

Effects of foliar application of BAP on source and sink strength in four six-rowed barley (*Hordeum vulgare* L.) cultivars

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Abstract A field experiment was conducted to investigate the effects of foliar application of a synthetic cytokinin (BAP) on source and sink strength of four different six-rowed barley (*Hordeum vulgare* L.) cultivars. Different spraying treatments consisting of *spraying on whole plant*, *spraying only on leaves* and *spraying only on ears* started at anthesis and continued for 7 days. One additional spraying was carried out on late period of grain filling. Results showed that *spraying only on leaves* did not affect ear weight, grain yield and 1,000-grain weight, while the two other treatments increased all above mentioned traits. Neither of treatments affected stem weight, biological yield and contribution of stem reserves in grain filling. Exogenous cytokinin did not increase photosynthetic rate and chlorophyll content in treated leaves until late period of grain filling, although there was no significant increase in final grain weight due to late application of BAP. Our results suggested that effects of foliar application of BAP were mostly due to increased sink size soon after anthesis and increased sink demand probably met by current photosynthesis of organs other than leaves, like ear green tissues.

Keywords Cytokinin · Foliar application · Grain weight · Photosynthesis · Barley

Abbreviations

BAP	6-Benzyl aminopurine
DAA	Days after Anthesis
Pn	Photosynthetic rate
SMW	Stem maximum weight
WSC	Water soluble carbohydrates

Introduction

Grain yield of barley, like other cereals, is controlled by interactions of current photosynthesis and redistribution of reserves in vegetation tissues (Schnyder 1993); however sink strength as a major determinant in attracting assimilates and final grain yield has long been a matter of discussion. Numerous studies of source-sink relations in cereals have reported that although assimilation rates after 15–20 days of anthesis exceeded the demands of growing kernels (Hay and Walker 1989; Bingham et al. 2007a), there are still sink limitations in wheat (Borrás et al. 2004) and barley (Bingham et al. 2007b). Studying sink limitation in barley has revealed that potential sink size is determined by endosperm cell number established during early grain development (Michael and

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Seiler-Klebitch 1972; Cochrane and Duffus 1983). Endosperm cell number is regulated by cytokinins rather than available carbohydrates (Radley 1978) and there is close association between cytokinin levels in grains and rate of cell division (Banowitz et al. 1999; Yang et al. 2002b). Several studies have attempted to increase cytokinin level of grains during its early phase of development by application of natural or synthetic cytokinins by spraying or injection (Peltonen-Sainio 1997; Wang et al. 2001; Yang et al. 2003; Gupta et al. 2003) and in most cases, a considerable increase has been found both in final grain weight and grain number, depending on time of application (i.e. growth stage).

On the other hand, cytokinins have positive effects on photosynthetic capacity of leaves and delaying senescence (Gan and Amasino 1995; Soejima et al. 1995; Wingler et al. 1998; Yang et al. 2002a; Ookawa et al. 2004). Double effects of cytokinin on both sink and source strength have been neglected in some of foliar application studies, so it is not clear whether increased grain weight has been caused by increase in photosynthetic ability of leaves and availability of more assimilates for grain or by increased sink capacity in attracting assimilates.

This study was undertaken to explore the effects of exogenous cytokinin on source and sink strength by investigating changes in stem and grain weight as well as photosynthetic capacity and chlorophyll accumulation after flowering. In addition, it was determined that whether changes in remobilization could affect source sink relations.

Materials and methods

Plant material and growth conditions

Seeds of four six-rowed barley (*Hordeum vulgare* L.) cultivars were provided from the cereal department of The Institute of Seed and Plant Improvement of

Karaj, Iran. Cultivars included: M80-7 line, Hull-less, Reihan and Walfajr which were selected based on the different agronomical characteristics (Table 1). All are long-day and adapted to arid and semi-arid environments. The experiment was carried out at the Research Farm of College of Agriculture, University of Tehran, Karaj, Iran (35°47' N, 51°10' E). The sowing date was 18 Nov. 2005. To prevent lodging, no fertilizer was used. Each plot consisted of six rows, 4 m long, 20 cm apart and planted at a rate of 420 seeds m⁻².

