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Effects of Selected Plant Growth Regulators on Bread Wheat Spike Development

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Abstract

Although the grain yield of wheat is finally determined after anthesis, the yield potential is largely dependent on early growth and development. At the specific stage from double ridge to terminal spikelet, spikelet initiation occurs and can affect the number of grains per spike and the grain yield. A factorial experiment using a randomized complete blocks design with six replicates was used to study the effect of three growth regulators (3-indoleacetic acid [IAA], gibberellic acid [GA_3], and 6-benzylaminopurine [6-BAP]) on two bread wheat (*Triticum aestivum* L.) cultivars (Rijaw and Azar-2), at the Campus of Agriculture and Natural Resources of Razi University, in Kermanshah, Iran, during the 2013–2014 and 2014–2015 cropping seasons. The effect of the hormones was not significant for spikelet initiation number or spikelet initiation rate based on days and growing degree days (GDDs), but apical meristem length and rate of elongation of the apical meristem were affected by exogenous application of hormones in both years. The Rijaw genotype was better than Azar-2 with respect to apical meristem traits. As well, biplot diagrams showed that the treatment combination 6-BAP × Rijaw was the best in terms of shoot apex length and rate of shoot apex elongation and that the treatment combination GA_3×Rijaw was the best in terms of spikelet number and rate of spikelet initiation. It is concluded that each hormone can improve specific apical meristem characteristics and that the rate of each hormone's effect depends on the plant's genetic feature and on the environmental conditions.

Keywords: apical meristem, plant hormone, spikelet, wheat

1. Introduction

Bread wheat (*Triticum aestivum* L.) is a main food crop and a strategic cereal crop around the world. Because wheat can be used directly, for thousands of years it has provided most of the daily food for the world's population: today, wheat provides 20% of the consumed calories in the world and more than 40% to 45% of daily calories and 50% of daily protein for people in Iran (Iran-Nejad & Shahbaziyan, 2005; Kalantari et al., 2005; Braun et al., 2010). Thanks to its high capacity for adaptation to different environmental climates, wheat has a wide distribution in the world (Cakmak, 2008; Amiri et al., 2015). In recent decades, increasing food demand and water deficit have created a challenge in terms of food security around the world (Zwart & Bastiaannsen, 2004; Reynolds et al., 2011). Although great successes have been achieved in improving the yields of crops, especially wheat, through crop breeding methods, we have a long way to go before we reach the theoretical wheat yield potential (20 t/ha) that is estimated by cereal physiologists (Evans, 1993). Studies show that gaining adequate knowledge of the formation and physiology of crop yield, being able to distinguish changes created by different factors in the life cycle of the crop, and identifying the relationship between the impacts of these factors on the formation of yield components can be effective in making genetic achievements to improve grain yield (Pedró et al., 2012; Reynolds et al., 2012).

The final grain yield of wheat consists of three main components, namely, the number of spikes per ground unit, the number of grains per spike, and thousand grain weight, and each component is shaped during a specific stage of wheat growth and development (Figure 1) (Itoh et al., 1998; Acreche & Slafer, 2006). However, there are two main methods for classifying the different growth stages of wheat: morphological classification and physiological classification. The morphological characteristics of wheat are presented using the Zadoks scale

(Zadoks et al., 1974), and the physiological development of the wheat apical meristem is showed on a quantitative scale (Waddington et al., 1983), on which each code represents a particular stage of development of the wheat spike (apical meristem). [Figure 1] [Figure 2]

Studying the developmental stages of wheat based on morphological characteristics in order to assess the plant requirements at different growth stages is important, but these divisions do not provide physiologists with accurate information to distinguish the effects of wheat management and environmental factors on spike formation and grain size, which will later determine the grain yield.

Based on developmental classification, the appearance of a double ridge on the shoot apex is an indication of the transition of wheat from the vegetative phase to the reproductive phase (Figure 2), because spikelet and floret differentiation starts during this period (double ridge to terminal spikelet). In other words, the terminal spikelet marks the end of spikelet primordia initiation (grain set potential) (Figure 1) (Pask et al., 2012), and thus the potential grain yield is largely dependent on the pre-anthesis events (Li et al., 1999; Wang et al., 2001). One to two thirds of the florets that form before the terminal spikelet phase will be aborted around the booting stage (Bancal, 2009). Finally, grain weight will be formed after the anthesis phase until physiological maturity (grain filling).

