and enhance yield in many crop species (Grossman 1992). During the 1980s the use of plant growth regulators increased more rapidly than any other agricultural chemical group (Cooke 1987). Gibberellin (GA) biosynthesis inhibitors are the most widely used plant growth regulators in agronomic and horticultural crops (Davis and Curry 1991).

Paclobutrazol, a member of the triazole plant growth regulator group, is a broad spectrum GA biosynthesis inhibitor (Davis and Curry 1991). The primary mode of action of paclobutrazol is inhibition of *ent*-kaurene oxidase, which catalyzes the sequential oxidations from *ent*-kaurene to *ent*-kaurenoic acid in the early sequence of GA biosynthesis (Graebe 1987, Rademacher et al. 1987). Recently an additional mode of action for triazole compounds has been suggested (Grossman 1992) which is related to increased antioxidant content (Upadhyaya et al. 1989). This is particularly important for the plant's protection against environmental stresses such as drought, high or low temperature (Fletcher and Hofstra 1985, Wang 1985), and gaseous sulfur dioxide (Lee et al. 1985). Paclobutrazol reduces plant height (Cox and Keever 1988, Davis et al. 1988) and increases chlorophyll content (Hawkins et al. 1985) in various plant species. Because paclobutrazol has been very effective for the reduction of vegetative growth, many studies have been initiated to investigate prevention of lodging in cereal crops (Froggatt et al. 1982, Kang et al. 1985), canopy control of fruit trees (Quinlan 1987, Tukey 1981), and growth control of turfgrass (Dalziel and Lawrence 1984), ornamentals (Keever and Cox 1989), bedding plants (Cox and Keever 1988, Tayama and Carver 1990), and floricultural crops (Davis et al. 1988, Suh et al. 1992). Paclobutrazol also increased in vitro shoot regeneration and improved the quality of regenerated plantlets (Sankhla et al. 1992).

Different concentrations of GA are required for plant development at different stages of growth during the life cycle (Takahashi 1992). In rice plants, GA_{19} and GA_1 are

---

Abbreviations: GA, gibberellin; FW, fresh weight; ANOVA, analysis of variance; LSD, least significant difference.

*Author for correspondence.

the most abundant forms, and the total amount of GA decreases following anthesis (Takahashi 1986). The tall rice variety Nihonbare has significantly higher levels of GA than the semidwarf variety Tongil (Takahashi 1986). Rice varieties with the dwarf gene Dee-geo-woo-gen have reduced levels of GA biosynthesis (Harada 1985). GA increases the plant height of rice seedlings (Hanada 1964) by elongation of leaves and stems and by inhibiting tiller production (Jung 1986). GA-treated tissues act as strong sinks to induce carbohydrate translocation (Weaver et al. 1969). However, GA-treated plants have been shown to decrease overall starch accumulation (Davis et al. 1988).

GA biosynthesis inhibitors are not only used for plant growth regulation but also to study the effect of GA by lowering the endogenous level of GA. The reduction in the endogenous level was proportional to the concentration of paclobutrazol, and leaf length was correlated linearly to the log concentration of GA_1 (Lenton and Hedden 1987). Paclobutrazol is translocated primarily apoplastically through the xylem to its site of action where it decreases the rate of cell division and elongation, which ultimately results in a reduction of the vegetative growth. In cereal crops, the use of paclobutrazol has been focused on the prevention of lodging and not on improvement of seedling quality. Good seedling quality (substantiality) is essential for early establishment and growth and is reflected through enhanced yield components and ability to overcome environmental stresses. Substantiality may be expressed by shoot dry weight/unit of plant height. In this study the effects of paclobutrazol and GA_3 on rice seedling photosynthesis, allocation of assimilates, utilization of stored starch, growth morphology, and rooting ability were evaluated.

Materials and Methods

Rice seeds (var. Minehikari) were planted with 1.5 × 1.5-cm spacing density in plastic pots (10 × 10 × 10 cm). For paclobutrazol (ICI Co.) treatment, 50 mL of paclobutrazol solution containing 0.7 mg of a.i. paclobutrazol (4.8×10^{-5} M) was sprayed uniformly onto each pot just prior to seedling. For GA treatment, 20 mL/pot 6.5×10^{-5} M GA_3 solution was sprayed onto seedings at 20 days after seeding. At 20 days after seeding, usually the fifth leaf was emerging in control plants.

