Effects of salicylhydroxamic acid on relative levels of starch and total sugars in different grains growing in the same spikelet of wheat

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Abstract: The effects of salicylhydroxamic acid on relative levels of starch and total sugars were studied in different grains (bold and small) growing in the same spikelet of wheat (*Triticum aestivum* L. var. *PBW-343*). The plants were grown in a screen covered hall under otherwise natural conditions. A concentration of 10 ppm salicylhydroxamic acid was applied at anthesis stage with the help of cotton plugs, which remained on ears of mother shoots (MS) for 48 hours. Labeled spikes were sampled five times, seven-day intervals started from seventh day after anthesis (DAA) up to 28th DAA, and at maturity. The application of salicylhydroxamic acid presented the unique observations. The inhibitor behaved in an enigmatic way and proved to be a promoter when being assessed under the criterion of relative levels of starch and total sugars. The salient points emerging through the use of salicylhydroxamic acid were that (i) both bold and small grains showed an increase in relative levels of starch and total sugars from 14th and 28th DAA stages respectively ($P<0.01$) and (ii) in spite of aforementioned increment, they continued to exhibit the disparity between them and at maturity the smaller grains still showed lower starch and higher total sugars than the bolder grains.

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1. Introduction

Starch is the major constituent of cereal's end product and is a measure of the activity of processes contributing to its deposition in the grain (Chinnusamy and Khanna-Chopra, 2003). Sucrose, the primary product of photosynthesis and assimilated carbon, acts as the main raw material for its formation (Porter and May, 1955). Berry *et al*. (1971) isolated, studied and compared the output of starch among triticale, rye hard red spring and durum wheat. They reported that the greatest percentage of starch occurred in the triticale flour samples as compared to wheat and rye. Jenner (1980) correlated the starch synthesis in endosperm to concentration of sucrose in tissue. Starch accumulation appeared to cease during development in the oat prior to the total dry weight accumulation, while soluble carbohydrates primarily sucrose and glucose remained at higher levels (Koch and Peterson, 1991). Black *et al*. (1996) studied starch in embryos of wheat and reported that its levels accumulated in the axis and scutella from 20th DAA to reach a maximum at approximately 35th DAA and subsequently it declined to a very low value in late maturation. According to Jeng *et al*. (2003) starch content was initially low but increased rapidly during maturation while reducing sugars, sucrose and fructose decreased in two spring wheat cultivars. Jenner and Rathjen (1972) concluded that magnitude of photosynthesis is adequate to maintain the flow of sucrose into the wheat grains but flow of sucrose may be limited by the capacity of the processes transporting the sugars during the final stages of its passage into grains. Kumar and Singh (1980) showed that active starch synthesis started from 14th DAA onwards and continued until 35th DAA.

Many plant developmental, physiological and metabolic processes are regulated, at least in part, by nutrient availability. In particular, alteration in the availability of soluble sugars, such as glucose and sucrose, help regulate a diverse array of processes (Gibson, 2004). The accumulation of sugars in the storage cells is crucial for the size of grain. According to Sterans (1970) sugars constituted nearly 10 percent of dry matter of wheat aleurone cells. Paul *et al*. (1971) reported that reducing sugars were gradually converted into non-reducing forms during development in developing seeds of rice. Kerepesi *et al*. (2002) reported that the contents of reducing and non-reducing sugars decreased as grains matured and the contents of non-reducing sugars were higher than reducing at maturity stages in hard red spring wheat. They reported that the concentration of glucose and fructose decreased

while raffinose which appeared at later stages increased with maturity. Duffus and Rosie (1973) found changes in soluble reducing sugars and studied that reducing sugars remained low throughout development.

Singh and Singh (1982) noticed that total soluble sugars decreased during course of grain development in rice treated with IAA, GA_3 and kinetin. Caputo and Barneix (1999) have studied the relationship between amino acids and sugars export to the phloem in wheat. They showed that the sugar concentration in the phloem exudates was increased by higher light intensities, but there was no difference in the amino acid concentration of the phloem exudates and thus the amino acid to sugar ratio in the phloem decreased under high illumination. The present results suggest that amino acids can be exported to the phloem independently of the export of sugars.