Treatments

Treatments consisted of a factorial combination of four cultivars and four BAP treatments arranged in a randomized complete block design as split-plot with four replicates. Main plots consisted of the four cultivars (M80-7, Hull less, Reihan and Walfajr) and the sub-plots consisted of: Control (T₀), spraying BAP on whole plant (T₁), Spraying only on leaves (T₂) and spraying only on ears (T₃). One additional treatment was trimming of 20 spikes to half spikelets at anthesis by removal of grains on one side of ear (Navaro et al. 1993; Yong-Zhan et al. 1996) and spraying of BAP on spikes. In this treatment, controls consisted half-eared plants without spraying.

Application of BAP

Starting at anthesis, BAP (6-Benzylaminopurine) (Sigma) was dissolved with a small amount of 10N KOH and solution of 5 × 10⁻⁵ M was sprayed at I: whole plant, II: only on leaves and III: only on ears for seven consecutive days with 0.5% (v/v) Teepol (Sigma) as surfactant (Yang et al. 2003). Spraying was conducted on a whole sub-plot in final hours of day to avoid damage of hormone by intense light. For Walfajr, an additional application of BAP was

Table 1 Main agronomical characteristics of barley cultivars used in this experiment

Cultivar	Height	LAI	Tillering	Maturity	Yield	1,000-grain weight
M80-7	Tall	Medium	Low	Early	Medium	High
Hull-less ^a	Short	Low	Low	Early	Very low	Low
Reihan	Medium	Low	Low	Early	Low	Medium
Walfajr	Tall	High	High	Late	High	Medium

^a In Hull-less, glumes and glumelles will be separated from kernel when threshing

conducted at 20–23 DAA, when discoloration and senescence of leaves had fastened.

Sampling

The date of anthesis was taken as the day when anthers were extruded in 50% of the spikes in a plot. From anthesis until physiological maturity, six main stems (Bonnett and Incoll 1992) from the central rows with similar height were randomly sampled at 0, 6, 14, 21, 29, 36 and 50 DAA for M80-7, Hull less and Reihan, and at 0, 8, 15, 30, 37 DAA for Walfajr, because of different anthesis date and grain filling period in Walfajr and other cultivars.

Measurements

Stem and ear dry weights

Samples were separated to stem and ears, oven dried at 75°C for 48 h and then weighed.

Calculation of remobilization

According to Bonnett and Incoll (1992), contribution of stem reserves both pre- and post-anthesis was calculated:

Pre-anthesis remobilization (%)

$$= (\text{stem weight at anthesis} - \text{stem weight at maturity}) / \text{final ear weight} \times 100$$

Post-anthesis remobilization (%)

$$= (\text{stem weight at the time of stem maximum weight} - \text{stem weight at maturity}) / \text{final ear weight} \times 100$$

Photosynthetic rate

Photosynthetic rate of flag leaf of sprayed and control treatments were measured by an infrared gas-exchange analyzer (LCA4, ADC, UK) at one and two weeks after anthesis at 8:00–10:00 am in four consecutive days (each day for one replication). Also,

photosynthetic rates of spraying and control treatments of Walfajr in final stages of ripening (24–32 DAA) were measured.

Chlorophyll content

The chlorophyll content was assessed one and 2 weeks after anthesis on the flag leaf using chlorophyll meter (Minolta SPAD Meter; Minolta Camera Co., Tokyo, Japan) (Tahir and Nakata 2005). Again, chlorophyll content was measured for additional spraying for Walfajr at 24–32 DAA.