Plant height, chlorophyll content, leaf area, dry weight of shoots and roots, and rooting ability were measured on 35-day-old seedlings. The chlorophyll content of the youngest fully emerged leaves from 120 different seedlings was measured without sacrificing the leaf using a portable device designed to measure chlorophyll content, SPAD-501 (Minolta Co., Japan). The content of chlorophyll was expressed as mg of chlorophyll/g, FW, using the equation from the standard curve ($y = 0.1x + 0.578$, $r = 0.98^{**}$) which was derived from measurements taken with the SPAD-501 and photometric measurements of chlorophyll obtained by extraction in 80% acetone (Yoshida et al. 1972). Area of the youngest fully emerged leaf was measured from three different seedlings/pot with a leaf area meter (LI-3100-C, LI-Cor, Inc.). Soil was carefully washed from the roots of three sets of 20 seedlings from each treatment and separated into roots and shoots, and dry weight was measured after drying at 80°C in a forced air oven for 3 days. The root:shoot ratio was calculated from the dry weights. Substantiality was calculated as shoot dry weight/plant height. Rooting ability was observed from 10 seedlings of each treatment by removing roots 3 mm below the crown. The plants were then placed in distilled water at room temperature for 7 days after which the length of the new developing roots was measured and expressed as total length of new roots/seedling.

Each week the length of all leaves was measured for 30 seedlings, and leaf width was measured at the middle of the leaf, which usually represented the widest region. The number of fully emerged leaves, including tillers with at least one leaf, in each treatment was recorded from 30 seedlings every 5 days starting 10 days after seeding until 40 days after seeding.

The micromorphology of leaves was observed under a light and a scanning electron microscope. Replicas from the central section of the seventh leaf of 35-day-old seedlings were made by coating the leaf with collodion and staining with fast-green. Using a light microscope the number of veins/leaf and stomata/cm^2 was recorded for 20 different leaves in each treatment. The adjacent section of the same leaf was harvested in liquid nitrogen, freeze-dried (Uni-Trap 16-100, Virtis Co.) for 24 h, and coated with gold. The distance between veins and stomata and the length of the stomate were recorded using an electron scanning microscope (Stereoscan 250 Mk2, Cambridge Instrument Ltd.). Fifty observations were made from five leaves for each treatment.

Leaves, stems, crowns, and roots were harvested separately from 35-day-old seedlings and oven dried for 3 days at 80°C. A 100-mg ground sample was used for each analysis. Sugars were extracted with 80% ethyl alcohol, and starch was extracted with perchloric acid. The extracted sugars and starch were quantified with anthrone (Yoshida et al. 1972), and absorbence was read with a spectrophotometer (model Lambda 4B, Perkin-Elmer) at 630 nm. This analysis was repeated three times.

Photosynthesis measurements were made using the seventh leaf of 20 seedlings for each treatment at 35 days after seeding with a LI-600 Portable Photosynthesis System (LI-Cor Inc.).

Fresh leaf or crown tissue was harvested from 35-day-old seedlings and analyzed for starch degrading activity. One g of tissue was ground in 4 volumes of phosphate buffer (0.2 mM, pH 6.0) and centrifuged at 10,000 ×g for 25 min. The supernatant (0.25 mL) was diluted with 0.75 mL of distilled water and mixed with 2.5 mL of starch solution. Starch solution was prepared by dissolving 200 mg of pure potato starch in 200 mL of acetate buffer (0.2 M, pH 4.9). After incubation at 35°C for 20 min, the amount of degraded starch was determined by colorization with 0.5 mL of IKI solution, and absorbence was read at 660 nm using a spectrophotometer. This experiment was repeated three times.

All results were combined and subjected to analysis of variance (ANOVA) and followed by a comparison of means using the least significant difference (LSD). The statements made in the text are based on differences that were statistically significant using LSD at $P < 0.05$.