In addition to affecting a number of developmental processes, sugars have been implicated in the regulation of a large number of genes (Koch, 1996). The α-amylase gene family provides a particularly well-characterized example of sugar-regulated gene expression. Given their biological function, it is, perhaps, not surprising that the expression of many α-amylase genes has been shown to be repressed by soluble sugars, such as glucose and sucrose, thus providing a mechanism by which starch breakdown may be regulated to provide an adequate supply of soluble sugars (Gibson, 2004). The regulation of α-amylase expression by sugars is complicated, occurring at multiple levels as well as via multiple response pathways that can be dependent on sugar concentration or its fluxes. The comprehensive works of Liang *et al*. (2001) and Gibson (2004) have shown that α-amylase expression has been regulated by sugars at both the transcriptional and post-transcriptional levels.

The alternative oxidising pathway is a non-proton motive 'bye-pass' to main electron transport otherwise in operation through the cytochrome pathway. Despite its wasteful nature, in terms of energy conservation, the pathway is ubiquitous throughout the plant kingdom. A small alternative oxidising gene family probably exists and its members are differentially expressed in response to environmental, developmental and other cell signals. The alternative oxidising pathway enzymes possesses tight biochemical regulatory properties that determine its ability to compete with the cytochrome pathway for electrons. Studies show that alternative oxidising pathway can be a prominent component of total respiration in important crop species. All these characteristics suggest that this pathway plays an important role in metabolism and/or other aspects of cell physiology (McDonald *et al*., 2002).

Depending on the plant species and growth conditions, 30 to 70 percent carbohydrates fixed in photosynthesis get respired on the day of its synthesis (McDonald *et al*., 2002). The terminal part of the respiratory path, which starts with glycolysis, consists of the mitochondrial electron transport pathway, in which, among other components, two terminal oxidizing systems, cytochrome C oxidase or alternative oxidase may operate. The later branches from the main electron transport pathway at the ubiquinone pool and beyond the branch point, unfortunately does not contribute to ATP production. The energy conservation is less than maximal if a part of the respiration proceeds via this non-phosphorylating (alternative) pathway. Because of its energy wasting nature, it is most interesting (scientifically, as well as economically) to investigate under which conditions and to what extent alternative respiration is used, and how its activity is regulated.

Many reports have appeared, in which the activity of the alternative oxidase entity was assessed with the use of specific inhibitors of the cytochrome (e.g., CN^{-}, azide, antimycin) or (e.g., SHAM, benzhydroxamic acid, propyl gallate) pathways (Lambers, 1997). It was shown that the alternative pathway became active at very high reduction levels of the Q pool (Dry *et al*., 1989). There have been a few reports of this alternate oxidative pathway from some angiosperms and its values have been correlated with a few physiological parameters directly or indirectly associated with yield e.g., in *Vigna radiata* grown at 19°C the concentration of the alternative oxidase component increased over two-fold in both hypocotyls and leaves as compared to 28°C. This response could not be carried to *Glycine max* cotyledons (Gonzalez-Meler *et al*., 1999). Ribas-Carbo *et al*. (2000) reported that in a chilling-sensitive maize cultivar, the activity of the alternative pathway was higher during the recovery period than in a less chilling-sensitive cultivar. According to Millenaar and Lambers (2003) the alternative pathway is inhibited more at low oxygen concentrations compared with the cytochrome pathway. Therefore, the alternative pathway

does not have a function at low oxygen concentrations.