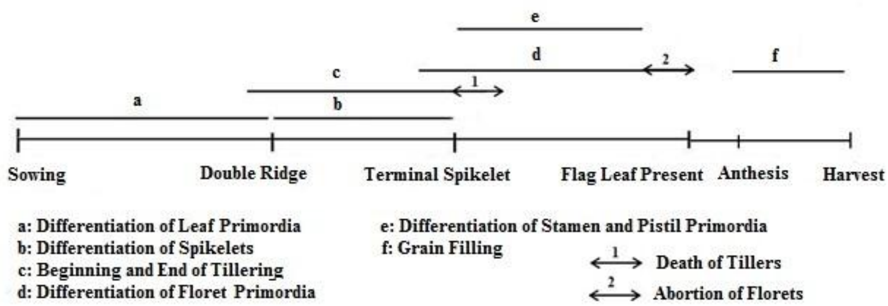


Figure 1. Formation stages of different components of wheat yield from sowing to harvest (adapted from McMaster et al., 1992 with minor changes)

Figure 2. Early Double ridge initiation. The photo was provided by the authors and was taken during the experiment

Plant hormones (plant growth regulators) are the most important internal factors for the regulation of plant growth in response to environmental and genetic factors. For example, water deficit is the main factor for the significant accumulation of abscisic acid in relation to corn kernel abortion (Ober & Sharp, 1994). Water deficit also increases abscisic acid levels in leaves and spikelets of wheat, which reduces the number of seeds (Wilkinson & Davies, 2002). Studies have shown that plant hormones could regulate the partitioning and translocation of photoassimilates during grain filling (Ahmadi & Baker, 1999). Both 3-indoleacetic acid (IAA) and cytokinins have been shown to play an important role in the transportation of assimilates to wheat spikes (Darussalam et al., 1998; Lejeune et al., 1998). As well, cytokinins are required for cell division during the early phase of grain filling (Yang et al., 2000). The exogenous application of abscisic acid was found to reduce chlorophyll in flag leaves, whereas remobilization and rate of grain filling were enhanced by increasing abscisic acid (Yang et al., 2003b/ 2006). The application of chlormequat and ethephon was found to increase wheat grain yield, because these substances reduced the plant height and improved the partitioning of dry matter into the spikes (Shekoofa & Emam, 2008).

However, most of the previous studies concerned the effects of plant hormones on the wheat yield formation processes that occur after anthesis. Investigating the relationships between hormones and their roles in the formation of wheat yield, especially at the early stages of spike physiological development, can be important. Thus, the objective of this study was to determine the effects of the exogenous application of plant growth regulators at a specific pre-anthesis stage, namely, the period from double ridge to terminal spikelet, on apical meristem characteristics in two wheat genotypes.

2. Material and Methods

2.1 Study location

The study was conducted for two cropping seasons in the experimental field at the Campus of Agriculture and Natural Resources of Razi University, in Kermanshah, Iran (34°21′N; 47°9′E; 319 m AMSL). This location is in a semi-arid zone. The soil texture was clay with a pH of 7.8. The rates of N, P_2O_5, and K_2O in the soil before the experiment were 0.012%, 8 ppm, and 400 ppm, respectively. Weather characteristics, including monthly average temperatures (℃) and total rainfall (mm), for both years of the experiment are shown in Figure 3.