Results and Discussion

Paclobutrazol-treated rice seedlings were shorter (70% of control) but had a higher chlorophyll content on a FW basis (Table 1) at 35 days after seeding. GA_3-treated seedlings were taller than the control (152% of control) and had a lower chlorophyll content. Although GA_3 treatment did not decrease the number of green leaves statistically, the number of green leaves was increased by paclobutrazol treatment. The total area of green leaves/

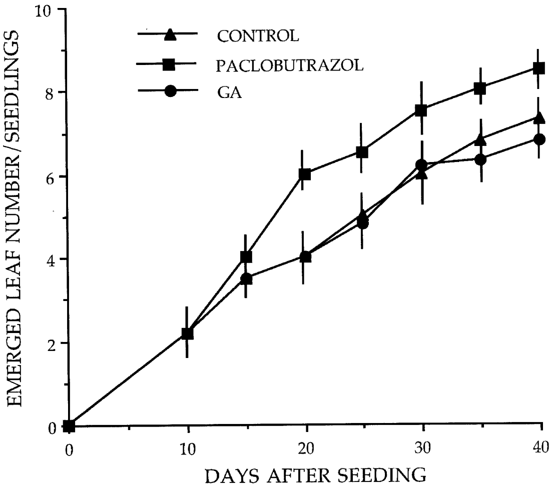

Fig. 1. Leaf emergence of rice seedlings treated with paclobutrazol or GA_3. Only fully emerged leaves were counted. Paclobutrazol solution (4.8×10^{-5} M) was sprayed uniformly onto the soil of each pot (10 × 10 × 10 cm) just prior to seeding. GA_3 solution (6.5×10^{-5} M) was sprayed onto seedlings at 20 days after seeding, at the four-leaf stage. *Vertical bars* indicate the standard error of the means ($n = 30$).

Table 1. Plant height, chlorophyll content, number of green leaves/seedling, and leaf area/seedling of paclobutrazol- and GA_3-treated rice seedlings at 35 days after seeding. Paclobutrazol solution (4.8×10^{-5} M) was sprayed uniformly onto the soil of each pot (10 × 10 × 10 cm) just prior to seeding. GA_3 solution (6.5×10^{-5} M) was sprayed onto the seedlings at 20 days after seeding, at the four-leaf stage.

	Control	Paclobutrazol[a]	GA_3[a]
Plant height (cm)	16.5	11.5*	25.0*
Chlorophyll content (mg/g FW)	1.74	2.14*	1.14*
No. of green leaves	3.4	3.9*	3.1
Area of green leaves/seedling (cm^2)	6.7	6.6	5.9*

[a] All values followed by an asterisk are statistically different from controls at the 5% level ($n = 120$ in plant height, chlorophyll content, and no. of green leaves; $n = 36$ in area of green leaves/seedling).

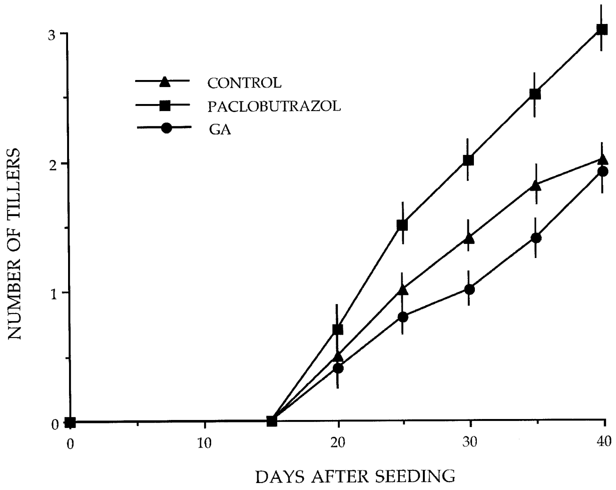

Fig. 2. Tiller formation of paclobutrazol- or GA_3-treated rice seedlings. The number of tillers with at least one leaf was counted. Paclobutrazol solution (4.8×10^{-5} M) was sprayed uniformly onto the soil of each pot (10 × 10 × 10 cm) just prior to seeding. GA_3 solution (6.5×10^{-5} M) was sprayed onto seedlings at 20 days after seeding, at the four-leaf stage. *Vertical bars* indicate the standard error of the means ($n = 30$).

Table 2. Dry weight of shoots and roots, rooting ability, and substantiality[a] of paclobutrazol- and GA_3-treated rice seedlings at 35 days after seeding. Paclobutrazol solution (4.8×10^{-5} M) was sprayed uniformly onto the soil of each pot (10 × 10 × 10 cm) just prior to seeding. GA_3 solution (6.5×10^{-5} M) was sprayed onto seedlings at 20 days after seeding, at the four-leaf stage.

