The Canon of Potato Science:

38. Carbohydrate Metabolism

Joseph R. Sowokinos

Published online: 15 May 2008 *#* EAPR 2008

What is it?

Carbohydrate metabolism is comprised of several interrelated pathways that ultimately serve to provide the carbon and energy necessary to support potato growth. In the presence of sunlight and carbon dioxide, photosynthesis leads to the formation of assimilation starch in the leaves with the release of molecular oxygen. At night, the assimilated starch is converted to the disaccharide, sucrose. This sugar is loaded into the phloem and translocated down through the vascular system, through the stem and the stolon, and is then unloaded when it reaches the tuber. The energy of the glucosidic bond in sucrose (6.6 kcal/mole) provides the chemical energy necessary to drive all biosynthetic processes that support plant growth and tuber development. The majority of tuber growth that occurs during bulking involves cellular expansion accompanied with starch accumulation. Starch comprises approximately 80% of the tuber dry weight.

Why is it Important in Potato Science?

Potato tubers are an excellent source with which to study the regulation of carbohydrate metabolism. Whole plant metabolism (including photosynthesis, dark respiration, transpiration, translocation, tuberization, and the processes involved in tuber bulking) can be studied in the field or in a glasshouse environment. Potato cells are a rich source of mitochondria that can be isolated to investigate the process of respiration i.e., production of energy (ATP), carbon dioxide, and water. Tissue culture cells can be used to study carbon metabolism with the understanding that the *in vitro* cells respond as wound tissue. Biotechnology has

J. R. Sowokinos (***)

Department of Horticultural Science, University of Minnesota, 311 5th Avenue NE, East Grand Forks, MN 56721, USA e-mail: sowok001@umn.edu

embraced the potato as a transformation tissue to investigate carbohydrate metabolism as well as to serve as a system to produce biologically active compounds related to human health.

The regulation of carbohydrate metabolism is complex and the final concentration of starch and free sugar is influenced by cultivar, biotic and abiotic stresses during growth and development, storage environment, and, among others, the physiological age of the potato. The actual concentration of free-sugar in potato cells, at any particular point in time, is certainly not the result of a single factor but involves the interaction of several pathways of carbohydrate metabolism, i.e., starch synthesis/ degradation, glycolysis, respiration, and hexogenesis or sweetening. A few levels of cellular control that affect carbohydrate balance include:

- (1) hormones;
- (2) membrane structure and function;
- (3) compartmentalization and concentration of enzymes, key ions, and substrates;
- (4) enzyme expression and/or activity.

Potatoes can be subjected to biotic or abiotic stresses (singly or in combination) to investigate which of the above cellular controls are initially most important in causing the resulting change in carbohydrate partitioning and/or content. Such information can further our scientific understanding of the regulation of carbohydrate metabolism in plants.

Why is it Important for the Potato Industry?

The balance between starch (complex carbohydrate) and simple-reducing sugars determines the quality and marketability of processing potatoes (i.e., crisps and French fries). There is a tremendous economic impact when excessive concentrations of reducing sugars accumulate following the placement of potatoes into cold storage. Cold induced sweetening (CIS) presents a management problem for the potato industry on a global basis. When tubers of most commercially used cultivars are stored at cold temperatures (2−4 °C), they accumulate high concentrations of reducing sugars, primarily glucose and fructose. The carbonyl groups of these sugars react with the amino group of free amino acids as slices or sections of raw potatoes are fried in oil at high temperature. This leads to the production of visually unacceptable, dark-pigmented products. To overcome this difficulty, potatoes are generally stored at warmer temperatures $(7-12 \degree C)$.

Developing new cultivars that are resistant to CIS is a high priority for most potato breeding programmes. Genes from wild species, that confer resistance to CIS, are also being incorporated into commercially acceptable cultivars. Accessibility of CIS-resistant cultivars would allow potatoes to be stored at lower temperatures, which, in turn, would help

- (1) to reduce the use of fungicides and bactericides in storage;
- (2) to reduce the loss of solids through respiration;
- (3) to reduce or eliminate the need for chemical sprout suppressants; and
- (4) to increase the marketing window.

