Gibberellin Biosynthesis Inhibitors Help to Control Plant Height and Improve Lodging Resistance in Tef (*Eragrostis tef*)

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ABSTRACT

Eragrostis tef, a highly nutritious cereal grown in East Africa, has a serious lodging problem reducing its productivity considerably. Certain plant-growth regulators are known to restrict growth and improve lodging resistance in cereals by affecting gibberellin biosynthesis. Effect on height of growth regulator chlormequat chloride (CCC) was determined for varieties Gea Lammie with a short and DZ-01-196 with a tall phenotype. Effects on growth and yield of DZ-01-196 were also determined after treatment with plant growth regulator PBZ. Chlormequat chloride decreased plant height by 27% in Gea Lammie and by 46% in DZ-01-196. In DZ-01-196, CCC and PBZ treatments also reduced culm length but had no effect on internode diameter. In DZ-01-196, CCC, although reducing plant height, had no effect on grain yield. The regulation of gibberellin biosynthesis could therefore be a key target for improving lodging resistance in *Eragrostis tef.*

KEYWORDS: *Plant height, Eragrostis tef, lodging resistance, plant growth regulators, chlormequat chloride, paclobutrazol*

INTRODUCTION

Eragrostis tef (*E. tef* Trotter) is a panicle-bearing, small-seeded nutritious cereal grown extensively in East Africa in diverse climatic and soil conditions with low risk of failure (Assefa et al. 2010). In Ethiopia, the grain is a staple food for an estimated 60 million people. It is grown on >2.6 million ha and accounts annually for about 28% of the total acreage of this cereal in the country. However, *E. tef* suffers from low productivity, with average yields of only 1.0 t ha^{-1}. Lodging is the most important factor contributing to the low yield (Assefa et al. 2010; Tefera et al. 2003; Yu et al. 2007).

Lodging generally affects productivity by interfering with water and nutrient transport as well as light interception. It also provides a favorable environment for disease and reduces grain yield and quality increasing harvesting cost and losses (Tripathi et al. 2003). Studies showed that lodging caused by stem bending at the basal internodes to be a frequent phenomenon when compared with root lodging or failure of the anchorage system (Ketema 1983; Asefa et al. 2000). Culm length and the strength of the basal part of the culm are also considered major factors associated with lodging sensitivity in many cereals (Rajala, 2003; Tripathi et al. 2003).

In cereals, improvement of lodging resistance has been predominantly achieved by reducing plant height, in particular by chemical inhibition of gibberellin (GA) production (Rademacher 2000) or by the use of semi-dwarf varieties with reduced GA biosynthesis or signal transduction (Hedden 2003). Chlormequat chloride (2-chloroethyl-N,N,N-trimethyl-ammonium chloride; CCC), the most commonly used plant growth regulator (PGR), blocks GA biosynthesis by inhibition of the cyclization of geranylgeranyl diphosphate (GGPP) to *ent*-copalyl diphosphate (CPP) by CPP synthase (Rademacher 2000). Triazole PGRs, such as paclobutrazol (PBZ), inhibit the conversion of the GA precursor *ent*-kaurene to *ent*-kaurenoic acid (Rajala 2003; Hedden & Graebe 1985). In general, these two PGRs and others that inhibit GA biosynthesis have been extensively used in many crops to reduce lodging through shortening of the stem and to maintain a steady improvement in grain yield (Rajala 2003; Berry et al. 2004). Reduction in plant height caused by PGR treatment is associated with reduced elongation of internodes, particularly of the uppermost internodes and peduncle (Sanvicente et al. 1999; Rajala 2003). Foliar treatment with a combination of CCC, ethephon and imazaquin reduced main stem length in barley, where shortening of the three uppermost internodes contributed significantly to the reduction of the main stem (Sanvicente et al. 1999). In rice, plant height of dwarf lines carrying the sd-1 gene was 72.1% of that of tall (wild type) lines and only the three uppermost internodes accounted for about 75% of the difference in height between dwarf and tall lines (Bin-mei et al. 2006). PBZ application was found to reduce stem length and lodging in rice and increased yield by about 15% compared with controls (French et al. 1990).

