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Full Length Research Paper

Effect of Gibberellic acid (GA_3) and α-naphthalene acetic acid (NAA) on the growth of unproductive tillers and the grain yield of rice (*Oryza sativa* L.)

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In the present study, GA_3 and NAA were used to inhibit the growth of unproductive tillers of rice plants, and we measured the tiller occur and the grain yield of different treatments, the object of this study was to determine the effect of external hormones on the tiller growth and grain yield, and whether we can regulate the tiller growth by some manipulations of the hormone levels. The results indicated that external 10 mg L^{-1} GA_3 and 1000 mg L^{-1} NAA significantly inhibit the growth of unproductive tillers, and the elimination of unproductive tillers promoted the growth of productive tillers at the middle and late growth stages, and promoted the development of heavy panicles, and finally increased the grain yield. However, the external 100 mg L^{-1} GA_3 (G100) significantly decreased the grain yield of Yangdao 6. The reason was that the most of the plants of G100 treatment of Yangdao 6 were lodging at filling stage, and the lodging significantly decreased the spikelet filling and grain weight, and finally decreased the grain yield. These results suggested that the application of GA_3 in field production may lead to lodging, especially for the indica cultivars. So in field production, GA_3 should be used carefully.

Key words: Rice (*Oryza sativa* L.), gibberellic acid (GA_3), α-naphthalene acetic acid (NAA), tiller, yield.

INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most important food crops that feeds more than half of the world's population, and the demand for rice will increase dramatically because of the steady increase in population (Wang et al., 2006). However, further expansion of rice plant area is difficult, because most arable land used for rice production is already converted into urban infrastructure (Horie et al., 2005). The additional rice must therefore be largely produced by increased yield per unit area. Therefore, improving rice yield potential has been the main objective of breeders and cultivators in many countries for several decades (Li et al., 2009).

The grain yield potential of rice can be dissected into four major components: grain weight, grain number per panicle, panicle number per plant, and ratio of filled grains. Tillering of rice, which determined the panicle number per plant, is an important agronomic trait for grain production, and also a model system for the study of branching in monocotyledonous plants (Li et al., 2003). The optimizing tiller production is essential for achieving high rice yield (Matsushima, 1966; Vergara, 1988; Counce et al., 1992; Jiang,. 1994; Peng et al., 1994). Too few tillers result in too few panicles, but excessive tillers degrade rice population quality (Ling, 2000) and lead to high tiller abortion, poor grain setting, small panicle size, and consequent reduce the grain yield (Peng et al., 1994).

Rice tiller number is dynamic and adjustable (Kariali and Mohapatra, 2007), and plant hormones play important role in regulating the tiller occurrence. Leopold (1949) indicated that shoot growth in grasses came under the same type of auxin-induced apical dominance as with dicotyledon, removal or suppression of auxin activity could release the tiller (lateral buds) from the apical control. Exogenous application of auxin inhibited tiller bud growth (Harrison and Kaufman, 1982). In addition, application of gibberellic acid (GA) inhibited the occurrence of rice tiller (Hong et al, 1998), and higher

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abscisic acid (ABA) content in stem and tiller stimulated wheat tiller declining (Liang and Ma, 1998).

However, little is known about the relationship between the regulation of hormones on tiller occurrence and the grain yield of rice. In the present study, gibberellic acid 3 (GA_3) and α-naphthalene acetic acid (NAA) were used to regulated the tiller growth, and we measured the tiller growth and the grain yield of different treatments, the object of this study was to determine the effect of external hormones on the tiller growth and grain yield, and whether we can regulate the tiller growth by some manipulations of the hormone levels.

MATERIALS AND METHODS

Plant materials and treatments

The first experiment

The first experiment was conducted in Qinglongshan experimental base of Nanjing Agriculture University (Nanjing, Jiangsu Province, China; 31°56'39"N, 118°59'13"E) during the growing season of 2008. The soil was Gleyed paddy soil with 16.1 g kg^{-1} organic C and available nitrogen-phosphorus-potassium at 74.7, 10.4 and 82.6 mg kg^{-1}, respectively. Nitrogen (in the form of urea, 120 kg ha^{-1} at basal and 120 kg ha^{-1} at panicle initiation), phosphorus (in the form of single superphosphate, 135 kg ha^{-1} at basal) and potassium (in the form of KCl, 90 kg ha^{-1} at basal and 90 kg ha^{-1} at panicle initiation) were applied during the growing season.