	Control	Paclobutrazol[b]	GA_3[b]
Shoot dry weight (g/20 seedlings)	0.66	0.54*	0.76*
Root dry weight (g/20 seedlings)	0.84	1.03*	0.37*
Root/shoot dry weight	1.27	1.91	0.49
Substantiality (g/cm)	0.0020	0.0024	0.0015
Rooting ability (cm/seedling)	14.2	18.0*	5.0*

[a] Substantiality: shoot dry weight/plant height.

[b] All values followed by an asterisk are statistically different from controls at the 5% level ($n = 3$ in shoot dry weight and root dry weight; $n = 10$ in rooting ability).

The root:shoot ratio was calculated from root and shoot dry weight, and shoot dry weight was divided by plant height (Table 1) for substantiality.

seedling was not different in the control and paclobutrazol-treated seedlings; however, the area of each leaf in the paclobutrazol treatment was reduced. Because the seedlings in GA_3 treatment had very narrow leaves, the total leaf area was significantly lower than the control or paclobutrazol-treated seedlings.

Leaf emergence in seedlings treated with paclobutrazol was greater at 20 days after seeding and maintained approximately a 0.5-leaf advantage compared with the control or GA_3-treated seedlings (Fig. 1). Paclobutrazol treatment increased tillering at 25 days after seeding, and these seedlings maintained a one-tiller advantage over the control or GA_3-treated seedlings (Fig. 2). Paclobutrazol treatment has been reported to increase fertile tiller production in velvet grass (Hampton et al. 1992). GA_3 treatment decreased tillering at 30 and 35 days after seeding, but at 40 days after seeding the control and GA_3-treated seedlings had a similar number of tillers. Inhibition of tiller production by GA treatments has been reported in rice (Jung 1986).

Paclobutrazol decreased shoot dry weight and increased root dry weight (Table 2). GA_3 treatment showed an effect that was the reverse of the paclobutrazol treat-

Table 3. Length[a] of fully developed leaves of rice seedlings treated with paclobutrazol or GA$_3$. Paclobutrazol solution (4.8×10^{-5} M) was sprayed uniformly onto the soil of each pot (10 × 10 × 10 cm) just prior to seeding. GA$_3$ solution (6.5×10^{-5} M) was sprayed onto seedlings at 20 days after seeding, at the four-leaf stage.

	Leaf length (cm)							
	1st	2nd	3rd	4th	5th	6th	7th	8th
Control	2.6	4.9	8.8	9.6	10.2	10.3	10.8	10.9
Paclobutrazol[b]	1.4*	2.4*	4.1*	6.4*	8.2*	8.9*	10.1	10.6
GA$_3$[b]					10.9*	11.6*	16.2*	18.5*

[a] Leaf length was measured every 5 days starting 10 days after seeding until 40 days after seeding.
[b] All values followed by an asterisk are statistically different from controls at the 5% level ($n = 30$).

Table 4. Width[a] of fully developed leaves of rice seedlings treated with paclobutrazol or GA$_3$. Paclobutrazol solution (4.8×10^{-5} M) was sprayed uniformly onto the soil of each pot (10 × 10 × 10 cm) just prior to seeding. GA$_3$ solution (6.5×10^{-5} M) was sprayed onto seedlings at 20 days after seeding at the four-leaf stage.

	Leaf width (mm)							
	1st	2nd	3rd	4th	5th	6th	7th	8th
Control	2.4	2.4	3.1	3.3	3.7	5.5	5.8	5.8
Paclobutrazol[b]	2.4	2.5	3.3*	3.7*	4.3*	6.2*	6.2*	6.4*
GA$_3$[b]					3.4*	5.0*	4.3*	4.3*

[a] Leaf width was measured at the middle of the leaf every 5 days starting 10 days after seeding until 40 days after seeding.
[b] All values followed by an asterisk are statistically different from controls at the 5% level ($n = 30$).

Table 5. No. of veins/leaf, distance between veins, no. of stomata/cm^2/leaf, distance between stomata and length of guard cells from middle portion of the fully developed seventh leaf of 35-day-old rice seedling. Paclobutrazol solution (4.8×10^{-5} M) was sprayed uniformly onto the soil of each pot (10 × 10 × 10 cm) just prior to seeding. GA$_3$ solution (6.5×10^{-5} M) was sprayed onto seedlings at 20 days after seeding, at the four-leaf stage.