In *E. tef*, cultivars bred for improved grain yield have a tall phenotype, such as variety DZ-01-196, and are highly susceptible to lodging (Assefa et al. 2010; Yu et al. 2007). Thus, lodging susceptibility has prevented the introduction of higher yielding varieties with good grain quality, and has also hampered the use of input-intensive husbandry. Currently, there is no detailed information available for *E. tef* on the effect of PGR treatment on lodging and yield responses. The objective of this study was therefore to investigate morphological and yield changes in *E. tef* varieties following treatment with GA biosynthesis inhibitors, CCC and PBZ, under controlled environmental conditions. In particular, a short (Gea Lammie) and a tall (DZ-01-196) *E. tef* variety were compared in this study in their response to GA_3 and CCC treatment. Further, the effect of two GA inhibitors, CCC and PBZ, on growth and yield traits of variety DZ-01-196 was investigated. This variety is the most widely grown commercial variety because of its yield, seed quality and adaptability to various environments, but critically suffers from lodging. Therefore, knowledge of the mechanism of increasing lodging resistance in *E. tef* is highly desirable.

MATERIALS AND METHODS

Plant Material and Growth

Seed material for the *E. tef* varieties DZ-01-196, an improved tall variety grown widely but susceptible to lodging, and Gea Lammie, a short landrace variety, were obtained from the Holetta Agricultural Research Center, Ethiopia. Variety DZ-01-196 was developed in a conventional breeding program and its plants have a high positive correlation between height and grain yield (Teklu & Teferea 2005).

Growth experiments were carried out in two sets. In the first, the two varieties DZ-01-196 and Gea Lammie were grown in a greenhouse at the University of Pretoria for only six weeks before panicle initiation. In the second set, plants of DZ-01-196 were grown at Rothamsted Research, UK in a greenhouse. Seeds were pre-germinated in moist pots and germinated seedlings were transplanted after 10 days to new pots [15 cm diameter (top) x 12.5 cm (height) and 10 cm (bottom)] with 3 seedlings per pot. Pots were filled either with a germination soil mix and watered with a Hoagland fertilizer solution (Kebede et al. 2008) or filled with a mix consisting of peat (75%), sterilized loam (12%), vermiculite (3%) and grit (10%) supplemented with a slow-release fertilizer containing 15-11-13 NPK plus micronutrients. Seedlings were grown for 14 weeks until plant maturity in an environmentally controlled growth chamber using a 16-h photoperiod provided by natural light supplemented with light from sodium lamps to maintain a minimum PAR of 350 μmolm^{-2}s^{-1}.

Plant Treatment and Growth Measurements

Plants were treated with gibberellic acid (GA_3) or the GA-biosynthesis inhibitor CCC dissolved in dsH_2O. Beginning 10 days after planting, GA_3 and CCC were applied to the lower surface of the uppermost young leaves each at concentrations of 0.1mM, 1.0 mM, 10mM and 100 mM using a hand sprayer for six weeks, spraying once every week.. In experiments comparing the action of CCC and PBZ, both inhibitors were dissolved in dsH_2O and solutions were applied every two weeks to the base of the pot during watering of plants. Inhibitor treatment started 3 weeks after seed germination.

Length of culm, individual internodes, panicle and tillers from the subtending nodes were measured with a ruler and internode and tiller number were also determined for each plant. Internode diameter was measured 3 mm above the node using a standard digital caliper. Dry weight was determined from above-ground biomass by drying it at 80^{o}C for 2 days in an oven. Grain yield was determined by measuring the weight of seeds from all tillers. All data were collected at plant maturity from 12 individual plants, including their tillers.

Data Analysis

Data analysis was done using the Statistical Analysis System package (SAS Institute Inc., Cary, NC, USA). Statistical significance of difference between treatment means was determined using the Tukey's Studentized Range (HSD) Test. A *P*-value ≤ 0.05 was considered as significant.

RESULTS AND DISCUSSION

Plant Height and Panicle Length

Application of GA_3 and CCC affected plant height in both Gea Lammie and DZ-01-196 (Figures 1A and B) and showed a GA-dependent control of plant height in *E. tef*. GA_3 application (100 mM) increased ($P < 0.05$) plant height by 43% in the short variety Gea Lammie and only some increase (13%) was found in the tall variety DZ-01-196 (Figure 1A). In contrast, CCC (100 mM) treatment significantly ($P < 0.05$) reduced plant height by 46% in plants of the tall variety DZ-01-196 and by 27% in Gea Lammie (Figure 1B). Concentrations lower than 100 mM GA_3 still increased plant height in the short variety Gea Lammie but had no significant ($P > 0.05$) effect on plant height in the tall variety DZ-01-196 when compared to the untreated control (Figure 1A). Concentrations lower than 100 mM CCC also significantly reduced ($P < 0.05$) plant height in the tall variety DZ-01-196 but did not affect plant height in the short variety Gea Lammie when compared to the control (Figure 1B). Results show the amenability of *E. tef* for GA mediated plant height control and regulation of plant height using PGRs in tall varieties usually grown for their high yield but susceptible to lodging.