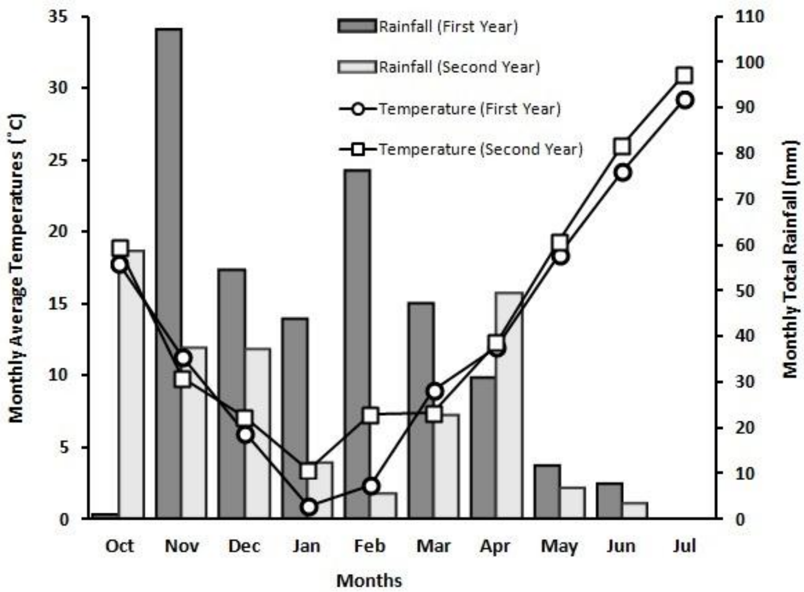


Figure 3. Monthly average temperatures (℃) and total rainfall (mm) in the two crop seasons (2013–2014 and 2014–2015) of the experiment

2.2 Experimental Design

Each experiment was carried out as factorial based on a randomized complete block design with six replications in the 2013–2014 and 2014–2015 cropping seasons. The factors were (i) exogenous application of different plant growth regulators, namely, IAA, gibberellic acid (GA_3), and 6-benzylaminopurine (6-BAP), and distilled water as the control at a specific physiological development stage of the apical meristem of wheat, namely, double ridge to terminal spikelet, and (ii) two dry-land wheat genotypes (cv. Rijaw and cv. Azar-2), which have optimum and low grain yield potential in Kermanshah province, respectively. The cultivar Rijaw is a newly released rain-fed cultivar. The hormone concentration applied for each hormone was 50 μM, in accordance with previous studies (Yang et al., 2002/ 2003a). Each plot contained six planting rows with 2.5 m length. The space between planting rows was 25 cm, and planting density was 300 seeds/ m^2. The distance between the plots was 50 cm. Sowing was performed manually. At the hormone application step, to ensure the absorption of the plant growth regulators, foliar application was done on three consecutive days after sunset (to prevent degradation of the plant growth regulators by sunlight).

2.3 Apical Meristem Measurement

Three main shoots from each plot were measured after the initiation of the double ridge (Figure 2). The developed spikelets were investigated using a quantitative scale (Waddington et al., 1983). The main shoot apex was dissected to determine the apex length and the number of spikelet primordia present on the apex. The number of spikelet buds and the apex length were measured using a binocular microscope at 40× magnification (Figure 2). The double unit of leaf primordium and spikelet bud was counted as one (Kirby, 1974). The rate of apex elongation (α) and the rate of spikelet initiation (β) were expressed per day and growing degree day (GDD). These parameters were calculated by dividing the number of spikelets (S) and length of the apex (L, in mm) by the duration between double ridge (D_1) and terminal spikelet (D_2), on the basis of days and GDDs (Table 1) (Kafi, 2001), as follows:

$$\beta = S / (D_2 - D_1)$$

$$\alpha = L / (D_2 - D_1) \rightarrow (\text{mm/day}), (\text{mm/GDD})$$

Table 1. Duration of the period from double ridge to terminal spikelet based on days and growing degree days (GDDs)

Year	Genotype	Double ridge to terminal spikelet based on days	Double ridge to terminal spikelet based on GDDs (℃d)
2014	Rijaw	14	68.5
2014	Azar-2	16	92.0
2015	Rijaw	10	67.4
2015	Azar-2	19	89.8

2.4 Statistical Analysis

The normality test of data, data analysis, mean comparisons, and diagram preparation were performed with the SPSS, SAS 9.1, GGEbiplot, and Excel software packages.