	Control	Paclobutrazol[a]	GA$_3$[a]
No. of veins/leaf	29.3	29.4	29.3
Distance between veins (μm)	126	173*	108*
No. of stomata/cm^2/leaf	257	295*	252
Distance between stomata (μm)	38	30*	45*
Length of guard cell (μm)	24	22	25

[a] All values followed by an asterisk are statistically different from controls at the 5% level ($n = 20$ in no. of veins/leaf, distance between veins and number of stomata/cm^2/leaf; $n = 50$ in distance between stomata and length of guard cell).

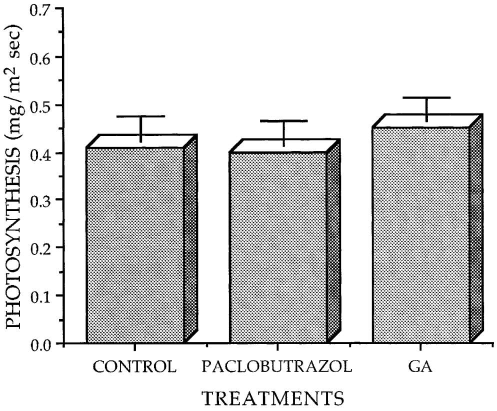

Fig. 3. Photosynthesis from the seventh leaf of paclobutrazol- or GA$_3$-treated seedlings at 35 days after seeding. Paclobutrazol solution (4.8×10^{-5} M) was sprayed uniformly onto the soil of each pot (10 × 10 × 10 cm) just prior to seeding. GA$_3$ solution (6.5×10^{-5} M) was sprayed onto seedlings at 20 days after seeding, at the four-leaf stage. *Vertical bars* indicate the standard error of the means ($n = 20$).

ment. The root:shoot ratio was increased in paclobutrazol-treated seedlings and decreased in GA$_3$-treated seedlings. The dry weight accumulation in the shoot as a result of the GA$_3$ treatment reflected the significant increase in seedling height (Table 1). Substantiality (relative dry weight accumulation in shoots), as expressed by dry weight/unit of plant height, was higher in paclobutrazol-treated seedlings (Table 2). Paclobutrazol-treated wheat seedlings showed higher root fresh and dry weight and increased root:shoot ratio (Pinhero and Fletcher 1994). Using citrus (Mauk et al. 1986) and apple seedlings (El Hodairi et al. 1988, Wang et al. 1985) paclobutrazol treatment caused basipetal transport of assimilates. These results suggest that altered GA levels resulting from GA$_3$ and paclobutrazol treatment cause different allocation patterns in plants. High GA level leads to a higher allocation of carbohydrates to the

Table 6. Content of starch and soluble sugars in different organs of 35-day-old rice seedlings treated with paclobutrazol or GA_3. Paclobutrazol solution (4.8×10^{-5} M) was sprayed uniformly onto the soil of each pot (10 × 10 × 10 cm) just prior to seeding. GA_3 solution (6.5×10^{-5} M) was sprayed onto seedlings at 20 days after seeding, at the four-leaf stage.

	Starch[a] (mg/g DW)			Soluble sugars[a] (mg/g DW)		
	Control	Paclobutrazol	GA_3	Control	Paclobutrazol	GA_3
Leaf	44	63*	28*	279	256*	310*
Stem	28	61*	34	113	118	122
Crown	89	110*	38*	91	95	73*
Root	4	18*	5	66	74*	65

[a] All values followed by an asterisk are statistically different from controls at the 5% level ($n = 3$).