Yield components

Three weeks after physiological maturity plants of each sub-plot, in area of 1 m² were harvested and threshed and grain yield, biological yield and 1,000-grain weight were determined. For de-graining treatment, only spikes of 20 half-eared stems were collected and grain weight of sprayed and control treatment was recorded.

Data analysis

Results were analyzed using SAS statistical analysis package (version 9; SAS Institute, Cary, NC, USA). Data of stem and ear weights were analyzed for all of sampling dates but to summarize the results, only results of samplings at anthesis, stem maximum weight and maturity are given. Means were compared using Duncan's Multiple Range Test ($P \leq 0.05$).

Results and discussion

Changes in stem dry matter after anthesis

Foliar application of BAP did not affect stem weight at any time while there was consistent difference between cultivars from anthesis till maturity (Table 2). It seems that exogenous cytokinin could not alter storing assimilates capacity in stem internodes, probably by increasing photosynthesis and/or remobilization efficiency after anthesis till maturity.

Table 2 Analysis of variance of effects of cultivars and foliar application of BAP for stem and ear dry mass (at anthesis, stem maximum weight and maturity) and for grain yield, biological yield and 1000-grain weight at harvesting

Source	df	Stem wt(g)			Ear wt(g)			Grain Yield (kg m ⁻²)	Biological Yield (kg m ⁻²)	1000 grain weight (g)
		Anthesis	SMW	Maturity	Anthesis	SMW	Maturity			
Block	3	0.0057	0.0149	0.018	0.0017	0.01208	0.0081	265.1	0.0234	0.038
Cultivar	3	0.67***	1.0641***	1.1616***	0.1107***	0.3908***	0.5111**	138833***	0.388***	281.9***
Block × Cultivar	9	0.0092	0.0050	0.0122	0.0019	0.0170	0.0031	1413.7	0.0036	0.837
Treatments (spraying)	3	0.0077	0.0019	0.0069	0.0009	0.0048	0.0549***	6364.705**	0.021	11.8***
Treat × Cultivar	9	0.0107	0.0009	0.0088	0.0009	0.00438	0.0156*	4989.354**	0.055	0.700271

Treatments were: control, spraying on whole plant, spraying only on leaves and spraying only on ears

*, **, ***Significant at 0.05, 0.01 and 0.001 probability level, respectively

Values within table are mean squares

Changes in ear weight after anthesis

Results indicated that cultivars responded to spraying treatments at physiological maturity (Tables 2, 3). Spraying on whole plant and on ears increased ear weight almost equally, while spraying on leaves had little effect. Apparently, BAP was not translocated from treated leaves to grains, because considerable increases in ear weight were observed only in treatments in which BAP was sprayed on ears. Borkovec and Procházka (1992) and Gupta et al. (2003) demonstrated that exogenous cytokinins do not move readily from the site of application/production to non-treated areas. Again, it seems that there was no effect of cytokinin on source strength or there was no source limitation in grain filling of these cultivars.

Since the only significant effect of foliar application of BAP on ear weight was observed at maturity, it is suggested that exogenous cytokinin can increase sink size probably by increased cell division in endosperm. Cell division process can continue up to 30 DAA in barley (Cochrane and Duffus 1983). So, induced changes in ear weight made by cytokinin were observed at maturity when starch deposition has been completed.

Several studies have emphasized the role of cytokinin in determining sink strength by increasing cell division (Michael and Seiler-Kelbitsch 1972; Yang et al. 2002b; Gupta et al. 2003). Table 3 shows that Hull-less had the highest increase in ear weight induced by cytokinin although this genotype has genetically low grain weight (Table 1) and probably

higher sink limitation. This observation is not in concert with the results of Dua and Bhardwaji (1979) who reported that wheat genotypes possessing larger grains were richer in cytokinins and their growth was further increased by exogenous application of cytokinin.