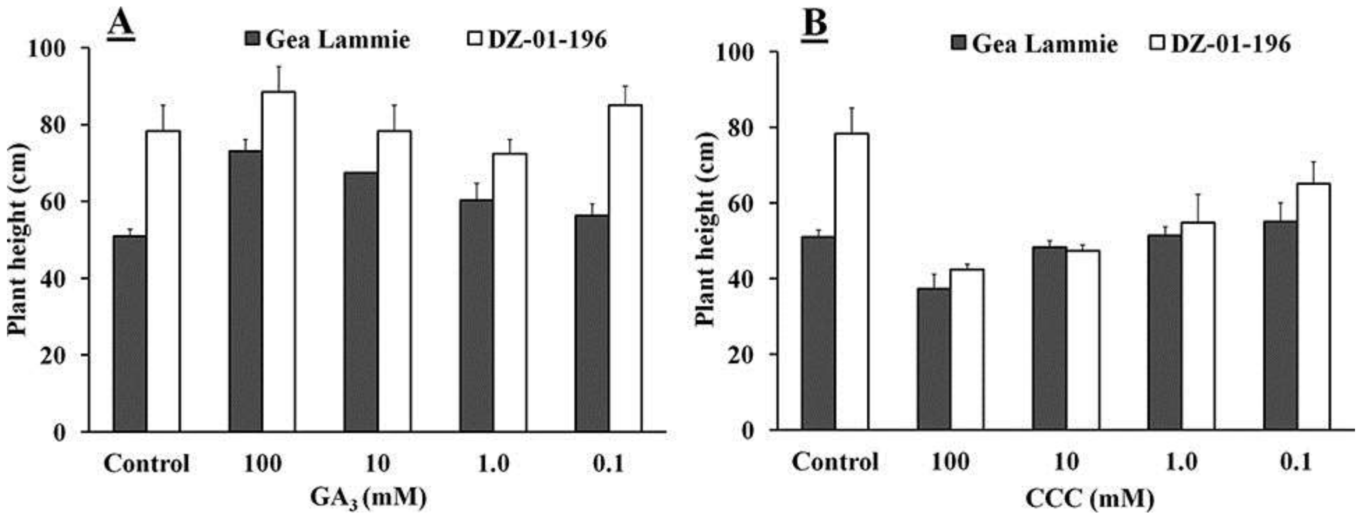

FIGURE 1 Plant height response of Gea Lammie and DZ-01-196 to exogenous application of various concentrations of GA_3 (A) and CCC (B). Data are the mean ± SEM of 12 plants. *indicates significant difference at 5% to the untreated control.

Based on our finding that CCC treatment reduces plant height in *E. tef*, the PGR effect on the taller variety DZ-01-196 was investigated in greater detail. The effect of GA inhibitors CCC and PBZ on DZ-01-196 was specifically studied. Both GA inhibitors CCC and PBZ significantly ($P < 0.05$) reduced stem growth in DZ-01-196, but with a much stronger effect of PBZ at a much lower concentration when compared to CCC (Table 1). Culm length was most responsive to inhibitor action and CCC significantly ($P < 0.05$) reduced culm length by one quarter without reducing panicle growth and grain yield (Figure 2; Table 1). Yield increase associated with CCC application, reported for other crops (Berry et al., 2004), was not found for *E. tef*. This could be due to absence of increased head bearing tillers following CCC application.

Table 1. Effect of CCC and PBZ on culm and panicle length, number of tillers and seed weight per plant of *E tef* variety DZ-01-196.

Treatment	**Culm length (cm)**	**Panicle length (cm)**	**Tillers (number)**	**Seed wt (g)**
Control	159.9± 3.7a	50.26±1.9c	5.0±0.6b	3.79±0.5a
CCC				
10mM	145.0±2.2b	53.93±0.9b	6.0±0.6b	3.63±0.7a
100mM	124.2±3.3c	61.50±0.7a	7.3±1.1b	3.78±0.3a
PBZ				
10 µM	11.5±1.1d	18.57±0.8d	17.3±2.8a	1.11±0.3b
100 µM	3.9±0.3e	5.87±0.3e	15.0±2.1a	0.05±0.03b
Significance	***	***	***	***

CCC = Chlormequate chloride; PBZ = Paclobutrazol

Letters within the column denote significance as determined using the Student's *t*-test. Data shown represent mean values±SE of 12 individual plants. Significance level was determined using ANOVA (*** P<0.001) and difference between treatment means was determined using the Tukey's Studentized Range (HSD) Test. Means followed by the same letter are not significantly different

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When plants were treated with PBZ (10 µM and 100 µM), culm length was significantly reduced (P < 0.05) by 92% and 98%, respectively. Elongation of the uppermost four internodes was in particular reduced or completely inhibited. However, CCC treatment only reduced culm length by 9.3% (10 mM) and 22.3% (100 mM) (Table 1). A further reduction of culm height might be achieved by increasing CCC concentration but such increased concentration should not affect panicle growth. Also, a lower PBZ concentration might be applied less affecting reduction of plant height reduction and with minimal effect on panicle growth and yield.

