

# The impact of temperature on the hydrolysis of potato starches into simple sugars

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## SUMMARY

Potatoes, underground tubers of the plant *Solanum tuberosum*, are staple foods in many cultures across the globe. In temperate climates, potatoes are harvested and stored throughout the cold season. In commercial storage facilities, they often undergo cold-induced sweetening (CIS), which negatively affects their taste. We aimed to determine why potatoes can also turn sweet during short-term storage in consumers' houses—especially when peeled and pre-cut—and to assess the impact of storage temperatures on this process. Specifically, we aimed to determine the effect of different storage temperatures on the breakdown of starches into simple sugars, which causes the undesirable sweet taste. To this end, we used a blood glucometer to measure sugar contents of juices squeezed from the tubers peeled, sliced, and exposed for 96h to three different temperatures: cold (4°C/39°F), ambient (approximately 20°C/68°F), and hot (37°C/98.6°F). Our initial hypothesis was that the hotter the storage temperature, the faster the rate of starch hydrolysis and the greater the content of simple sugars. Surprisingly, our data indicated that the highest levels of simple sugars were achieved during storage at the ambient temperature, while both the cold and hot storage conditions prevented the breakdown of starches, and the tubers remained relatively unsweetened. Thus, the rate of enzymatic breakdown as a function of temperature is not linear but follows a bell curve, with peak values achieved at the room temperature. Our findings suggest keeping freshly peeled potatoes in household refrigerators, where prolonged effects of CIS are unlikely to be a factor.

## INTRODUCTION

Potatoes are staple foods in many cultures, but their prolonged storage in commercial facilities and individual households often imparts the undesirable sweet taste. Human taste buds recognize certain foods as sweet when they contain monosaccharides, or simple sugars, such as glucose. However, rather than simple sugars, freshly harvested potatoes contain starch, a polymer with a complex chemical structure (1). Starches are polysaccharides that are made up of simple sugars bonded together. The two main components of starches are amylose and amylopectin, which are polymers of glucose arranged in linear and branched patterns, respectively (2). In the presence of the

enzyme amylase, amylose and amylopectin are subjected to hydrolysis, or breakdown by water (3). In the case of potato starches, amylase produces a disaccharide called maltose. Maltose is broken down further during additional hydrolysis steps by enzymes called  $\alpha$ -glucosidases. One common  $\alpha$ -glucosidase is maltase, which during hydrolysis produces two molecules of the monosaccharide glucose (2). As a result of these reactions, the potato becomes significantly sweeter. Unlike the sweetness of "sweet potatoes", which is an entirely different species (*Ipomoea batatas*), excessive sweetness in regular potatoes (*Solanum tuberosum*) is considered an undesirable trait, and much effort is dedicated to minimizing cold-induced sweetening (CIS) during long-term commercial storage (4,5).

We aimed to understand the effects of temperature on potato sweetening during short-term storage in consumers' houses, namely, to determine how storage conditions affect the breakdown of starches into simple sugars. Using common household appliances and a blood glucometer, we were able to test three different temperatures: cold (inside the refrigerator maintaining ~4°C/39°F), ambient (~20°C/68°F room temperature at the time of testing), and hot (inside an immersive circulator keeping water at 37°C/98.6°F).

At colder temperatures the intrinsic activities of most hydrolases are much lower, causing the reaction to take place at ~20-25% their optimal rates (6). Thus, we expected to detect very low sugar levels in peeled and cut potatoes stored in the refrigerator, which proved to be true. We also hypothesized that the higher the temperature, the faster the starch breakdown reaction and the higher the glucose levels. This also was found to be true, but only up to a point. While storage at 20°C indeed resulted in higher glucose levels (compared to storage at 4°C), further elevating the temperature to 37°C resulted in undetectable glucose levels. The biphasic effect we describe here has real-world implications for home and restaurant cooks wishing to avoid unnatural sweetness in their potato dishes.