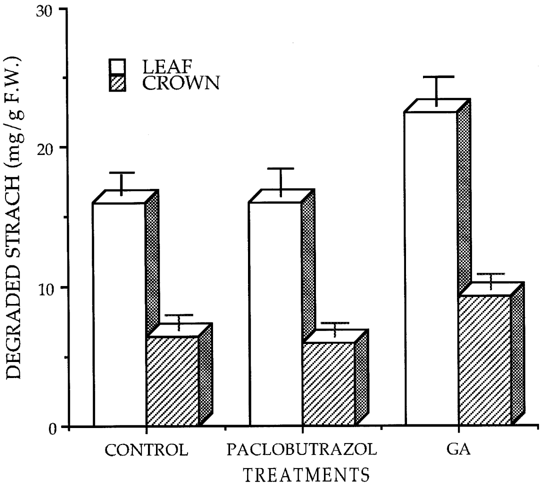

Fig. 4. Activity of starch degradation in control, paclobutrazol-, and GA_3-treated seedlings at 35 days after seeding. Paclobutrazol solution (4.8×10^{-5} M) was sprayed uniformly onto the soil of each pot (10 × 10 × 10 cm) just prior to seeding. GA_3 solution (6.5×10^{-5} M) was sprayed onto seedlings at 20 days after seeding, at the four-leaf stage. *Vertical bars* indicate the standard error of the means ($n = 30$).

shoots, whereas low GA level resulted in more dry matter accumulation in the roots (Table 2). It has been suggested that the inhibition of vegetative growth by paclobutrazol treatment alters the relative sink strength, which would indirectly affect the carbohydrate allocation pattern (Kohli 1985).

Rooting ability is an important index of seedling quality and is a critical factor for transplanting. Paclobutrazol-treated seedlings not only had higher root dry weight but also greater ability to produce new roots. Paclobutrazol-treated seedlings allocated more carbohydrates to the roots for an extended period of time following paclobutrazol treatment. GA_3-treated seedlings allocated fewer carbohydrates to the roots, which resulted in less root dry weight and lower rooting ability.

Paclobutrazol applied to the soil before seeding decreased the length of the first leaf by 46%, and the effects were maximized in the third leaf by a 53% reduction (Table 3). After the third leaf, the effect gradually diminished and had dissipated completely by the seventh leaf. GA_3 sprayed on leaves at 20 days after seeding caused significant leaf elongation starting with the fifth leaf, and the effect continued to increase through the eighth leaf, which was the last leaf measured in this experiment. Paclobutrazol increased leaf width significantly starting with the third leaf, whereas the GA_3 treatment decreased leaf width starting with fifth leaf (Table 4).

Because GA caused distinct changes in leaf shape, micromorphology of the leaf was investigated. Even though paclobutrazol-treated seedlings had wider leaves, the number of veins in a leaf was no different from the control or GA_3-treated seedlings (Table 5). The distance between veins was increased in paclobutrazol-treated seedlings and decreased in GA_3-treated seedlings. Thus the increased leaf width was due to the increased distance between veins rather than the number of veins. Paclobutrazol-treated seedlings had more stomata/unit area, whereas GA_3-treated seedlings had a similar density of stomata compared with the control. The distance between stomata was less in paclobutrazol-treated seedlings and greater in GA_3-treated seedlings when compared with control seedlings. However, there were no differences in the length of the guard cells regardless of treatments. When the number of stomata in a leaf was calculated from the density and leaf area, control, paclobutrazol- and GA_3-treated seedlings had similar number of stomata, approximately 500 stomata in the seventh leaf. Higher stomata density but a similar number of stomata/leaf has also been reported in paclobutrazol-treated soybean leaves (Hawkins et al. 1985).

Although there have been contradicting reports, paclobutrazol seems to have little effect on photosynthesis (Dalziel and Lawrence 1984). In this study, photosynthetic ability was not statistically different in all treatments (Fig. 3). Paclobutrazol-treated plants produced photosynthetic assimilates with efficiency similar to that of the control or GA-treated plants even though paclobutrazol-treated seedlings had a higher chlorophyll content (Table 1).

The effects of GA and paclobutrazol on starch and soluble sugar content in various tissues of rice seedlings were observed (Table 6). Starch was the most important storage material in rice and is utilized for the production of new leaves, tillers, and roots following conversion to the soluble sugars for mobilization or utilization in metabolism. Control plants showed a typical pattern of starch and soluble sugar distribution in rice seedlings with large amounts of starch accumulating in the crowns, stems, and leaves. No detectable starch was present in the roots. Soluble sugars were higher in the leaves than in the stems, crowns, and roots. Paclobutrazol- or GA_3-treated seedlings showed a pattern of starch and soluble sugar distribution similar to that of the control, but the amounts were quite different. Paclobutrazol treatment increased starch accumulation in the leaves, stems, crowns, and roots. An increase in starch content has been reported in various tissues in apple seedlings (Steffens et al. 1983). The amount of soluble sugars in the leaves was decreased, and the amount of soluble sugars in the roots was increased (Table 6). The increased amount of soluble sugars in the roots suggests a larger allocation of assimilates to the roots, which increased rooting activity and root dry weight (Table 2). Paclobutrazol influenced the allocation and utilization of photosynthates in young developing apples, which resulted in an increase in translocation and ultimately in an increase in yield (Quinlan 1987, Wang et al. 1985).