The activity of the cytochrome pathway depends on the availability of inorganic phosphate and ADP. If plants are exposed to very low phosphorus supply, its concentration along with that of ADP may become very low. Therefore, it has been postulated that under these conditions the activity of the alternative pathway is increased relative to that of the cytochrome pathway (Gonzalez-Meler *et al*., 2001). Some oxygen free radical scavenger enzymes (catalase and total peroxidase) are more active in P-deficient plants, while others do not change (ascorbate peroxidase and superoxide dismutase) (Juszczuk *et al*., 2001). Restriction of the cytochrome pathway by phosphorus limitation causes an increase in the formation of oxygen free radicals, which can be prevented (partly) by more active alternative oxidase pathway.

While studying the development of grains at basal and distal positions within a middle spikelet of mother shoot of wheat, Kumari and Ghildiyal (1998) observed that lesser growth of distal grains was associated with higher rate of alternative respiration compared to proximal grains, thereby inferring that lesser growth at distal position in a spikelet may be linked to high alternate oxidase system. Gonzalez-Meler *et al*. (1996) reported elevated CO_2 concentration inhibited the salicylhydroxamic acid-resistant cytochrome pathway, but had no direct effect on the cyanide-resistant alternative pathway. This response may be indicative of a shift in plant metabolism and the increased energy demand resulting from higher photosynthetic rates under CO_2 enrichment (Woodward, 2002).

In the present study, it is proposed to analyze the relative levels of starch and total sugars as affected by specific inhibitor of salicylhydroxamic acid in basal and apical grains growing in the same spikelet of wheat.

2. Material and Methods

2.1. Experimental setup

The investigation was conducted with a common bread wheat (*Triticum aestivum* L. var. *PBW-343*), which was sown in circular earthenware pots (50x30x30 cm) containing 35 kg of soil mixed with farmyard manure (4:1). Eight seeds per pot were sown and after 15 days, seedlings were thinned to two. Hoagland's nutrient solution (1939) was supplied to the pots. The plants were grown in a screen covered hall under otherwise natural conditions. A concentration of 10 ppm salicylhydroxamic acid was applied at anthesis stage with the help of cotton plugs, which remained on ears of mother shoots (MS) for 48 hours. Labeled main spikes were sampled five times, seven-day intervals started from seventh day after anthesis (DAA) up to 28th DAA, and at maturity. Grains were usually taken from three different segments in the ear. The labeled samples of grains were brought to laboratory and separated to two types of grains (small and bold) and the following biochemical analysis was carried out in the above aged grains.

2.2. Starch analysis

Starch contents were estimated by the method described by Hodge and Hofreiter (1962). The brief procedure is as follows:

(i) Extraction of Starch - One gram of powdered dry sample of grains was transferred to 100 ml of volumetric flask. The material was hydrated and gelatinised with 30 ml of distilled water by keeping the flask over boiling water bath for 30 minutes. The flasks were well stoppered so as to prevent any loss of water by evaporation. The flasks were cooled under running cold water for 10 minutes and 60 ml of 60 percent perchloric acid was added slowly with thorough agitation so as to avoid any momentary high concentration of acid. The mixture was allowed to stand, with occasional stirring, for 15 minutes and the volume were made up with distilled water. After shaking, the contents were allowed to settle. The supernatant was used for starch estimation.

(ii) Estimation of Starch - 5 ml of the above supernatant solution was pipetted out into 100 ml volumetric flask. To this, 6 ml of cold distilled water was added. The solution was made incipient alkaline with a few drops of 2N NaOH with the use of phenolphthalein as an indicator. The solution was made just acidic with a drop of 2N acetic acid till the pink colour disappears and to this, 2.5 of 2N acetic acid, 0.5 ml of 10 percent potassium iodide and 5 ml of 0.01 N potassium iodate were added for the colour to develop. The volume was raised to 100 ml and intensity of the colour was measured at 650 nm in a Bausch and Lomb Spectronic 20 using red filter. A single blank containing all the reagents was used to adjust the absorbance at zero. The unknown quantity was estimated from the standard curve prepared with tomato starch and results expressed as mg per grain.