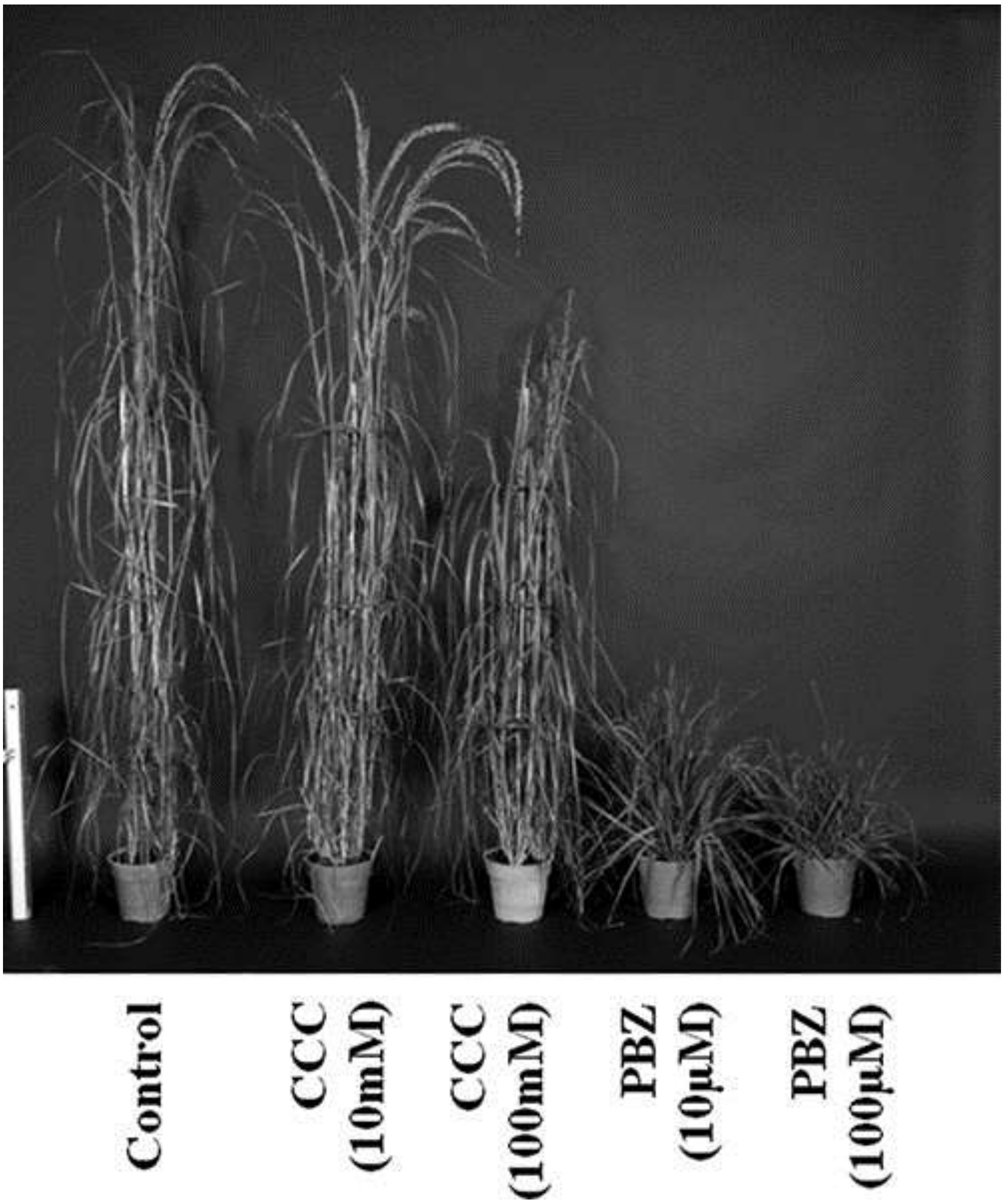

FIGURE 2 Effect of CCC (100mM) and PBZ (100µM) on plant height near plant maturity in comparison to the untreated control.