3. Results

Based on our data, the application of different exogenous plant hormones during the stage from double ridge to terminal spikelet had no significant effect on spikelet number and rate of spikelet initiation (based on days and GDDs) in both years of the experiment, whereas apical meristem length and rate of apical meristem elongation (based on days and GDDs) were affected by hormone application (Tables 2 and 3). The genotypes showed significant differences in all the apical meristem traits in both years (P = 0.01) (Tables 2 and 3). However, the interaction effects between genotypes and plant hormones were different in both years. The interaction effect of genotype × hormone in each year was significant on spikelet number, apical meristem length, and rate of apical meristem elongation (based on days) but was not significant on rate of spikelet initiation (based on GDDs), whereas that interaction had a significantly effect on rate of spikelet initiation (based on days) in the first year of the experiment only and on rate of apical meristem elongation (based on GDDs) in the second year of the experiment only (Tables 2 and 3). As shown in Figure 4, the Rijaw genotype was superior to Azar-2 for all the shoot apex traits with the different hormones used. There was a significant difference in the traits between the crops to which plant hormones were applied and the controls (to which distilled water was applied). In both years of the experiment, GA_3 and 6-BAP led to the initiation of more spikelets on the apical meristem, but this effect was observed only in the Rijaw genotype (Figures 4a and 5a). The highest spikelet initiation number was obtained by exogenous application of GA_3 and 6-BAP, with 19.3 and 18.6 spikelets (in the first year) and 18.1 and 17.8 spikelets (in the second year) per apical meristem, respectively (Figures 4a and 5a). In both years of the experiment, apical meristem length and rate of elongation of the apical meristem (based on days) in the Rijaw genotype were highest when the wheat plants were treated with 6-BAP (Figures 4b, c, and 5b, c), As well, the highest and lowest measured apical meristem lengths at the terminal spikelet stage were associated with the application of 6-BAP to the Rijaw genotype (4.2 and 3.7 mm in the first and second years) and the application of distilled water (control) to the Azar-2 genotype (3.2 and 3.3 mm in the first and second years), respectively (Figures 4b and 5b). Moreover, 6-BAP promoted higher apical meristem elongation rates based on days (in both years) in the Rijaw genotype, with 0.300 and 0.377 mm/d in the first and second years, respectively (Figures 4c and 5c). However, for rate of spikelet initiation (based on days) in the first year of the experiment, GA_3 was higher (Figure 4d), and for apical meristem elongation rate (based on GDDs) in the second year of the experiment, 6-BAP was higher, with 0.055 mm/GDD (Figure 5d); as with the previous two traits, the effects of these hormones were greater in Rijaw than in Azar-2. [Table 1] [Table 2] [Table 3] [Figure 4] [Figure 5]

Table 2. The ANOVA table for the shoot apex traits of two wheat genotypes (Rijaw and Azar-2) treated with different plant hormones (3-indoleacetic acid, gibberellic acid, and 6-benzylaminopurine) from double ridge to terminal spikelet stage in the first year of the experiment

Sources of variation	*df*	*F*					
		Spikelet number	Rate of spikelet initiation (days)	Rate of spikelet initiation (GDDs)	Apical meristem length	Rate of apical meristem elongation (days)	Rate of apical meristem elongation (GDDs)
Replication	5	70.4**	63.9*	52.4**	288.5**	269.7**	154.6**
Genotype (G)	1	114.0**	519.7**	1170.3**	2843.8**	10 269.3**	12 955.0**
Hormone (Hr)	3	1.4ns	1.5ns	1.3ns	253.1**	268.2**	134.0**
G ×Hr	3	3.3*	3.0*	2.6ns	7.0**	3.8*	2.6ns
CV%	-	3.44	3.62	4.00	1.00	0.96	1.33

*$P \le 0.05$; **$P \le 0.01$; ns, not significant.

Table 3. The ANOVA table for the shoot apex traits of two wheat genotypes (Rijaw and Azar-2) treated with different plant hormones (3-indoleacetic acid, gibberellic acid, and 6-benzylaminopurine) during the period from double ridge to terminal spikelet stage in the second year of the experiment

Sources of variation	*df*	*F*					
		Spikelet number	Rate of spikelet initiation (days)	Rate of spikelet initiation (GDDs)	Apical meristem length	Rate of apical meristem elongation (days)	Rate of apical meristem elongation (GDDs)
Replication	5	79.0**	35.2**	62.9**	22.9**	73.5**	239.8**
Genotype (G)	1	111.4**	8183.8**	3696.3**	1194.7**	257 758.0**	225 297.0**
Hormone(Hr)	3	1.3ns	0.9ns	1.4ns	107.3**	266.2**	890.2**
G ×Hr	3	3.0*	1.6ns	2.6ns	3.1*	17.8**	14.9**
CV%	-	1.70	2.55	1.90	0.75	0.46	0.26

*$P \le 0.05$; **$P \le 0.01$; ns, not significant.