Remobilization

According to Bonnett and Incoll method (1992), contribution of stem reserves at both pre- and post-anthesis stage was calculated (Table 4). Results showed that post-anthesis remobilization was not affected considerably by foliar application treatments. Since there was no significant difference between stem weights at SMW and maturity, but there was significant difference between ear weights at maturity (Table 3), it can be hypothesized that other sources have provided extra assimilates for increased sink sizes induced by exogenous cytokinin. Current photosynthesis of ear parts (awns, glumes and glumelles) has been speculated as a major component contributing in grain filling in barley (Ziegler-Jöns 1989; Bort et al. 1996) and probably could be an important source to supply assimilates for grains. M80-7 and Reihan had the highest ear weights at maturity which were related to least contribution of post-anthesis remobilization among cultivars (Tables 3, 4). This finding suggested that there were considerable differences between cultivars in utilizing reserves. On the other hand, pre-anthesis contribution of stem reserves was calculated negative

Table 3 Mean comparisons of ear weights and grain yields at maturity for different cultivars under spraying treatments

Cultivar	Spraying treatment	Ear weight (g)	Relative increase *(%)	Grain yield (kg m ⁻²)	Relative increase *(%)	Biological yield (kg m ⁻²)	HI
M80-7	T0	2.097 de	0	0.520 d	0	1.52 ± 0.060	34.26 ± 0.020
	T1	2.21 abc	5.4	0.582 c	11.9	1.78 ± 0.130	32.62 ± 0.013
	T2	2.124 def	1.23	0.538 d	3.5	1.7 ± 0.104	31.65 ± 0.020
	T3	2.273 a	8.43	0.622 c	19.7	1.57 ± 0.067	39.71 ± 0.019
Hull-less	T0	1.666 h	0	0.394 f	0	1.23 ± 0.044	32.94 ± 0.015
	T1	1.942 g	16.6	0.444 e	12.8	1.37 ± 0.033	32.50 ± 0.025
	T2	1.685 h	1.2	0.421 ef	7.0	1.35 ± 0.050	31.21 ± 0.022
	T3	1.902 h	14.2	0.450 e	14.1	1.23 ± 0.065	36.58 ± 0.033
Reihan	T0	2.005 efg	0	0.593 c	0	1.45 ± 0.065	40.93 ± 0.020
	T1	2.185 bcd	8.9	0.674 ab	13.5	1.58 ± 0.044	42.56 ± 0.017
	T2	2.007efg	0.12	0.630 b	6.15	1.47 ± 0.033	42.95 ± 0.016
	T3	2.175 bcd	8.5	0.682 ab	15.0	1.53 ± 0.033	44.51 ± 0.016
Walfajr	T0	1.979 fg	0	0.643 b	0	2.15 ± 0.074	29.92 ± 0.017
	T1	2.141 def	8.1	0.748 a	16.3	2.29 ± 0.033	32.60 ± 0.016
	T2	2.075 fg	4.6	0.654 bc	2.0	2.17 ± 0.067	30.16 ± 0.008
	T3	2.185 cde	10.4	0.682 ab	6.1	2.06 ± 0.075	33.08 ± 0.012

Biological yields are shown to calculate harvest index (HI)

*Percentage increase over control

Means in a column with similar letter are not significantly different ($P \leq 0.05$); Means ± SE ($n = 4$)

T₀: Non-treated (control), T₁: Spraying on whole plant, T₂: Spraying only on leaves and T₃: Spraying only on ears

(or very low in some cases) because stem weights for all treatments were greater at maturity than anthesis. In this study leaves weights were omitted from remobilization calculations because 1: most of retranslocated reserves are water soluble carbohydrates (WSC) which accumulate mostly in stem internodes (Bonnett and Incoll 1993b) and 2: shedding of dead leaves after anthesis occurs and would lead to an overestimation of reserves mobilization (Schnyder 1993). Gebbing et al. (1998) using balance sheets of WSC and protein estimated pre-anthesis contribution of reserves in wheat by 19%. Bonnett and Incoll (1992) found that in winter barley post-anthesis contribution was higher than pre-anthesis and net loss of stem matter between SMW and maturity could account for 62–92% of increasing in grain weight during this period. Kuhbauch and Thome (1989) found that in wheat pre-anthesis remobilization had not significant effect on grain filling. Some authors have suggested that remobilization of reserves will be crucial in the presence of stress during final stages of grain filling (Bidinger et al. 1977, Austin et al. 1980,

Blum et al. 1983) while others have noted that their role would be important even in common environments (Daniels et al. 1982, Bonnett and Incoll 1992).