The panicle to culm length ratio of 1.61 (10 µM PBZ) and 1.51 (100 µM PBZ) decreased to 0.37 and 0.49 when plants were treated with either 10 mM CCC or 100 mM CCC, respectively (ratio computed based on Table 1). Treatment with PBZ had a stronger effect on culm than on panicle length indicating a differential *E. tef* response to GA inhibitor treatment. Panicle length positively correlated with culm length and dry weight as well as total above-ground shoot dry weight but negatively correlated with number of tillers per plant and dry weight to height ratio (Table 5).

Internode Growth

In variety DZ-01-196, both internode length and diameter were significantly reduced by soil application of PBZ when compared to CCC treatment or to the untreated control (Tables 2 and 3). In PBZ-treated plants, length was reduced in all internodes. The two uppermost internodes of plants treated with 10 µM PBZ and the four uppermost internodes treated with 100 µM PBZ completely failed to elongate (Table 2). In CCC-treated plants, reduction in internode length varied between the different internodes. Shortening was most significant ($P < 0.05$) in the lowermost internodes with a 2.6-fold reduction when compared to the control (Table 2). The lowermost two internodes (I1+I2) of CCC-treated plants were further more positively correlated ($r = 0.70$, $P < 0.05$) to culm length when compared to the uppermost two internodes (I7+I8) ($r = -0.04$, $P < 0.05$) (data not shown). Shortening of basal internodes, if associated with stem wall thickening or increase in dry weight per unit of basal internodes, may minimize the lodging risk. For example, the basal internode length and plant height in wheat are the two most important culm traits closely associated with lodging (Kelbert et al. 2004). Further, foliar application of CCC reduced most of the length of the two uppermost internodes (Gebre unpublished data) indicating a possible differential response in *E. tef* to CCC application. *E. tef* might also benefit more from a foliar than from a soil application of CCC. Soil application can cause chemical decomposition of CCC due to prevailing temperature and humidity (Radmacher 2000; Pintus 1973).

The internode diameter was unaffected by either PBZ or CCC treatment. In control and CCC-treated plants, the internode diameter steadily increased from the base up to internode 6. This shows a poor tapering characteristic of *E. tef* plants under the selected growth conditions (Table 3). Such acropetal increase in stem diameter might exacerbate lodging susceptibility because the basal part of the culm should be thicker to hold the plant upright. This problem might even become more serious with increasing N-fertilization. This will decrease lignification of the stem and reduces stem strength (Crook & Ennos 1995) allowing minimum wind speed or rain to cause lodging. This also indicates that *E. tef* plants have a weak transition from shoot to root with a smaller plant-base diameter causing poor tapering. Absence of an effect on stem-base diameter by CCC is not unique to *E. tef* has also been reported in wheat and barley (Gendy & Hofner 1989; Berry et al. 2000).

Table 2. Effects of CCC and PBZ on length of different internodes of *E. tef* variety DZ-01-196.

	Internode (cm)							
Treatment	**I-1**	**I-2**	**I-3**	**I-4**	**I-5**	**I-6**	**I-7**	**I-8**
Control	8.6±0.9a	14.3±0.85a	18.7±0.5a	18.3±1.1a	21.9±0.9a	23.0±2.0a	27.2±1.1a	28.4±3.3a
CCC								
10 mM	8.1±0.9a	12.3±0.5b	15.1±0.9b	17.3±0.8a	20.4±0.1b	22.7±0.9a	24.1±0.9b	25.0±2.7a
100 mM	3.3±0.6b	8.9±0.6c	12.8±0.7c	15.8±0.5b	17.0±0.6c	18.3±0.8b	20.5±0.7c	27.6±1.3a
PBZ								
10 µM	1.3±0.5c	2.0±0.5d	3.0±0.5d	4.0±0.7c	1.7±0.8d	0.8±0.1c		
100 µM	0.45±0.1d	0.9±0.3e	1.0±0.3e	0.8±0.2d				
Significance	***	***	***	***	***	**	**	NS

CCC= Chlormequate chloride; PBZ= Paclobutrazol Letters within the column denote significance as determined using the Student's *t*-test. Data shown represent mean values±SE from 12 individual plants. Significance level was determined using ANOVA (** $P<0.01$; *** $P<0.001$; NS = not significant) and difference between treatment means was determined using the Tukey's Studentized Range (HSD) Test. Means followed by the same letter are not significantly different.

Table 3. Effect of CCC and PBZ on diameter of different internodes of *E. tef* variety DZ-01-196.

