REVIEW

Maltose Generation by Beta-amylase and its Relation to Eating Quality of Steamed Storage Roots of Sweet Potato Cultivars, Including Recently Developed Varieties in Japan

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Abstract

The sweetness and texture of heat-cooked storage roots are major factors regarding the eating quality of sweet potatoes. The sweetness (Brix%) of steamed storage roots stored for not longer than three months after harvesting correlated with the concentration of maltose (wt.%) in the roots. The concentration increased to a peak of approximately 10 wt.%, with beta-amylase activity in the fresh roots increasing up to about 0.2 mmol maltose min⁻¹ mg⁻¹ protein of the enzyme solution. However, the concentration did not increase along with increased activity even if it exceeded these levels. The maltose concentration also exhibited a negative correlation with the pasting temperature of starch isolated from the fresh roots. Such new varieties with high sweetness as 'Quick Sweet' and 'Beniharuka' produced a larger amount of maltose due to their higher beta-amylase activity and/or lower starch pasting temperature than older varieties. Beta-amylase activity also remarkably affected the texture of steamed storage roots of sweet potato relative to the remaining content of starch in the steamed roots after digestion by the enzyme during steaming. The difference in starch content between fresh and steamed roots was closely correlated to the amount of starch digested into maltose by beta-amylase, whose activity was significantly correlated to the digestion rate of starch in the six varieties investigated with different levels of beta-amylase. From these results, maltose generation by beta-amylase was significantly associated with the eating quality of steamed sweet potato.

Discipline: Food

Additional key words: starch, starch pasting temperature, sweetness, texture

Introduction

Sweet potato (Ipomoea batatas [L.] Lam) is ranked tenth among ordinary crops in terms of production quantity (ca. 110 million tons annually) from a cultivation area of approximately 8 million ha worldwide (FAOSTAT 2014). It has been cultivated mostly in African and Asian countries, particularly in China, which accounts for ca. 70% of worldwide production. In Japan, the latest reported production of sweet potato (Ipomoea batatas [L.] Lam) was about 0.9 million tons, with about half of this amount being consumed as food and in processed food (Ministry of Agriculture, Forestry and Fisheries 2016). Although the Japanese people

consume on average no more than 1 kg (fresh weight) of sweet potato per capita each year, they pay great attention to the eating quality of sweet potato (Yamakawa & Yoshimoto 2001, Komaki & Yamakawa 2006) as they consume sweet potato in relatively simple styles, such as baked and hoshi-imo - a local, traditional processed food made from steamed sweet potato (Kuranouchi et al. 2010, 2012).

The breeding of sweet potato varieties in Japan has continued for about 100 years since the first breeding crosses made in Okinawa in 1914. The main targets in the first 50 years of breeding were high yield, high starch content, and resistance to disease and insect damage. Japanese sweet potato breeding in the subsequent 50 years also

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focused on improving the eating quality and functionality of sweet potatoes, as starch production from sweet potato has decreased drastically since 1963. In the past 30 years, various sweet potato varieties with high eating quality and/or unique physiological functions have been developed in Japan (Katayama et al. 2014, Takahata 2014). For example, purple-fleshed varieties containing a high amount of anthocyanin, which is expected to have antioxidant activity, as well as varieties containing starch with lower pasting temperature than any other traditional varieties had higher sweetness in their heat-cooked storage roots. In the present Japanese system for breeding sweet potato for food, the eating qualities of breeding lines and materials were evaluated according to the sweetness and texture of their steamed storage roots. Sweetness is quantified as the Brix% value, and texture was investigated by sensory evaluation. The final evaluations of total eating quality were conducted by a sensory comparison of test samples against a standard variety ("Kokei 14"). Analytical methods for evaluating the eating quality of sweet potato are needed in order to prescribe an international criteria for sweet potato quality.

The sweetness and texture of heat-cooked sweet potato are also major factors for the eating quality and processability of sweet potato. Sweet potato rich in starch and high in beta-amylase activity, which predominantly hydrolyzes gelatinized starch, results in maltose generation (Walter et al. 1975, Walter 1987). Such starch gelatinization parameters as the pasting temperature and beta-amylase activity in sweet potato could thus be available for an analytical indication of the eating quality of sweet potato. This review describes the effects of starch pasting temperature and beta-amylase activity on the sweetness and texture of steamed storage roots of sweet potato from current cultivars (varieties and breeding lines), including such recently developed varieties as 'Beniharuka' and 'Quick Sweet' in Japan.

Maltose generation by beta-amylase and its association with the sweetness of steamed storage roots of sweet potato

Sweet potato storage roots produced a large amount of maltose during heating due to the hydrolysis of their inner starch by beta-amylase, and the maltose produced is largely responsible for the sweetness of heat-cooked sweet potato (Ito et al. 1968, Picha 1986, Takahata et al. 1992). Nakamura et al. (2014b) demonstrated that the sweetness of steamed storage roots stored for not longer than three months after harvesting, measured using a refractometer, and expressed as Brix% value had increased linearly with maltose concentrations (wt.%) in the roots of current Japanese sweet potato cultivars that consist of 12 varieties and 23 breeding lines (Fig. 1). They also reported that the maltose concentrations (wt.%) in the roots of the cultivars investigated ranged from approximately 0 to 15 wt.% (Nakamura et al. 2014b). Older varieties such as 'Kokei

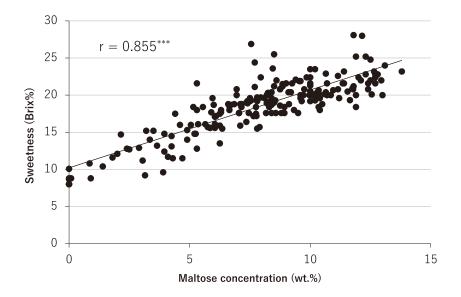


Fig. 1. Relationship between maltose concentration and the sweetness values of steamed storage roots of Japanese cultivars of sweet potato (modified from Nakamura et al. 2014b).