Two rice cultivars, Nanjing 44 (a japonica cultivar, higher tillering capacity) and Yangdao 6 (an indica cultivar, lower tillering capacity), were used. Seedlings were raised in the seedbed on 20 May, and transplanted on 25 June at a hill spacing of 30.0 cm × 13.3 cm with two seedlings per hill. Plot dimension was in 2 m × 2 m.

Two hormones, GA_3 and NAA, were used. Each hormone has four levels: 1, 10, 100 and 1000 mg L^{-1}. When the main stem has 12 leaves for the two cultivars, GA_3 or NAA was sprayed on leaves by the help of a sprayer (700 ml m^{-2}) for 2 days and during 6:00 to 7:00 A.M. on each day. The control plants received an equal amount of distilled water. Each treatment had 3 repetitions in a complete randomized block design.

The second experiment

The second experiment was conducted in Danyang experimental base of Nanjing Agriculture University (Zhenjiang, Jiangsu Province, China; 31°44'52"N, 119°23' 15"E) during the growing season of 2009 and 2010. The soil was Gleyed paddy soil with 21.0 g kg^{-1} organic C and available nitrogen-phosphorus-potassium at 80.3, 15.6 and 80.9 mg kg^{-1}, respectively. Nitrogen (in the form of urea, 120 kg ha^{-1} at basal and 120 kg ha^{-1} at panicle initiation), phosphorus (in the form of single superphosphate, 135 kg ha^{-1} at basal) and potassium (in the form of KCl, 90 kg ha^{-1} at basal and 90 kg ha^{-1} at panicle initiation) were applied during the growing season.

Two rice cultivars, Nanjing 44 (a japonica cultivar) and Yangdao 6 (an indica cultivar), were used. Seedlings were raised in the seedbed on 22 May for 2009 and 27 May for 2010, transplanted on 24 June for 2009 and 26 June for 2010 at a hill spacing of 30.0 cm × 13.3 cm with two seedlings per hill. Plot dimension was in 5 m × 4 m.

According to the results of the first experiment, each cultivars had four treatment: G100: 100mg L^{-1} GA_3; G10: 10mg L^{-1} GA_3; N1000: 1000mg L^{-1} NAA. When the main stem has 12 leaves for the two cultivars, GA_3 or NAA was sprayed on leaves by the help of a sprayer (700 ml m^{-2}) for 2 days and during 6:00 to 7:00 A.M on each day. The control plants received an equal amount of distilled water. Each treatment had 3 repetitions in a complete randomized block design.

Sampling and measurements

Both in the two experiments, after seedlings were transplanted to the field, fifty hills were marked from each plot to record the number of main stems plus tiller. In the second experiment, five hills were sampled from each subplot at treating, jointing stage, heading stage and maturity stage. Stem (main stems plus tillers) and panicle numbers were record. Plant samples were separated into green leaf blades (leaf), culms plus sheathes (include dead tissues) and panicles (at heading stage and maturity stage). The area of the green leaf was measured with LI-3000 (LI-COR, Lincoln, NE, USA) and expressed as LAI. All the fresh samples were placed in a forced-air oven, killed for an hour at 105°C, and dried until they reached a constant weight at the temperature of 85°C. Then the dry weights of samples were measured.

Five hill plants were sampled from each plot at maturity stage. Spikelets per panicle and grain-filling percentage were calculated, then panicles were hand-threshed and the filled spikelets were separated by submerging them in tap water. The filled spikelets were then oven-dried at 70°C to constant weight for determining individual grain weight and the values were adjusted to 13.5% water content. The grain yield was the multiplicator of the four components.

Statistical analysis

Data were analyzed using the analysis of variance (SPSS 16.0 for windows). Means were tested by least significant difference at $P_{0.05}$ ($LSD_{0.05}$).

RESULTS

Tillering dynamics

The result of 2007 showed that the maximum tiller number per hill of Nanjing 44 was 42.9 % higher than that of Yangdao 6 in the control (Table 1). The external GA_3 and NAA play important roles in the regulation of rice tiller growth (Table 1), compare to control plants, the external 1000 mg L^{-1} GA_3, 100 mg L^{-1} GA_3, 10 mg L^{-1} GA_3 and 1000 mg L^{-1} NAA significantly reduced the maximum tiller number per hill of Nanjing 44 and Yangdao 6. Because the rice plants of G1000 treatment of the two cultivars all lodging in 2008, so in 2009 and 2010 we selected external 100 mg L^{-1} GA_3, 10 mg L^{-1} GA_3 and 1000 mg L^{-1} NAA to inhibit the growth of rice tiller.