	Internode (mm)							
Treatment	**I-1**	**I-2**	**I-3**	**I-4**	**I-5**	**I-6**	**I-7**	**I-8**
Control	3.2±0.1a	3.7±0.1a	4.2±0.2a	4.34±0.2a	4.6±0.3a	4.8±0.3a	4.7±0.3a	4.0±0.3a
CCC								
10 mM	2.8±0.1b	3.5±0.1a	3.9±0.1a	4.25±0.1a	4.6±0.1a	4.9±0.1a	4.9±0.1a	4.2±0.4a
100 mM	3.2±0.1a	3.9±0.12	4.1±0.1a	4.22±0.1a	4.4±0.1a	4.4±0.1b	4.4±0.2a	3.8±0.2a
PBZ								
10 µM	3.7±0.5a	3.9±0.4a	3.7±0.6a	3.66±0.6a	2.0±0.8b	0.8±0.6c		
100 µM	3.8±0.5a	4.1±0.4a	3.7±0.6a	0.56±0.4b				
Significance	***	NS	NS	**	*	**	NS	NS

CCC= Chlormequate chloride; PBZ= Paclobutrazol

Letters within the column denote significance as determined using the Student's *t*-test. Data shown represent mean values ± SE of 12 individual plants. Significance level was determined using ANOVA (**P < 0.01; ***P < 0.001; NS = not significant), and difference between treatment means was determined using the Tukey's studentized range (HSD) test. Means followed by the same letter are not significantly different.

Tillering, Biomass and Yield

Treating DZ-01-196 plants with PBZ had a three-fold increase significant (P < 0.05) in the number of tillers per plant whereas CCC-treated plants had no significant (P > 0.05) increase (Table 1). Increased number of productive tillers is a desired trait in *E. tef* breeding when positively associated with high yielding (Hailu et al. 2000). However, after PBZ treatment most tillers had no panicles or panicles with less fertile florets and without seeds (data not shown). Treatment with CCC did not increase panicle bearing tillers. Previous studies have also shown a growth stage-dependent increase in head-bearing tiller formation following CCC treatment (Peltonen & Peltonen-Sainio 1997; Naylor & Saleh 1987). The PBZ treatment also reduced culm and panicle dry weight in both the primary and secondary tillers (Table 4) and suppressed significantly ($P < 0.05$) above-ground shoot dry weight by 43.2% and 75.9% at 10 µM and 100 µM PBZ, respectively (Figure 3).

Table 4. Effect of CCC and PBZ on dry weight of culm and panicle tillers of *E. tef* variety DZ-01-196.

Treatment	**Primary tiller (g)**		**Secondary tiller (g)**		**T**
	Culm	**Panicle**	**Culm**	**Panicle**	**otal shoot (g)**
Control	7.1±0.3a	2.0±0.2a	25.7±1.8b	5.5±0.6b	40.3±1.9b
<u>CCC</u>					
10 mM	6.7±0.3a	2.2±0.2a	31.1±1.3a	6.93±0.6a	46.9±1.7a
100 mM	4.6±0.3a	1.9±0.1a	19.9±1.6b	6.5±0.6ab	34.5±1.9c
<u>PBZ</u>					
10 µM	0.72±0.1b	0.73±0.2b	11.8±1.2c	2.8±0.6c	16.1±1.8d
100 µM	0.41±0.1c	0.31±0.1c	5.6±0.3d	0.29±0.1d	6.4±0.4e
Significance	**	**	**	**	**

CCC= Chlormequate chloride; PBZ= Paclobutrazol

Letters within the row denote significance as determined using the Student's *t*-test. Data shown represent mean values ± SE from 12 individual plants. Significance level was determined using ANOVA (** $P<0.01$) and difference between treatment means was determined using the Tukey's Studentized Range (HSD) Test. Means within a column followed by the same letter are not significantly different.