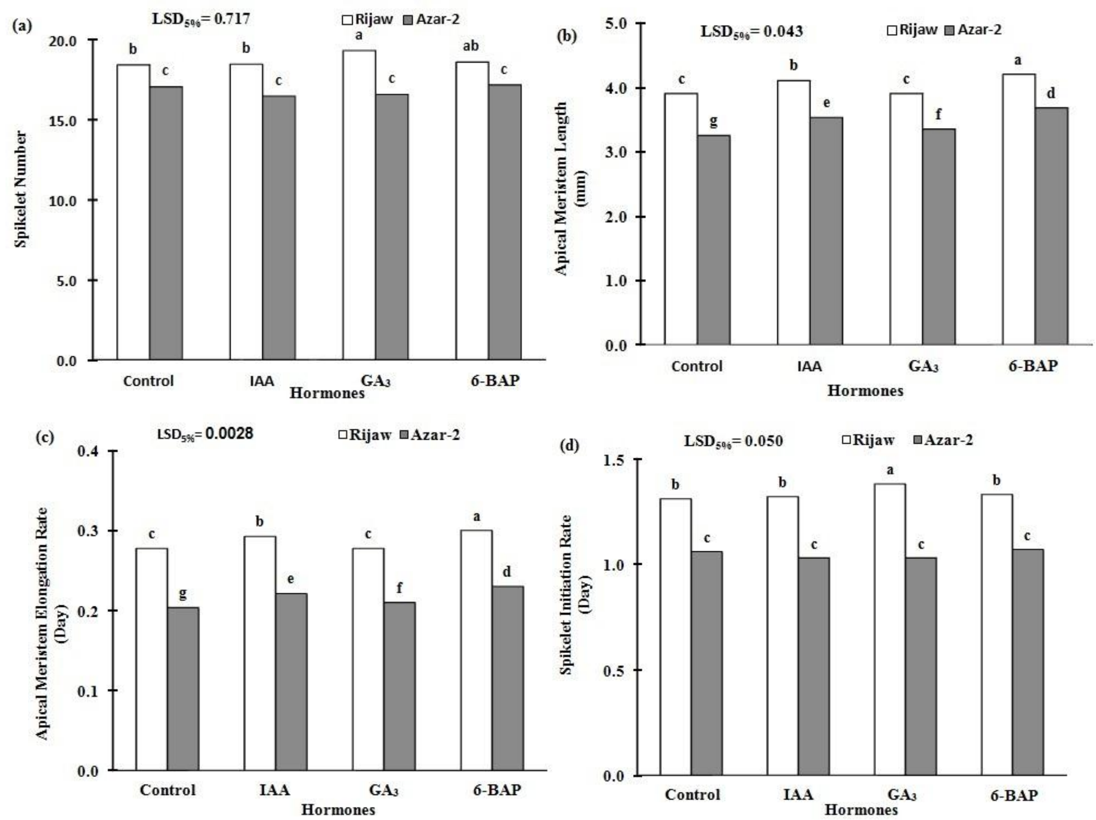


Figure 4. Interaction effects between exogenous applications of different plant growth regulators (3-indoleacetic acid [IAA], gibberellic acid [GA_3], and 6-benzylaminopurine [6-BAP]) and two wheat genotypes (Rijaw and Azar-2) on shoot apex traits during the stage from double ridge to terminal spikelet in the first year of the experiment. Means with the same letter are not significantly different