The commercial evaluation of a tuber's sucrose and glucose concentration during harvest and storage has assisted the potato industry in fine-tuning management decisions to minimize the effects that reducing sugars have on colour-quality of crisps and French fries. The monitoring of the 'chemical maturity' (CM) of the potato has been made possible through the use of the YSI (Yellow Springs Instrument) Industrial Sugar Analyzer. Injection of potato juice directly into the analyzer rapidly yields the concentration of sucrose and glucose simultaneously in mg/g tuber on a fresh weight basis. The relative concentration of these two sugars has helped farm managers in determining:

- (1) timing for vine-kill;
- (2) which fields to harvest first;
- (3) whether a short, preconditioning period is necessary for removing sugars in early storage;
- (4) the potential for holding a potato bin long-term; and
- (5) when the process of irreversible senescent-sweetening is imminent.

Scientific Developments

Sucrose translocated into the stolon tip is unloaded via the enzyme sucrose synthase (Susy). Studies with potato suspension cultures have revealed that Susy is induced during the lag phase of cellular growth, i.e., prior to the initiation of cell division and starch formation processes. This induction occurred when the intracellular concentration of sucrose reached 2 to 3 mM. High intracellular concentrations of the hexoses glucose or fructose were not able to lead to Susy induction. During the period of rapid cellular division, total Susy activity remains constant per cell and then declines during the stationary phase of growth.

Two candidate genes and their products have been shown to play a major role in regulating the formation of reducing sugars in potatoes, i.e., UGP-Glucose pyrophosphorylase (UGPase) and vacuolar acid invertase (VAcInv). Potatoes contain different profiles of UGPase isozymes (i.e., slightly different charge forms of the enzyme). The major isozyme of UGPase found in cold sweetening-sensitive cultivars is UGP3 (e.g., Norchip); in cold sweetening-resistant cultivars it is UGP5 (e.g., Snowden). The kinetic property that distinguishes UGP3 from UGP5 is that the latter is catalytically less active and limits the amount of sucrose (i.e., substrate for reducing sugar formation via hydrolysis by VAcInv) that is formed. The genes responsible for expressing UGP3 and UGP5 have been cloned and are designated $UgpB$ and $UgpA$, respectively. Cultivars with a predominance of the $UgpA$ allele demonstrate a 4.5-fold decrease in reducing sugar concentration at cold temperatures compared to cultivars that have a predominance of the UgpB allele. Two cultivar traits that collectively contribute to cold sweetening resistance are

- (1) a predominance of the $UgpA$ allele; and
- (2) low VAcInv activity.

Cultivars with high VAcInv activity, even in the presence of UgpA, can result in the production of crisps and French fries with unacceptable colour. This is most likely due to the fact that the 'reduced sucrose pool', obtained with UGP5, is more efficiently turned-over or hydrolysed to yield undesirable concentrations of reducing sugars. The UgpA allele is being used to transform cultivars used for crisp and French fry production that demonstrate low VAcInv activity, but lack the coldsweetening resistant gene.

Further Reading

- Gupta SK, Sowokinos JR (2003) Physiochemical and kinetic properties of unique isozymes of UDP-Glc pyrophosphorylase that are associated with resistance to sweetening in stored potato tubers. J Plant Physiol 160:589−600
- Hofius D, Börnke FAJ (2007) Photosynthesis, carbohydrate metabolism and source-sink relations. In: Vreugdenhil D (ed) Potato biology and biotechnology: advances and perspectives. Elsevier, Amsterdam, pp 501−523
- McKenzie MJ, Sowokinos JR, Shea IM, Gupta SK, Lindlauf RR, Anderson JAD (2005) Investigations on the role of acid invertase and UDP-glucose pyrophosphorylase in potato clones with varying resistance to cold induced sweetening. Am J of Potato Res 82:231−239
- Sowokinos JR (2007) Internal physiological disorders and nutritional and compositional factors that affect market quality. In: Vreugdenhil D (ed) Potato biology and biotechnology: advances and perspectives. Elsevier, Amsterdam, pp 501−523
- Sowokinos JR, Varns JL (1992) Induction of sucrose synthase in potato tissue culture: Effect of carbon source and metabolic regulators on sink strength. J Plant Physiol 139:672−679
- Sowokinos JR, Vigdorovich V, Abrahamsen M (2004) Molecular cloning and sequence variation of UDP-Glucose pyrophosphorylase cDNAs from cold sweetening and resistant potatoes. J Plant Physiol 161:947−955