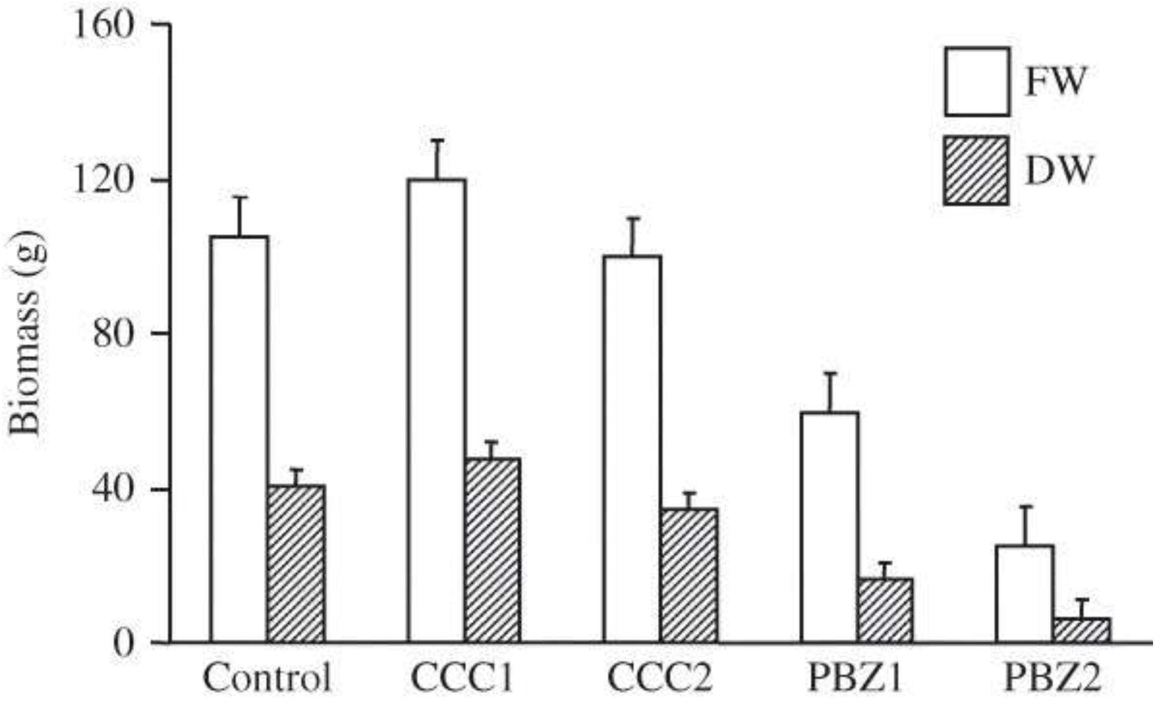

FIGURE 3 Effect of different concentrations of CCC and PBZ on biomass measured as fresh weight (FW) or dry weight (DW) per plant in comparison to biomass of untreated control plants. Data represent the mean ± SE of 12 individual plants. CCC1 = 10 mM CCC; CCC2 =100 mM CCC; PBZ1 =10 mM PBZ; and PBZ2 = 100 mM PBZ.

In plants treated with 10 mM CCC, secondary tiller culm and panicle dry weight and total above-ground shoot dry weight increased significantly ($P < 0.05$). However, increase in panicle growth did not result in a grain yield increase per plant. In CCC-treated plants, change in above-ground shoot dry weight was caused by either increase (10 mM CCC) or decrease (100 mM CCC) in secondary tiller growth (Figure 3) with a lower CCC concentration stimulating plant growth. In all GA inhibitor-treated plants, tiller number per plant was further negatively correlated to above-ground shoot dry weight but positively correlated to the ratio of dry matter to shoot height (Table 5).

Table 5. Correlation coefficients for morphological and yield components of *E. tef* variety DZ-01-196.

	PL	PaL	TH	IN	NT	CDW	PDW	TSDW	DW/Ht	S/P
CL	0.5352	0.9281	0.9872	0.9291	-0.6415	0.8872	0.7779	0.8966	-0.8687	0.7191
PL		0.5555	0.5663	0.5579	-0.2571	0.5012	0.4383	0.5065	-0.4561	0.4557
PaL			0.9511	0.9276	-0.6028	0.8356	0.8251	0.8748	-0.8585	0.7587
TH				0.9321	-0.6145	0.8609	0.7859	0.8833	-0.8848	0.7538
IN					-0.6252	0.8486	0.7447	0.8634	-0.8532	0.6522
NT						-0.4258	-0.4248	-0.4307	0.8029	-0.4401
CDW							0.7904	0.9803	-0.7199	0.6682
PDW								0.8809	-0.6543	0.8923
TSDW									-0.7372	0.7511
DW/Ht										0.9869

CL = Culm length; PL = Peduncle length; PaL = Panicle length; TH = Total height; IN = Internode number; NT = Number of tillers; SFW = shoot fresh weight; CDW = Culm dry weight; PDW = Panicle dry weight; SDW = Shoot dry weight; DW/Ht = shoot dry weight per height ratio; S/P = seed weight per plant. Significance level for the Pearson Correlation Coefficients was determined using the SAS statistical package and all values are significant at $P<0.001$.