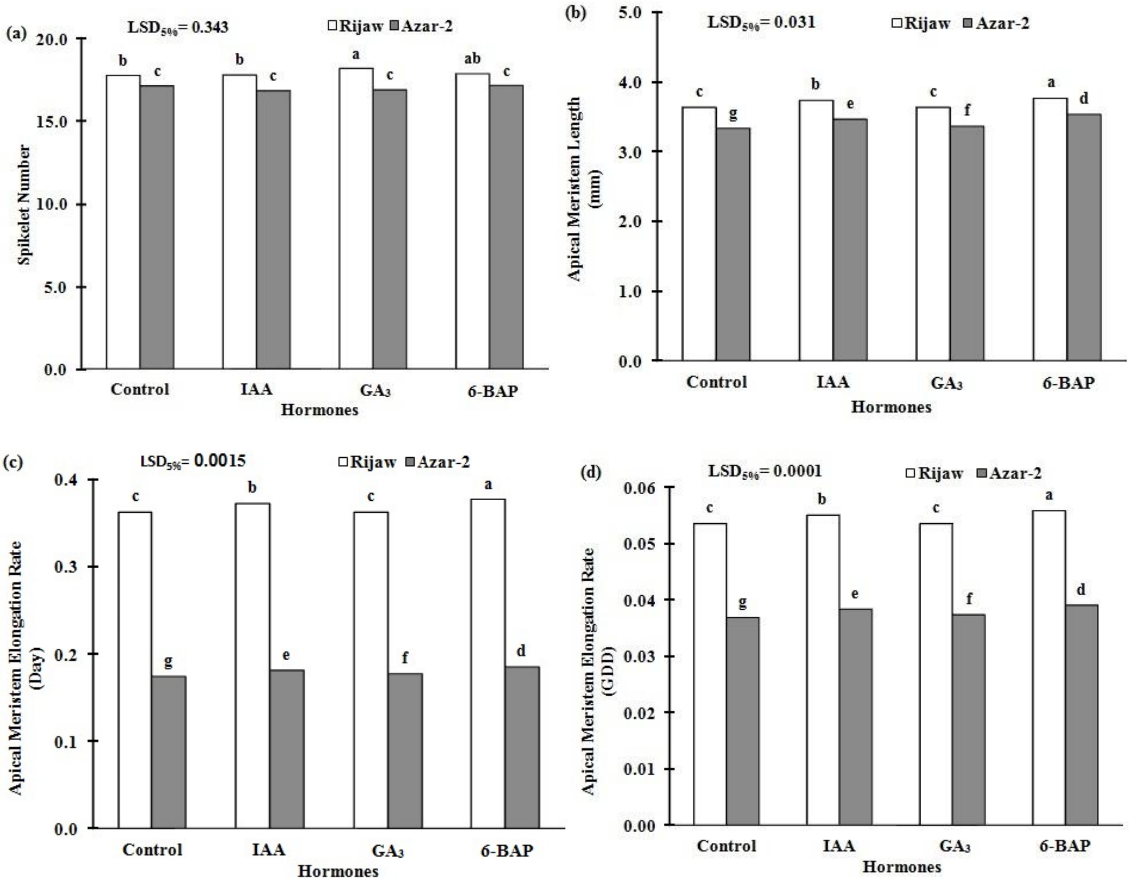


Figure 5. Interaction effects between exogenous applications of different plant growth regulators (3-indoleacetic acid [IAA], gibberellic acid [GA_3], and 6-benzylaminopurine [6-BAP]) and two wheat genotypes (Rijaw and Azar-2) on shoot apex traits during the stage from double ridge to terminal spikelet in the second year of the experiment. Means with the same letter are not significantly different