2.3. Total sugars analysis

Total sugars were estimated by the method of Dubois et al. (1956) with some

modifications as follows:

(i) Extraction of total sugars - Fresh grains weighing 1 g at different intervals of time after anthesis were cut into small cubes of 1 sq. mm and taken into a vial containing 5 ml of 80 percent ethanol and stored overnight. The samples were extracted with boiling ethanol the next day. The supernatant was decanted into 50 ml beaker. The residue was repeatedly extracted 4 times with 80 percent boiling ethanol. The volume of the combined supernatant was made upto 25 ml with 80 percent ethanol and then centrifuged at 6000 g for 20 minutes. The supernatant so obtained was used for the estimation of total sugars.

(ii) Estimation of total sugars - Total sugars were estimated using the reagents included phenol 5 percent and concentrated H_2SO_4. A suitable amount of the supernatant (0.2 – 0.5 ml) was taken in a test tube and to this 1 ml of phenol reagent and 5 ml of concentrated H_2SO_4 were added and mixed thoroughly. The absorbance was recorded after 20 minutes of colour development at 490 nm. The total sugars content were calculated from a calibration curve prepared with glucose and expressed as mg per grain.

3. Results

3.1. Relative levels of starch and total sugars

All the grains, irrespective of their size or positions in an ear, revealed a positive correlation between their ages and the levels of starch (Table 1). The first five spikelets, constituting as proximal, the next ten and the last five spikelets as middle and distal segments respectively had their own characteristic variations with a common generalization that the bolder grains possessed a higher levels of starch than the smaller grains at all the stages of grain development. The disparity between the bold and small grains in the levels of starch was maximum at 7th DAA in all the three segments (44.8, 30.0 and 55.6 percents lesser in smaller grains than bolder grains in proximal, middle and distal segments respectively) and further the disparity tended to taper with maturity. Interestingly, during the initial phases of grain growth, there were significant disparities within the smaller grains amongst themselves whether growing at proximal, middle or distal segments, while on the other hand, bolder grains reflected insignificant differences amongst them.

The data on total sugars are also presented in Table 1. The total sugars increased upto third week after anthesis in small grains in the proximal, middle or distal spikelets, while its values enhanced upto fourth week in the bolder grains in the same segments. Their values were significantly lower in the bolder grains as compared to smaller grains in all the segments by a margin ranging from 8.1 to 46.9 percents. These disparities were maximum around three weeks after anthesis and this generalization was true for all the three segments under (45.6, 46.9 and 46.3 percents higher in smaller than bolder grains in proximal, middle and distal segments respectively). Interestingly the gap amongst the bold and small grains tended to taper with the grains' progression to maturity.

Table 1. Levels of starch and total sugars (mg grain^{-1}) at different location within developing grains of wheat (*Triticum aestivum* L. var. *PBW-343*) as influenced by SHAM

Relative levels (mg grain^{-1})	Grain type	Day after anthesis (DAA)				
		7th	14th	21st	28th	Maturity
Starch	Bold	2.0 (+5.3)	12.8 (+39.1)	21.9 (+23.7)	31.2 (+20.5)	32.7 (+18.5)
	Small	1.4 (+7.7)	9.1 (+35.8)	17.9 (+27.0)	26.9 (+24.5)	28.3 (+22.5)
Total sugars	Bold	3.48 (+1.8)	4.26 (+2.2)	4.86 (+4.1)	4.64 (+10.0)	4.62 (+14.9)
	Small	4.74 (+1.9)	6.04 (+3.1)	7.08 (+6.9)	6.54 (+14.9)	6.10 (+18.9)

Values within parenthesis indicate percentage of increase (+) in the level of starch/total sugars over control

3.2. SHAM effects on relative levels of starch and total sugars

The application of salicylhydroxamic acid presented the unique observations. Ironically, the inhibitor behaved in an enigmatic way and proved to be a promoter when being assessed under the criterion of relative levels of starch and total sugars.

The salient points emerging through the use of salicylhydroxamic acid were that (i) both bold and small grains showed an increase in relative levels of starch and total sugars from 14th and 28th DAA stages respectively (Table 1) and (ii) in spite of the aforementioned increment, they continued to exhibit the disparity between them and at maturity the smaller grains still showed lower starch and higher total sugars than the bolder grains (Figures 1 and 2).