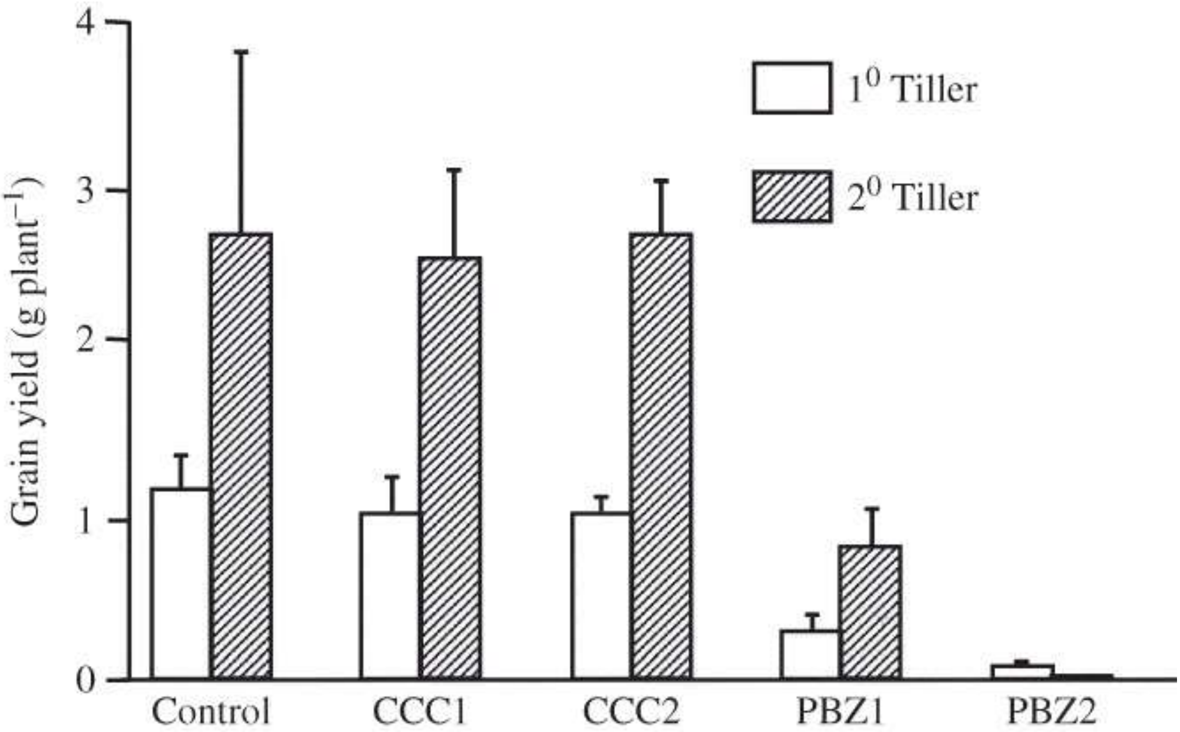

FIGURE 4 Effect of different concentrations of CCC and PBZ on primary (1^o) and secondary (2^o) tiller grain yield per plant in comparison to the untreated control. Data represent the mean ± SE of tiller grain yield of 12 individual plants. CCC1 = 10 mM CCC; CCC2 =100 mM CCC; PBZ1 = 10 mM PBZ; and PBZ2 = 100 mM PBZ.

Seed weight per plant was significantly ($P < 0.05$) reduced by PBZ treatment but not by CCC treatment. Panicle length increased due to CCC (10 mM) application, but this increase was not related to any change in seed weight per plant. In CCC-treated plants, panicle-bearing secondary tillers contributed 63.4% to the total yield per plant (Figure 4). Absence of a CCC effect on *E. tef* panicles possibly indicates a low demand for bioactive endogenous GA for panicle growth and therefore inhibition of GA biosynthesis does not greatly affect yield while reducing plant height.

In *E. tef* breeding, high tillering and taller plants have been the main focus for grain yield improvement. It is therefore important to develop a lodging-resistant *E. tef* ideotype differentially controlling plant height and yield. This study has demonstrated that GA biosynthesis is a prime target for plant height regulation. Since CCC reduces plant height without affecting grain yield, this compound might be suitable for lodging prevention providing the advantage of high productivity. Treatment with CCC did not increase stem diameter, the diameter to height ratio however increased and CCC treatment would therefore also improve plant standability. Although PBZ is probably useful at lower concentrations, cost and persistence in the soil would restrict its wider application. However, future fine-tuning might be required to optimize CCC use for commercial application in lodging prevention without compromising seed yield. Results presented also imply that genetic modification of GA metabolism and targeting genes, such as the rice *sd-1* and the wheat *Rht* orthologs in *E. tef*, could be a strategy for plant height control in *E. tef*.

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