4. Discussion

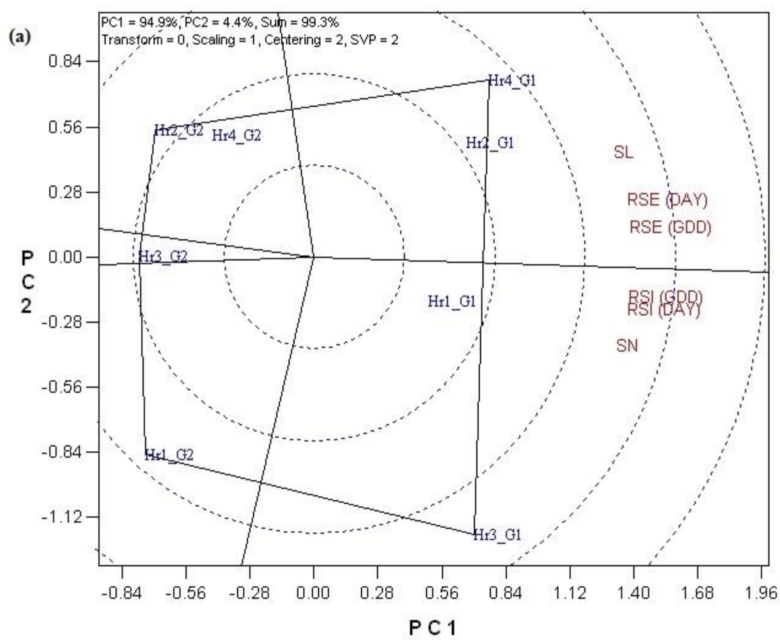
The period from double ridge to terminal spikelet is an important stage in grain set of wheat spikes. When the wheat apical meristem enters the double ridge stage, spikelet initiation starts and will continue until the terminal spikelet stage. The number of initiated spikelets per spike, spikelet initiation rate, and the length of the shoot apex from double ridge to terminal spikelet are important, and the final grain yield will be higher if those traits are higher. Thus, during the period from double ridge to terminal spikelet, two important traits, namely, number of spikelets per spike and number of florets per spikelet, are shaped, and they have an effect on the final grains number, consequently, the grain yield can be increased (Itoh et al., 1998), because there is a close positive relationship between the grains number per spike and the final grain yield (Duggan et al., 2000; Brancourt-Hulmel et al., 2003; González et al., 2003). Also, the relationship between the spikelet and the spike can determine the yield production capacity (Duggan & Fowler, 2006). According to our results, the exogenous application of different plant hormones increased grain yield in comparison with the controls, and thus the wheat treated with 6-BAP was significantly different from the controls and had improved grain yield and grain number (Table 4). The increasing ratios for grain yield were higher in the second year even though the grain yields were lower than they were in the first year (Table 4). This result may have been related to differences in rainfall amount and temperature in February (time of double ridge appearance) between the first and second years (Figure 3), because the rainfall amount was much lower and the temperature was higher in the second year of the experiment than in the first year, and such differences would influence which hormones were more effective on the final grain yield. In other words, the grain yield of the control plots decreased more, so that the increasing ratios were high for the wheat treated with plant hormones (Table 4). However, this relationship was not true for the number of grains per spike, because the number of initiated spikelets was lower in the second year than in the first year, leading to a decrease in grain number. Although previous studies reported that an acceleration in apical meristem development led to a reduced spikelet number in each shoot apex and thus lower yield potential (Maas & Grieve, 1990; Munns & Rawson, 1999; Kafi, 2001), in the present experiment the plant hormones increased the rate of spikelet initiation and rate of apical meristem elongation, both of which are necessary for a higher final grain set per spike. [Figure 6] [Table 4]

Table 4. Increasing ratios of grain yield and number of grains per spike for the application of different plant hormones (3-indoleacetic acid [IAA], gibberellic acid [GA_3], or 6-benzylaminopurine [6-BAP]) in comparison with the controls in two dry-land wheat genotypes (Rijaw and Azar-2).

Hormone	First year			
	Grain yield (kg/ha)	Increasing ratio (%)	Grains per spike	Increasing ratio (%)
Control	2105.1c	0	32.7b	0
IAA	2491.1b	15.5	34.0b	3.8
GA_3	2529.3b	16.8	38.6ab	15.3
6-BAP	2930.1a	28.1	42.2a	22.5
*LSD*5%	295.23	-	6.54	-
Hormone	Second year			
	Grain yield (kg/ha)	Increasing ratio (%)	Grains per spike	Increasing ratio (%)
Control	1797.8c	0	33.6b	0
IAA	2298.8b	21.8	34.0b	1.2
GA_3	2399.3ab	25.1	36.2ab	7.2
6-BAP	2802.5a	35.8	38.5a	12.7
*LSD*5%	480.44	-	2.98	-

Means with the same letter are not significantly different.