Similar to 2008, the results of 2009 and 2010 showed that the maximum tiller number per hill of Nanjing 44 was 30 and 27.6% higher than that of Yangdao 6 in the control, respectively, in 2009 and 2010 (Figure 1). Both external 100 mg L^{-1} GA_3, 10 mg L^{-1} GA_3 and 1000 mg L^{-1} NAA significantly reduced the maximum tiller number per hill of the two cultivars, the productive tiller percentage (the ratio of the panicle number per hill/ the maximum tiller number per hill) of G100, G10 and N1000 treatments between the two years were 8.8 to 25.7% higher than that of control plants in Nanjing 44, and 9.4 to 19.8% in Yangdao 6.

Yield and yield component factors

The external GA_3 and NAA significantly affect the grain

Table 1. Effect of GA_3 and NAA on the tiller growth of Yangdao 6 and Nanjing 44 (2008).

Cultivar					
Nanjing 44			Yangdao 6		
Treatment	Tiller number per hill		Treatment	Tiller number per hill	
	Treating	Maximum		Treating	Maximum
G1000	12.8^{a}	13.9^{f}	G1000	9.4^{a}	10.7^{d}
G100	12.5^{a}	14.7^{ef}	G100	9.3^{a}	11.2^{cd}
G10	12.3^{a}	16.4^{cd}	G10	9.4^{a}	11.7^{bc}
G1	12.4^{a}	18.5^{a}	G1	9.5^{a}	12.1^{ab}
N1000	12.5^{a}	15.5^{de}	N1000	9.0^{a}	11.1^{cd}
N100	12.3^{a}	17.1^{bc}	N100	9.4^{a}	12.0^{ab}
N10	12.7^{a}	17.8^{ab}	N10	9.4^{a}	11.8^{abc}
N1	12.2^{a}	17.9^{ab}	N1	9.5^{a}	12.1^{ab}
Control	12.2^{a}	18.0^{ab}	Control	9.5^{a}	12.6^{a}

After seedlings were transplanted to the field, fifty hills were marked from each plot to record the number of main stems plus tiller. Treating: tiller number per hill at treating. Maximum: the maximum tiller number per hill. G1 or N1: 1 mg L^{-1} GA_3 or NAA, G10: 10 mg L^{-1} GA_3 or NAA, G100: 100 mg L^{-1} GA_3 or NAA, G1000: 1000 mg L^{-1} GA_3 or NAA. Values within a column followed by different letters are significantly different at P=0.05.

yield of the two cultivars. The external 10 mg L^{-1} GA_3 and 1000 mg L^{-1} NAA increased the grain yield of the two cultivars both in 2009 and 2010 compare to control (Table 2). However, external 100 mg L^{-1} GA_3 had different effects on grain yield of the two cultivars, external 100 mg L^{-1} GA_3 significantly increased the grain yield of Nanjing 44 both in 2009 and 2010 compare to control, but the grain yield of G100 treatment of Yangdao 6 was significantly lower than control both in 2009 and 2010.

Besides this, from the results of 2009 and 2010 we found that there was no significant difference in panicles per m^2 among all of the treatments for the two cultivars. The external GA_3 and NAA significantly increased the spikelets per panicle compare to control for the two cultivars. For Nanjing 44, there was no significant difference in spikelet filling and grain weight among all of the treatments, but for Yangdao 6, the spikelet filling and grain weight of G100 treatment were significantly lower than the other treatments. Analysis of variance showed that among the yield components, the external hormones had significantly effect on spikelets per panicle, spikelet filling and grain weight.

Dry matter and LAI

External GA_3 and NAA significantly increased the LAI at heading stage of the two cultivars in 2009 and 2010, and the LAI at heading stage of Yangdao 6 was significantly higher than Nanjing 44 (Table 3). At jointing stage, the total dry weights (TDWs) of G100, G10 and N1000 treatments were significantly lower than control treatment, however, the TDWs of G100, G10 and N1000 at heading and maturity stages were significantly higher than CK. The two cultivars had similar trends. The harvest index (HI) among the treatments had no significantly difference for Nanjing 44 both in 2009 and 2010; however, for Yangdao 6, the HI of the G100 treatments was significantly lower than the other treatments.