As apparent from the Figure 1, the relative levels of starch in bold and small grains showed a significant disparity with respect to its distribution in the two types of grains. In comparison to bolder grains, the smaller grains possessed significantly low levels of starch. The disparity was sustainable throughout the ontogeny of grains development with maximum gap at 21st DAA (30.0 percent lower than bold grains) with a recorded gap of 28.9, 18.3 and 13.8 percent at 7th, 14th and 28th DAA and

ending up with a final disparity of 13.4 percent at maturity, respectively.

Furthermore, as apparent from the Figure 2, the relative levels of total sugars in bold and small grains also showed a significant disparity with respect to its distribution in the two types of grains. In comparison to bolder grains, the smaller grains possessed significantly high levels of total sugars. The disparity was sustainable throughout the ontogeny of grains development with maximum gap at 21st DAA (55.7 percent higher than bold grains) with a recorded gap of 36.2, 41.7, 40.9 and 32.6 percent at 7th, 14th, 28th DAA and maturity, respectively.

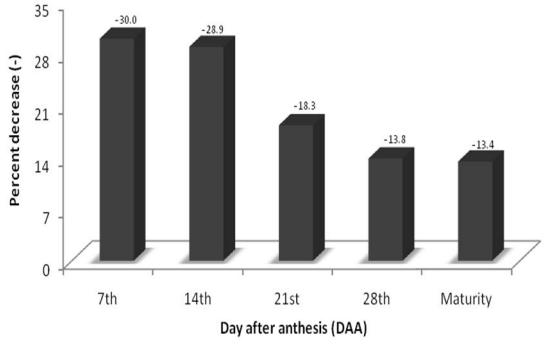

Figure 1. Percentage decrease (-) in relative levels of starch in small grains over their counterparts bold grains as affected by SHAM

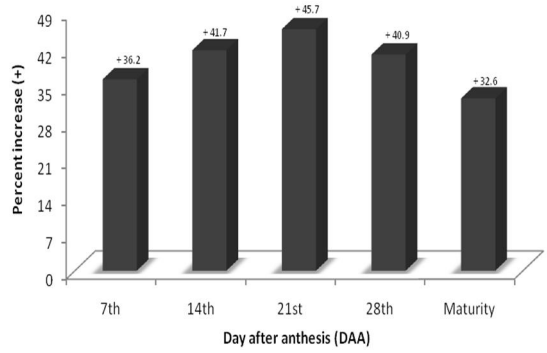

Figure 2. Percentage increase (+) in relative levels of total sugars in small grains over their counterparts bold grains as affected by SHAM

4. Discussions

We have investigated the relative levels of starch and total sugars as affected by salicylhydroxamic acid in basal and apical grains growing in the same spikelet of wheat. The results bring forth, in no uncertain terms, the findings that the ear of wheat is a developing place for a definite number of grains which intern are separate biological entities endowed with their inherent potentials. This axiom was advocated by Abolina (1959) and is in line with the observations of innumerable workers (Cook and Evans 1978; Larsson and Hensen 1992; Wang *et al.* 1998; Yang *et al.* 2003). Nevertheless, the sequence of events, piloting the yielding ability, is the metabolic profile and if augmented through the use of plant growth regulators (Yang *et al*. 2000; Houshmandfar and Eradatmand-Asli 2011) or by imposing a shift in metabolic events (Dua *et al*. 1990) promotery effects are achievable (Hayashi 1961; Michael and Beringer 1980).

In present context, the central point which came to light in the present endeavor is that an unusual path of aerobic respiratory chain (CN-resistant respiration) plausibly switches-on during the grain filling stage and if checked, through the immaculate use of salicylhydroxamic acid, can increase the relative levels of starch and total sugars in the grains. Of course, SHAM or regulator of alternate oxidase pathway was not successful in eliminating the disparities between the two types of grains.

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