In both years of the present study (Figure 6a, b), the first two principal components accounted for 99.3% and 98.9% of total variation in the data set, respectively. The polygon for “which is best for what” indicates the best treatment combination (genotype × hormone) for each trait. In both panels of Figure 6, the biplot was divided into five sections. The peak treatment combination for each section was the one that gave the highest amount for the traits that fall within that section. The treatment combinations $Hr_4\_G_1$ (6-BAP and Rijaw) followed by $Hr_2\_G_1$ (IAA and Rijaw) were the best in terms of shoot apex length and rate of shoot apex elongation (based on days and GDDs). The treatment combination $Hr_3\_G_1$ (GA_3 and Rijaw) was the top treatment combination in terms of spikelet number and rate of spikelet initiation (based on days and GDDs).



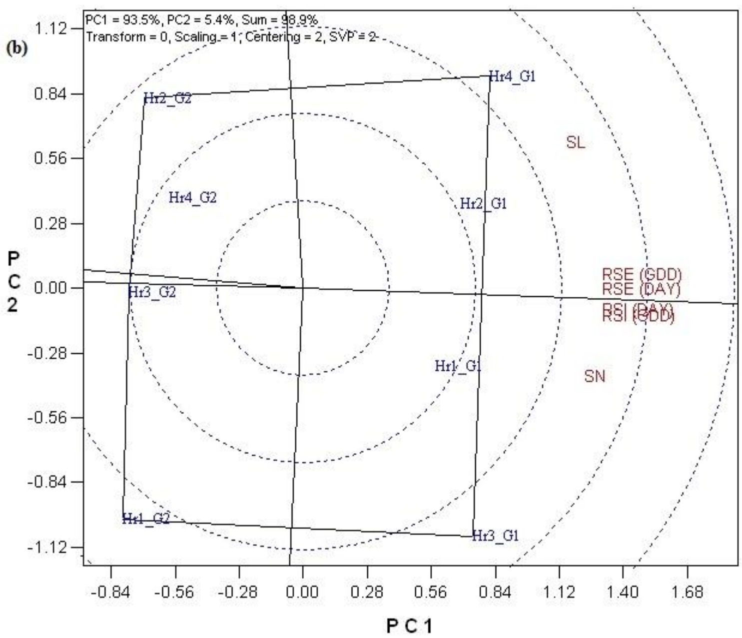


Figure 6. Polygon view of the principal component (PC) analysis biplot showing "which is best for what" for wheat shoot apex traits in the first year (a) and second year (b) of the experiment. RSE, rate of shoot apex elongation; SL, shoot apex length; RSI, rate of spikelet initiation; SN, spikelet number; G_1,genotype 1 (Rijaw); G_2,genotype 2 (Azar-2); Hr_1,control; Hr_2,3-indoleacetic acid(IAA); Hr_3,gibberellic acid (GA_3); Hr_4,6-benzylaminopurine (6-BAP)

In this experiment, a difference was found among the number of days from double ridge to terminal spikelet in each year based on days. The duration of this period was 14 and 16 d for Rijaw and Azar-2 genotypes in the first year, respectively, in comparison with 10 and 19 d in the second year (Table 1). The number of GDDs received by the plants was the same in both years (68.5 ℃d and 67.4 ℃d for the Rijaw genotype and 92 ℃d and 89.8 ℃d for the Azar-2 genotype) (Table 1).

5. Conclusion

In summary, the present study found that plant growth regulators could change the characteristics of the wheat apical meristem during the period from double ridge to terminal spikelet when grain set was being shaped. The present study showed also that hormone could affect a specific trait. Indeed, GA_3 improved the spikelet initiation rate and the number of spikelets per shoot apex, whereas 6-BAP, which is a cytokinin, affected the length and elongation rate of the shoot apex.

As well, the duration of this critical stage was affected not only by genotype and the application of hormones but also by temperature. However, each wheat plant, depending on its genetic characteristics, had to receive a specified number of GDDs to complete this phase, and the transition time varied based on differences in daily temperature; therefore, the rates of spikelet initiation and apical meristem elongation were changed.

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