## RESULTS

We aimed to determine the effects of various storage temperatures on glucose levels in potato juices. We tested three different potatoes, and analyzed each potato slice multiple times, to assess the suitability of using the Livongo glucometer as well as to determine individual variations and measurement errors. All three sliced potatoes used in this initial experiment were kept at ambient temperature (~20°C) for 96 h prior to measurement. Then the slices were cut into smaller pieces, juices were extracted from each sample, and glucometer strips were immersed in the juices for 3s and read in the glucometer, in triplicate.

Using this workflow, we obtained the following mean  $\pm$  SD values: 240  $\pm$  5.0 mg/dL (potato #1), 180  $\pm$  2.5 md/dL (potato #2), and 331  $\pm$  6.1 md/dL (potato #3) (**Figure 1**). For each individual potato, these measurements were very consistent, attesting to the reproducibility of our approach. Potato #3 showed the largest deviation from the mean, 6.1 mg/dL, or  $\pm$  4.1 mg/dL experimental uncertainty commonly understood to be two-thirds standard deviation (7). Among the three potatoes, the standard deviation value and the experimental uncertainty were much higher, 66.5 mg/dL and  $\pm$  44.3 mg/dL, respectively.

Having established the extent of technical errors and sample variability, we tested the effects of temperature on glucose levels. We placed multiple slices from the same potatoes in Ziploc bags and stored them for 96h at 4°C, 20°C, or 37°C. After that, we tested potato juices as described above. We used freshly sliced potatoes as baseline controls and observed that they yielded negligible values, below the detection limit of the glucometer.

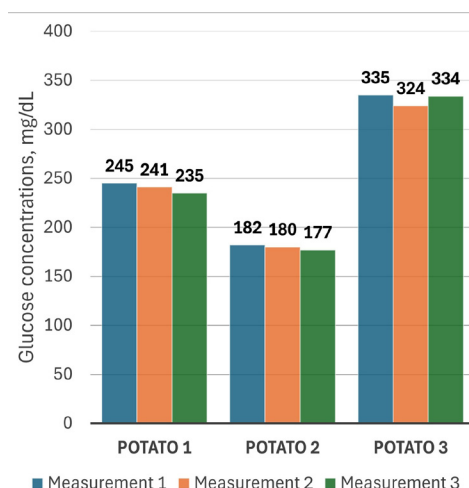
We found that glucose levels in potatoes stored at both 4°C and 37°C remained below the detection level of 20 mg/dL. In contrast, for the potato slices stored at 20°C, the glucometer returned higher values: 181 mg/dL (potato #1), 89 mg/dL (potato #2), and 218 mg/dL (potato #3) (**Figure 2**). Without adjusting for the undetermined baseline, this corresponded to the mean value of 162.6 mg/dL, standard deviation of 54.2 mg/dL, and the uncertainty of  $\pm$  36.1 mg/dL. This variability was similar to that observed in the previous experiment, attesting to the consistency of our results.

## DISCUSSION

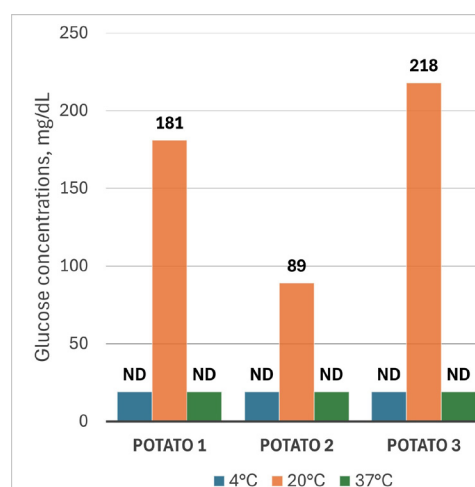
In our study, we aimed to investigate how different storage temperatures affect the breakdown of potato starches into simple sugars, which increase potato sweetness. Despite the simplicity of the central question, whether it could be addressed without access to a professional analytical chemistry lab was unclear. After investigating available options, we settled on the use of a blood glucometer designed for individuals with diabetes.