According to our results at most 3.9 to 16.5% of final grain weight comes from remobilization of reserves (Table 4), which is similar to the finding of Borrel et al. (1989), and current photosynthesis would be prominent factor in determining grain weight.

Photosynthetic rate and chlorophyll content

Spraying of BAP 1 and 3 weeks after anthesis on different organs (ears, leaves and whole plant) affected neither photosynthetic rate of leaves nor ear chlorophyll content (data not shown). However, at final stages of grain filling periods in Walfajr (24–32 DAA) spraying of BAP significantly increased both photosynthetic rate and greenness of flag leaf (Fig. 1), nevertheless ear weight was not changed (data not shown). There are evidences from other studies that there is close relationship between cytokinin content

Table 4 Estimation of contribution of pre- and post-anthesis assimilation in grain filling of four barley cultivars under different BAP spraying treatments

Cultivar	Spraying treatments	Stem weight (g)			Grain wt (g)	Remobilization (%)	
		Anthesis	SMW	Maturity		Pre-anthesis	Post-anthesis
M80-7	T0	1.020 ± 0.025	1.480 ± 0.071	1.354 ± 0.079	2.097 ± 0.020	-0.16 ± 0.08	6.0 ± 0.04
	T1	1.153 ± 0.058	1.491 ± 0.041	1.372 ± 0.039	2.210 ± 0.042	-0.10 ± 0.03	5.4 ± 0.03
	T2	1.081 ± 0.038	1.451 ± 0.049	1.449 ± 0.077	2.124 ± 0.029	-0.17 ± 0.12	3.9 ± 0.05
	T3	1.090 ± 0.029	1.495 ± 0.075	1.423 ± 0.089	2.273 ± 0.037	-0.15 ± 0.05	3.1 ± 0.06
Hull-less	T0	0.861 ± 0.058	1.040 ± 0.028	0.766 ± 0.065	1.666 ± 0.030	0.06 ± 0.03	16.5 ± 0.04
	T1	0.815 ± 0.053	1.035 ± 0.027	0.763 ± 0.035	1.942 ± 0.024	-0.01 ± 0.03	14.8 ± 0.02
	T2	0.747 ± 0.042	1.019 ± 0.048	0.770 ± 0.055	1.685 ± 0.025	-0.10 ± 0.05	14.7 ± 0.08
	T3	0.819 ± 0.046	1.062 ± 0.059	0.799 ± 0.037	1.902 ± 0.033	0.01 ± 0.04	13.8 ± 0.06
Reihan	T0	0.675 ± 0.070	1.253 ± 0.035	1.078 ± 0.066	2.005 ± 0.033	-0.20 ± 0.03	3.8 ± 0.02
	T1	0.801 ± 0.040	1.283 ± 0.015	1.154 ± 0.037	2.185 ± 0.013	-0.17 ± 0.02	5.9 ± 0.03
	T2	0.771 ± 0.057	1.239 ± 0.028	1.233 ± 0.092	2.007 ± 0.037	-0.23 ± 0.07	5.8 ± 0.03
	T3	0.733 ± 0.066	1.238 ± 0.023	1.133 ± 0.070	2.176 ± 0.025	-0.22 ± 0.04	4.8 ± 0.02
Walfajr	T0	1.264 ± 0.023	1.649 ± 0.040	1.348 ± 0.078	1.979 ± 0.039	0.01 ± 0.07	15.2 ± 0.09
	T1	1.206 ± 0.021	1.640 ± 0.054	1.332 ± 0.044	2.140 ± 0.057	-0.06 ± 0.03	14.4 ± 0.05
	T2	1.184 ± 0.019	1.635 ± 0.054	1.384 ± 0.043	2.070 ± 0.034	-0.09 ± 0.03	12.1 ± 0.06
	T3	1.149 ± 0.027	1.627 ± 0.035	1.300 ± 0.047	2.185 ± 0.059	-0.07 ± 0.02	14.9 ± 0.03