DISCUSSION

Tiller of rice is dissected into productive tiller and unproductive tiller. After jointing stage, most of the nutrients in rice plants were transported to mother stems and panicles (Jiang et al., 1994). The tillers which had more than three leaves at the jointing stage can be fed by themselves and produce a panicle, these tillers is called productive tiller; if the tiller had less than three leaves at the jointing stage, it cannot be fed by themselves and cannot produce a panicle, these tillers are called unproductive tiller (Ling, 2000).

Nanjing 44 and Yangdao 6 were used in the present study. In the experiments of 2005, 2006 and 2007, we found that the two cultivars were jointing when they had fifteen leaves at main stems. So we applied GA_3 and NAA when the main stems had 12 leaves, the tillers which occurred before this stage could had at least four leaves at jointing stage. From the results we found that the number of tillers and stems of control treatments at treating had no significantly difference compared to the panicles number at heading and maturity stages (Figure 1). This means that the tillers occurred later than 12 leaf stage were the unproductive tillers, and external GA_3 and NAA significantly inhibited the growth of unproductive tillers for the two cultivars.

Unproductive tillers compete for light and nutrients with productive tillers (Ao et al., 2010). Many researchers believe that optimizing tiller production by regulating

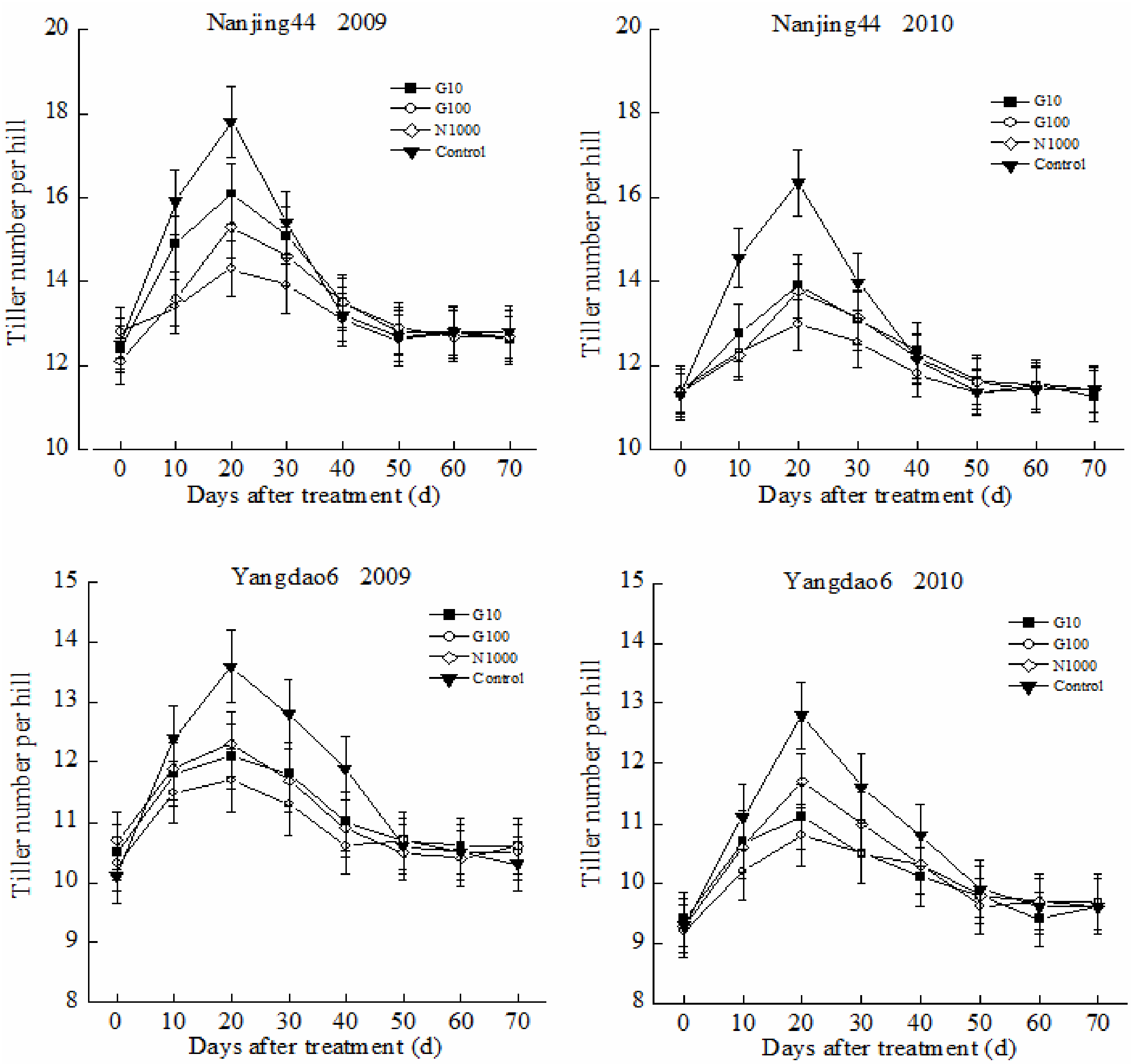

Figure 1. Changes of tiller number per hill of Nanjing 44 and Yangdao 6 after different treatments. G100: 100 mg L^{-1} GA_3; G10: 10 mg L^{-1} GA_3; N1000: 1000 mg L^{-1} NAA. Error bars represent ±standard error of mean.