Our first experiment was to determine whether the Livongo glucometer could detect glucose in potato juices. Notably, glucometers are allowed to deviate from the actual value by as much as 20%, as reflected in the International Organization for Standards (ISO) Standard 15197, which is used by the Food and Drug Administration, the lead health authorities in the United States (8). We determined that the uncertainty of the Livongo glucometer was low (4.1 mg/dL), suggesting that the glucometer we chose had sufficient precision. We didn't measure the accuracy of the instruments since we didn't have access to standard glucose solutions. While we could not rule out a possible bias, its impact on our results could be considered minimal, since we were primarily interested in relative, not absolute, changes in glucose levels. Additionally, the type of glucometer we used does not report values below 20 mg/dL or above 600 mg/dL. Thus, we were unable to quantitate baselines for freshly peeled and sliced potatoes or potato slices stored at 4°C and 37°C.

Our experimental data indicated that, as expected, increasing the temperature up to a certain level (from 'cold' to 'ambient') increased glucose levels inside peeled and cut potatoes. However, further increasing the temperature (from 'ambient' to 'hot') had the opposite effect: glucose levels



**Figure 1. Variations in glucometer readings across technical and biological replicates.** Three slices representing individual potatoes were stored separately at 20°C/68°F for 96 h and then tested for glucose content three times each. Numbers above bars are raw readings used to calculate standard deviation values. Independent measurements are color-coded, as shown in the legend.



**Figure 2. Variation in glucose levels across different storage conditions.** Slices from the same three potatoes were stored at indicated temperatures for 96 h and then tested for glucose content once. In the 20°C group, numbers refer to glucometer measurement. In the 4°C and 37°C groups, numbers represent baseline levels assumed to be just below the detection level of 20 mg/dL. ND, not detected.

remained below detection levels. This suggests that for the optimal breakdown of starches, the temperature cannot be too cold nor too hot, but just right, which is known as the Goldilocks Principle (9). As there were limits to the number of temperatures that we could test without special equipment, we were unable to reproduce the classic bell curve graph seen in most analytical chemistry reports (10). Nor were we able to perform a Student's t-test to determine the statistical significance of increased glucose levels at 20°C, because at 4°C and 37°C glucose levels were undetectable. Still, the biphasic, 'pyramid' pattern is clearly seen in **Figure 2**.

Testing the potatoes kept at 4°C supported our initial hypothesis that storage in colder conditions would result

in unsweetened tubers. Indeed, this low temperature would cause amylase and  $\alpha$ -glucosidases to be much less active, hence limiting the enzymatic breakdown of starches into glucose molecules (6). The glucose levels observed in potatoes kept at 20°C were also easily explained. We reasoned that the warmer temperature would increase the kinetic energy within the tubers, resulting in more collisions between the starch molecules and the amylase, and between the maltose molecules and  $\alpha$ -glucosidases. These frequent collisions should increase the glucose levels over the same period of time (11). Indeed, glucose levels were much higher when the potatoes were kept at room temperature (**Figure 2**). The 37°C dataset was the only part of our experiment that did not support our original hypothesis. We anticipated that the enzymatic activities would be the highest at 37°C, thus producing the greatest glucose levels. However, this was not the case, as the glucose concentrations at 37°C remained below the detection level (**Figure 2**). Scientific literature indicates that 37°C is not hot enough to inactivate the enzyme amylase, which only starts denaturing at 70°C (12). Therefore, some other factors must be negatively affecting starch breakdown at 37°C – but not at 20°C.

One such factor could be absolute levels of hydrolytic enzymes, which are independent of their intrinsic activities. Potatoes thrive at mildly warm (approximately 20°C) but not exceedingly hot (37°C) temperatures (13). In fact, at 20°C potatoes begin to germinate, or form new sprouts; and cutting them into slices, as we did for our experiment, is known to accelerate that process (14). During germination, potatoes need carbon sources to support sprouting. Starch cannot be used for this purpose—not only are its granules insoluble in water, but they are also stored in special organelles called amyloplasts (15,16). Thus, simple sugars must be used as a carbon source. Having considered this requirement, we formulated a new hypothesis: that during germination the genes encoding amylase and maltase are activated at the level of gene transcription, and more enzymes are produced. This activation at 20°C might be primarily responsible for higher rates of hydrolysis, even though the enzymes are acting at suboptimal temperatures.