GA_3 treatment decreased starch accumulation in leaves and crowns and increased the content of soluble sugars in the leaves (Table 6). Starch was decreased dramatically by 43% in the crown. This may explain the delayed production of new leaves and tillers and lower rooting ability in GA_3-treated seedlings (Fig. 1, 2, Table 1).

GA activates the enzymes for utilization of starch (Weaver et al. 1969, Mulligan and Patrick 1979). The activity of starch degradation in the leaf and crown was increased by 40 and 45% in GA_3-treated leaves and crowns, respectively (Fig. 4), resulting in rapid growth in GA_3-treated seedlings. Paclobutrazol-treated seedlings had an efficiency in starch degradation similar to that of the control, which would indicate that the accumulated starch was utilized in a manner similar to the control.

References

Cooke AR (1987) The future of specialty plant growth regulators. Proc Plant Growth Regul Soc Am 14:2–7

Cox DA, Keever GJ (1988) Paclobutrazol inhibits growth of zinnia and geranium. HortScience 23:1029–1030

Dalziel J, Lawrence DK (1984) Biochemical and biological effects of kaurene oxidase inhibitors, such as paclobutrazol. In: Menhenett R, Lawrence DK (eds) Biochemical aspects of synthetic and naturally-occurring plant growth regulators. British Plant Growth Regulator Group, Wantage pp 43–57

Davis TD, Curry EA (1991) Chemical regulation of vegetative growth. Crit Rev Plant Sci 10:151–188

Davis TD, Steffens GL, Sankhla N (1988) Triazole plant growth regulators. Hort Rev 10:63–105

El Hodairi MH, Canham AE, Buckley WR (1988) The effects of paclobutrazol on growth and the movement of ^{14}C-labeled assimilates in Red Delicious apple seedlings. J Hort Sci 63:575–581

Fletcher RA, Hofstra G (1985) Triadimefon, a plant multi-protectant. Plant Cell Physiol 26:775–780

Froggatt PJ, Thomas DW, Batch JJ (1982) Opportunities for manipulation of cereal productivity. In: Hawkins AF, Jeffcoat E (eds) Recent developments in the use of plant growth retardants. British Plant Growth Regulator Group, Wantage pp 71–74

Graebe JE (1987) Gibberellin biosynthesis and control. Annu Rev Plant Physiol 38:419–465

Grossman K (1992) Plant growth retardants: Their mode of action and benefit for physiological research. In: Karssen CM, Van Loon LC, Vreugdenhil D (eds) Progress in plant growth regulation. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 788–797

Hampton JG, Tolentino MS, Hill MJ (1992) Effect of plant growth regulators on seed yield in velvet grass (*Holcus lanatus* L.) cv. Massey Basyn. NZ J Agric Res 35:35–40

Hanada K (1964) Studies on branching habits in crop plants. 3. Effects of leaf removal or addition of gibberellic acid through leaf blade on the growth of tillering buds in rice seedlings. Crop Sci Soc Japan 33:247–254

Harada J (1985) High-yielding semi-dwarf rice and gibberellins. International seminar on plant growth regulation in agriculture. Tokyo, Japan, pp 15–20

Hawkins AF, Hughes HK, Hart CA (1985) Effects of the growth regulator, paclobutrazol, on structure and photosynthesis of soybean leaves. In: Jeffcoat E, Hawkins AF, Stead AD (eds) Regulation of sources and sinks in crop plants. British Plant Growth Regulator Group, Wantage pp 127–142

Jung J (1986) Aims and possibilities of applied plant bioregulation. In: Yopp M (ed) Plant growth substances 1985. Springer-Verlag, Berlin, pp 46–67