Table 2. Yield and yield components of the two cultivars under different treatments (2009-2010).

Year	Cultivar	Treatment	Panicles per m^2	Spikelets per panicle	Spikelet filling (%)	Grain weight (mg)	Grain yield (t ha^{-1})
2009	Yangdao6	G100	266.4^a	192.4^a	68.9^b	25.3^b	8.9^c
		G10	264.4^a	173.9^b	89.3^a	27.6^a	11.3^a
		N1000	263.1^a	169.2^b	88.1^a	27.5^a	10.8^{ab}
		Control	262.2^a	156.7^c	88.3^a	27.1^a	9.8^b
	Nanjing44	G100	318.9^a	163.4^a	90.3^a	25.5^a	11.9^a
		G10	318.1^a	142.6^b	91.4^a	25.4^a	10.5^b
		N1000	319.8^a	158.3^{ab}	89.9^a	25.3^a	11.5^{ab}
		Control	319.8^a	121.8c	91.6^a	25.4^a	9.1^c
2010	Yangdao6	G100	240.5^a	194.6^a	48.4^b	23.1^b	5.2^c
		G10	242.1^a	173.6^b	88.7^a	27.4^a	10.2^a

Table 2. Contd.

	N1000	242.9^{a}	167.1^{b}	89.4^{a}	27.8^{a}	10.1^{a}
	Control	244.6^{a}	158.3^{c}	87.9^{a}	27.3^{a}	9.3^{b}
Nanjing44	G100	287.4^{a}	154.6^{a}	90.5^{a}	25.6^{a}	10.3^{a}
	G10	286.3^{a}	139.1^{b}	89.8^{a}	25.4^{a}	9.1^{b}
	N1000	287.8^{a}	151.6^{a}	90.2^{a}	25.5^{a}	10.1^{a}
	Control	285.8^{a}	119.9^{c}	90.6^{a}	25.3^{a}	7.9^{c}
Analysis of variance	Year(Y)	316.37**	6.01*	13.26**	1.69	887.97**
	Cultivar(C)	1079.5**	1279.04**	159.35**	16.06**	243.01**
	Hormones(H)	0.04	53.59**	98.02**	7.24**	735.02**
	Y×C	12.8**	0.09	9.10**	1.78	86.88**
	Y×H	0.19	0.15	10.36**	0.94	12.21**
	C×H	0.07	9.65**	97.23**	8.50**	107.62**
	Y×C×H	0.56	0.26	13.24**	0.79	6.39**

Values within a column and for the same year and the same cultivar followed by different letters are significantly different at *P*=0.05. * Values within column are significantly different at the 0.05 probability level. ** Values within column are significantly different at the 0.01 probability level.

Table 3. LAI at full heading and aboveground total dry weight (TDW) of two cultivars under different treatments (2009-2010).