T₀: Non-treated (control), T₁: Spraying on whole plant, T₂: Spraying only on leaves and T₃: Spraying only on ears
Means ± SE (*n* = 4)

(endogenous or exogenous), photosynthesis attributes (rate, genes, proteins), chlorophyll accumulation or maintenance and delay in senescence (Gan and Amasino 1995; Soejima et al. 1995; Wingler et al. 1998; Yang et al. 2002a; Ookawa et al. 2004). Most of these studies have used in vitro and not field techniques. Murchie et al. (2002) in two different rice varieties did not find consistent relationship between the rate of grain-filling and maximum rate of photosynthesis and chlorophyll content, both of which remained mostly unchanged throughout grain filling. They concluded that Rubisco accumulated to a level in excess of photosynthetic requirements, serving as a store of nitrogen for grain filling. Also Guinn and Brummet (1993) observed that in cotton leaves cytokinins changed little with leaf age, while free IAA decreased and was significantly correlated with photosynthesis. On the contrary, Yang et al. (2002a) observed significant correlation between content of cytokinins in root exudates and photosynthetic rate of flag leaves in rice; nevertheless this is a correlation and not cause and effect relationship.

Based on our findings, it is suggested that exogenous cytokinin could facilitate photosynthesis and

chlorophyll maintenance at final stages of ripening. Since this action was not reflected in increased grain weight, the importance of this role is being questioned. Peat (1985) and Hay and Walker (1989) expressed that ripening in cereals is limited mainly by capacity of grains in converting sucrose to starch and not by sucrose availability.

Yield components

Application of BAP had not significant influence on biological yield but significant increase in grain yield and 1,000-grain weight were observed; however the extent of increase was not similar in cultivars (Tables 2, 3). It seems that increase in grain yield was due to increase in 1,000-grain weight which was reflected in ear weight in previous section. Again, results indicated that only application of exogenous cytokinin on sink organ (spikes) were able to induce changes in grain weight. In this study, effects of cytokinin on grain number per unit area was not investigated because it is obvious that potential sink size in terms of grain number per plant is determined

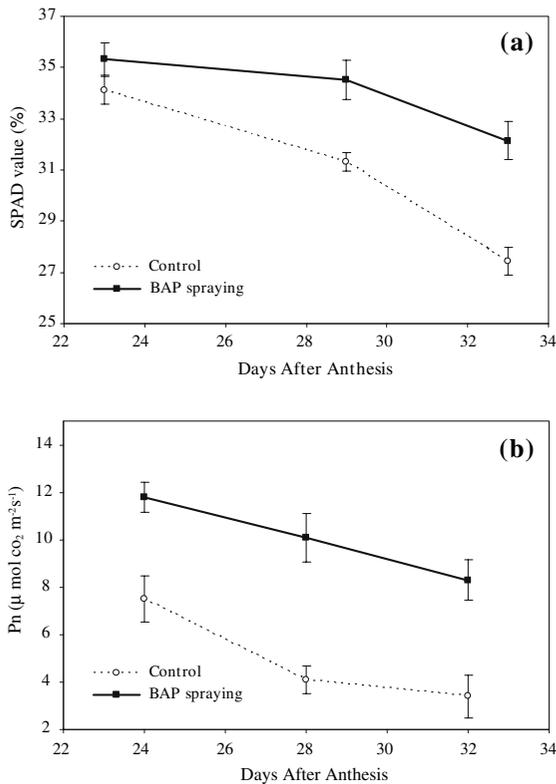


Fig. 1 Changes in chlorophyll content (a) and photosynthetic rate (b) of flag leaf in Walfajr after spraying with BAP. Spraying started at 20 DAA and continued for four consecutive days. Vertical bars show one standard error of means ($n = 4$)