We could test this hypothesis by measuring enzyme concentrations using iodine reaction tiles, as originally suggested by Paul Scott (the “starch & amylase experiment”) (17). The more amylase present in the potato extracts, the faster the hydrolysis reaction. We would expect to observe a sharp increase in amylase levels at 20°C but not 37°C, even though the enzyme activity might be higher at 37°C. Such data would increase confidence in our germination-based data interpretation.

Even though we presently lack such data, there is considerable support for this model in scientific literature. The multi-factorial regulation of starch hydrolysis has been uncovered previously by directly measuring both  $\alpha$ -amylase levels and its enzymatic activity in fresh sweet potato tubers (10). Note that Tavano *et al.* only used two temperatures (25°C and 60°C), a range similar to ours (4°C–37°C), but shifted toward higher temperatures (10). In parallel, other investigators have shown that after dormancy and right before visible sprouting could be observed, there is a sharp increase in the activity of enzymes involved in starch biosynthesis, such as ADP-glucose pyrophosphorylase (AGPase), which in turn produces more substrates for amylases (18,19).

Another factor not controlled for in our study but known to affect the breakdown of starches is pH. The same study by Tavano *et al.* clearly demonstrated that both amylase activity and stability have a narrow optimal range of pH value between 5.5 and 6.5 (10). The possible shifting of pH towards these values at 20°C (but not 37°C) could help explain why potatoes stored at 20°C have the highest levels of simple sugars.

One last factor that affects the breakdown of starches is time. Potatoes are known to undergo CIS when stored at 4°C (4). Admittedly, we didn’t observe this shift. However, CIS occurs over the course of weeks and months (5). In contrast, our experiment only took place over 96h and involved the peeling and slicing of potatoes. It is possible that if we were to store the potato slices in the refrigerator for several weeks, they would turn sweet.

Despite these limitations, we have high confidence in our central conclusion that in the short term, storing potatoes in consumers’ homes at 4°C is the most practical way to avoid unnatural sweetening, which might be desirable in other root crops, like carrots and parsnips (20), but not in *S. tuberosum*.

## METHODS

To test the effects of temperature on the breakdown of starches, we used ~8-10 oz store-bought Idaho potatoes. We peeled them with a manual peeler, cut into uniform ¼-inch slices, and placed them into Ziploc bags. The air was squeezed out, and the bags were sealed tight and placed into the three environments: the fridge (cold, ~4°C), countertop in an air-conditioned room (ambient, 20°C), or the Anova Precision® immersive circulator (hot, 37°C) (**Figure 3**). After 96h, potato slices were removed from the bags, cut in small pieces, and a garlic press was used to squeeze enough juice out of the potato to fill the 1.5 mL Eppendorf tubes. Potato debris were pelleted by spinning the tubes in the mini-centrifuge for 1 minute at 6,000 rpm (**Figure 3**).

To test for baseline glucose levels, the same three



**Figure 3. Select equipment and consumables used in the study.** 1) Ziploc bags; 2) potato slices; 3) 1,000- $\mu$ l automatic pipettes; 4) pipette tips; 5) 1.5-ml Eppendorf tubes; 6) glucometer testing strips; 7) – glucometer; 8) iPad; 9) mini-centrifuge. Not shown: Anova immersive circulator and garlic press.



potatoes were processed in the same manner but without the 96h incubation period. To measure the levels of simple sugars, we used a blood glucometer (Livongo) designed to measure the glucose content in blood samples from diabetic patients (21). Glucometer strips were inserted first into the glucometer, and the strips were then inserted into the tubes for 3s to absorb the juice. Testing was done in technical triplicates using individual strips to determine the variability of glucometer results. Glucose levels expressed in mg/dL were recorded on an iPad. Standard deviations were calculated using the STDEV function as implemented in Microsoft Excel.

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