Year	Cultivar	Treatment	LAI	TDW (t ha^{-1})			Harvest index
				Jointing	Heading	Maturity	
2009	Yangdao6	G100	7.32^{a}	3.78^{b}	12.88^{a}	19.34^{a}	0.38^{b}
		G10	7.31^{a}	3.97^{b}	12.49^{a}	19.69^{a}	0.49^{a}
		N1000	7.27^{a}	4.01^{b}	12.69^{a}	17.78^{b}	0.50^{a}
		CK	6.82^{b}	4.80^{a}	11.06^{b}	17.35^{b}	0.49^{a}
	Nanjing44	G100	7.18^{a}	3.49^{b}	12.18^{a}	19.87^{a}	0.50^{a}
		G10	7.21^{a}	3.81^{b}	11.69^{ab}	19.25^{a}	0.49^{a}
		N1000	7.15^{a}	3.78^{b}	11.57^{b}	19.74^{a}	0.51^{a}
		CK	6.63^{b}	4.35^{a}	10.59^{c}	16.44^{b}	0.48^{a}
2010	Yangdao6	G100	7.23^{a}	3.23^{b}	12.76^{a}	18.57^{a}	0.25^{b}
		G10	7.17^{a}	3.22^{b}	12.42^{a}	17.72^{a}	0.49^{a}
		N1000	7.25^{a}	3.16^{b}	12.51^{a}	17.49^{a}	0.49^{a}
		CK	6.68^{b}	4.36^{a}	11.39^{b}	16.04^{b}	0.49^{a}
	Nanjing44	G100	7.06^{a}	3.29^{b}	12.21^{a}	17.23^{a}	0.51^{a}
		G10	7.03^{a}	3.25^{b}	11.65^{b}	16.15^{a}	0.50^{a}
		N1000	7.09^{a}	3.26^{b}	11.73^{ab}	16.97^{a}	0.49^{a}
		CK	6.48^{b}	4.13^{a}	10.86^{c}	14.95^{b}	0.48^{a}
	Analysis of variance	Year(Y)	33.20**	90.62**	0.45	77.37**	27.97**
		Cultivar(C)	39.81**	7.36*	97.11**	8.35**	12.04**
		Hormones(H)	150.24**	69.75**	82.65**	30.06**	399.33**
		Y×C	0.07	6.62*	0.59	9.50**	6.14*
		Y×H	2.85	3.00*	1.36	2.47	18.95**
		C×H	0.10	1.48	1.84	4.95	4.71**
		Y×C×H	0.28	0.15	0.35	1.62	4.85**

Values within a column and for the same year and the same cultivar followed by different letters are significantly different at *P*=0.05.
* Values within column are significantly different at the 0.05 probability level. ** Values within column are significantly different at the 0.01 probability level.

tillering through in-season crop management and by selecting rice varieties with appropriate tillering ability is essential for achieving high rice yield (Matsushima, 1966; Vergara, 1988; Counce et al., 1992; Jiang, 1994; Peng et al., 1994). Jiang et al. (1994) reported that reducing unproductive tillers by water or nitrogen at the middle growth stage promoted the development of heavy panicles and improved canopy structure and photosynthetic efficiency at the late growth stage. In the present study, the external 10 mg L^{-1} GA_3 and 1000 mg L^{-1} NAA significantly increased the LAI and TDW at heading stage and the TDW at maturity stage. Ling (2000) indicated that the dry weight of plants at heading stage was positively and significantly correlated with spikelets per panicle in rice. In the present study, we found that the spikelet per panicle of G10 and N1000 treatments were significantly higher than that of CK for the two cultivars. These results suggested that the elimination of unproductive tillers promoted the growth of productive tillers at the middle and late growth stages, and promoted the development of heavy panicles, and finally increased the grain yield. Ao et al. (2010) indicated that reduction of unproductive tillers did not increase the grain yield of irrigated rice, this result is inconsistent with the present study, and this inconsistency may be due to the different methods to inhibit the unproductive tillers. Two methods were used in the experiment of Ao et al to reduce tillers: the first was the removal of tillers manually at different crop growth stages and the second was to grow rice plants through holes in styrofoam slats, which provided a physical restriction on tiller emergence (Ao et al., 2010). Our experiment used external GA3 and NAA to inhibit the growth of unproductive tillers. From the result we found that the methods which were used in the experiments of Ao et al. (2010) significantly decreased the panicles per m^2, but the panicles per m^2 among all of the treatments had no significant difference in the present study. This may be the main reason for the inconsistence between the two experiments.

Besides to G10 and N1000, the external 100 mg L^{-1} GA_3 also significantly increased the LAI and TDW at heading stage and the TDW and spikelet per panicle at maturity stage, however, the grain yield of G100 of Yangdao 6 was significantly lower than CK treatments. The reason of this phenomenon was that at filling stage, most of the plants of G100 treatment of Yangdao 6 were lodging, and the lodging significantly decreased the spikelet filling and grain weight of G100 treatment, and finally decreased the grain yield. These results suggested that the application of GA_3 in field production has a potential menace: it may lead to lodging, especially for the indica cultivars. So in field production, GA_3 should be used carefully.

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