in early growth stages of spike primordium (double ridge stage, Hay and Walker 1989) and exogenous cytokinin after anthesis could not enhance it. Gupta et al. (2003) did not observe any increase in grain number by BAP injection to wheat stems; however Trckova et al. (1992) and Wang et al. (2001) reported significant increase in grain number by application of cytokinin at early floret development stages in wheat.

Since in this study exogenous cytokinin was applied after anthesis, when leaf number and area as well as grain and tillers number per plant have already been determined, it is reasonable that there was no influence of cytokinin on biological yield. The increase in harvest index as a result of BAP application is a reflection of the changes in dry matter accumulation by enhanced sink size in ear-sprayed treatments, although rate of increase was relatively low in some cases (Table 3). Yang et al. (2002a) reported significant decrease in grain yield (per pot) and remobilization of well watered rice cultivars by application of cytokinin but they did not mentioned any cause for this observation.

De-graining treatment

Cultivars responded to de-graining (and BAP spraying) treatments although the response was different (Table 5). Most increases in grain weight caused by de-graining were in Reihan and Walfajr which indicated high sink limitation in these two cultivars while M80-7 and Hull-less showed highest increase in grain weight of half-eared spikes to spraying BAP. Apparently, cytokinin can induce more increase in endosperm cells of these two cultivars. The effects of partial spikelet removals on weight of remaining grains have been different. In some case there has been no significant increase in weight (Bonnett and Incoll 1993a, Yong-Zhan et al. 1996). It has been suggested that exceeded assimilates are redistributed to tillers or to stem to increase water soluble carbohydrates content in vegetative parts. This fact that extra photosynthates are transported to vegetative tissues like stem and tillers emphasizes on the

Table 5 Final grain weight of cultivars in response to de-graining and de-graining + BAP treatments on ears at anthesis

Cultivar	Grain weight (mg)		Relative increase * (%)	Grain weight (mg)	Relative increase * (%)
	Control	Half-eared			
M80-7	48.72 ± 0.63	51.16 ab	5.02	52.68 a	8.13
Hull-less	36.31 ± 0.76	38.67 e	6.50	41.23 d	13.55
Reihan	42.26 ± 0.69	49.28 b	16.62	49.72 b	17.65
Walfajr	42.30 ± 0.67	46.22 c	9.27	46.69 c	10.38

*Percentage over control

Mean comparison letters are only to compare half-eared and half-eared + BAP treatments ($P \leq 0.05$)

presence of sink limitation which is not due to deficiency of assimilates.

Conclusion

Our results showed that application of exogenous cytokinin soon after anthesis can increase grain weight, although the rate of increase varied in different cultivars. Since there was no considerable change in stem weight and remobilization of stem reserves, we hypothesized that current photosynthesis may provide extra assimilates to compensate for increased sink demand; although there was no significant increase in photosynthetic rate of flag leaf by exogenous cytokinin. So it was concluded that photosynthetically active tissues of ears can provide considerable amounts of photoassimilates for developing grains. Increased grain weight and yield as a result of application of cytokinin showed that sink limitation may be an important factor in determining potential grain yield. Generally, we speculate that in arid and semi-arid regions (like Iran) where illumination and day length are sufficient to support high photosynthesis rate and on the other hand, efficiency of remobilization (pre- and post-anthesis) is relatively low, sink size (number of endosperm cells within grains) is a major factor which limits final grain weight.

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