Kang KK, Kwon YW, Yoo CY (1985) Effects of applied GA_3 and paclobutrazol, an inhibitor of GA biosynthesis, on the growth of internodes and panicle of the rice plants. J Crop Sci Korea 30:4–10

Keever GJ, Cox DA (1989) Growth inhibition of marigold following drench and foliar-applied paclobutrazol. HortScience 24:390

Kohli A (1985) Paclobutrazol, a versatile new plant growth regulator as an effective tool in crop management. International Seminar of Plant Growth Regulation in Agric. Tokyo, Japan, pp 125–130

Lee EH, Byun JK, Wilding SJ (1985) A new gibberellin biosynthesis inhibitor paclobutrazol (PP_{333}) confers increased SO_2 tolerance on snapbean plants. Environ Exp Bot 25:265–275

Lenton JR, Hedden P (1987) Gibberellin insensitivity and depletion in wheat: Consequences for development. In: Hoad GV, Lenton JR, Jackson MB, Atkin RK (eds) Hormone action in plant development: A critical appraisal. Butterworths, London, pp 145–160

Mauk CS, Bausher MG, Yelenosky G (1986) Influence of growth regulator treatments on dry matter production, fruit abscission and ^{14}C-assimilate partitioning in citrus. J Plant Growth Regul 5:111–120

Mulligan DR, Patrick JW (1979) Gibberellic-acid-promoted transport of assimilates in stems of *Phaseolus vulgaris* L. Planta 145: 233–238

Pinhero GR, Fletcher RA (1994) Paclobutrazol and ancymidol protect corn seedlings from high and low temperature stresses. Plant Growth Regul 15:47–53

Quinlan JD (1987) Use of paclobutrazol in orchard management to improve efficiency of fruit production. In: Hawkins AF, Stead AD, Pinfield JN (eds) Plant growth regulators for agricultural and amenity use. British Crop Council and British Plant Growth Regulator Group, Thornton Heath pp 45–49

Rademacher W, Fritsch H, Graebe JE, Sauter A, Jung J (1987) Tetcyclacis and triazole plant growth retardants: Their influence on the biosynthesis of gibberellins and other metabolic processes. Pesti Sci 21:241–252

Sankhla D, Davis TD, Sankhla N (1992) Effect of gibberellin biosynthesis inhibitors on shoot generation from hypocotyl explants of *Albizzia julibrissin.* Plant Cell Rep 13:115–118

Steffens GL, Wang SY, Steffens CL, Brennan T (1983) Influence of paclobutrazol (PP_{333}) on apple seedlings growth and physiology. Proc Plant Growth Regul Soc Am 10:195–206

Suh JK, Park NB, Franssen JM, De Munk WJ (1992) The use of anti-gibberellin in the production of tulip as pot plants. In: Karssen CM, Van Loon CL, Vreugdenhil D (eds) Progress in plant growth regulation. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 852–858

Takahashi N (1986) Plant growth substances in regulation of life cycle of higher plants. Proceedings International Symposium of Korean Weed Science Society pp 1–5

Takahashi N (1992) Gibberellins in regulation of the life cycle of plants. Proc Plant Growth Regul Soc Am 19:1–8

Tayama HK, Carver SA (1990) Zonal geranium growth and flowering responses to six growth regulators. HortScience 25:82–83

Tukey LD (1981) The growth regulator PP_{333} on apples. HortScience 16:401

Upadhyaya A, Davis TD, Walser RH, Galbraith AB (1989) Uniconazole-induced alleviation of low-temperature damage in relation to antioxidant activity. HortScience 24:955–957

Wang CY (1985) Modification of chilling susceptibility in seedlings of cucumber and zucchini squash by the bioregulator paclobutrazol (PP_{333}). Sci Hort 26:293–298

Wang SY, Byun JK, Steffens GL (1985) Controlling plant growth via the gibberellin biosynthesis system. II. Biochemical and physiological alteration in apple seedlings. Physiol Plant 63:169–175

Weaver RJ, Shindy W, Kliewer MW (1969) Growth regulator induced movement of photosynthetic products into fruits of Black grapes. Plant Physiol 44:183–188

Yoshida S, Douglas AF, James HC, Kwanchai AG (1972) Laboratory manual for physiology studies of rice. International Rice Research Institution, Philippines, pp 36–41