(n=221, 2012 and 2013)

The experiments were conducted within three months after the storage roots were harvested. ***: significant at p < 0.001.

14' (released in 1945) and 'Tamayutaka' (released in 1960) contained maltose at concentrations less than 10 wt.% in their steamed storage roots, whereas such new and recently developed varieties as 'Beniharuka' (released in 2007) and 'Himeayaka' (released in 2009) contained maltose at concentrations higher than 12 wt.%, and thus exhibited higher sweetness in their steamed roots than the older varieties (Katayama et al. 2014). These new varieties also exhibited higher beta-amylase activity in their fresh storage roots than older varieties (Nakamura et al. 2014b, 2017). In contrast, varieties with extremely low sweetness in their steamed roots have also been developed over the past 30 years, such as 'Satsumahikari' (released in 1987) and 'Okikogane' (released in 2002). The sweetness of their steamed storage roots was very low (ca. 7-9 Brix%) as hardly any maltose was produced during heating due to extremely low beta-amylase activity (Baba et al. 1987, Kukimura 1988, Kumagai et al. 1990). Kumagai et al. (1990) reported that a variant lacking or having only traces of beta-amylase in sweet potato storage roots was controlled by a single recessive allele and inherited in a hexasomic or tetradisomic manner. They also described that a new type of sweet potato with or without extremely low beta-amylase activity could easily be developed as the allele was frequently detected in cultivated germplasm of the genetic resources of sweet potato.

The maltose concentrations of steamed storage roots of the cultivars investigated increased with increasing betaamylase activity, which was determined by quantification of the reducing sugar produced via starch hydrolysis by beta-amylase isolated from fresh roots of the cultivars, up to about 0.2 mmol maltose min⁻¹ mg⁻¹ protein of enzyme solution. However, the concentrations did not clearly increase with increasing activity even if the activity increased over this level (Fig. 2). The results suggested that maltose generation in sweet potato storage roots could be regulated not only by beta-amylase but also by other factors regarding the roots, particularly those with higher (higher than 0.2 mmol maltose min⁻¹ mg⁻¹ protein) beta-amylase activity. Another factor could be starch gelatinization that is required prior to maltose generation by beta-amylase in sweet potato, which is not able to digest raw starch (Kiribuchi & Kubota 1976). The maltose concentration exhibited a negative correlation $(r = -0.53^{***} n = 221)$ with the pasting temperature of starch isolated from the fresh storage roots of all cultivars investigated (Fig. 3). This negative correlation between maltose concentration and starch pasting temperature was stronger (r = -0.69^{**} n = 111) for roots with higher betaamylase activity (higher than 0.2 mmol maltose min⁻¹ mg⁻¹ protein of enzyme solution).

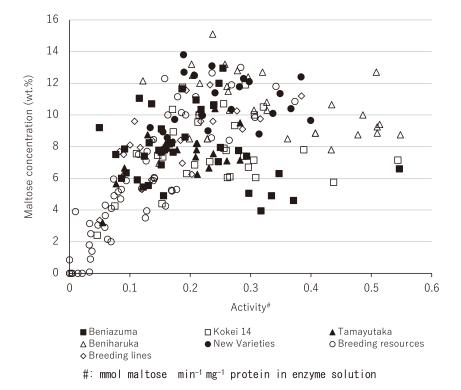
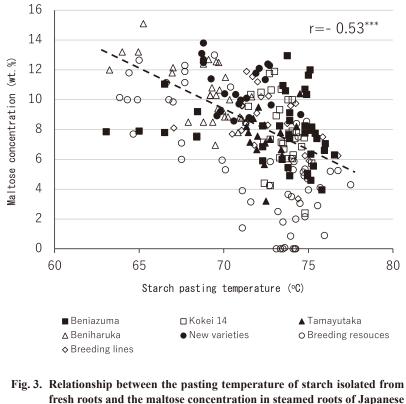


Fig. 2. Relationship between the beta-amylase activity of fresh roots and maltose concentration in steamed roots of Japanese cultivars and resources of sweet potato (Nakamura et al. 2014b).

(n=221, 2012 and 2013)

The starch pasting temperature of sweet potato starch is closely related to the molecular structure of its amylopectin (Noda et al. 1998), and greatly affected by the soil temperature during the growth period of sweet potato (Noda et al. 2001). Table 1 shows that the storage roots of 'Beniazuma' and 'Beniharuka' cultivated in Hokkaido, the northernmost prefecture of Japan, generated higher amounts of maltose than those of the same varieties cultivated in Ibaraki located ca. 700 km south of Hokkaido, despite lower beta-amylase activity in the roots cultivated in Hokkaido (Nakamura et al. 2014b). The pasting temperatures of starch isolated from the roots harvested in Hokkaido was 5-7°C lower than those



cultivars and resources of sweet potato (Nakamura et al. 2014b). (n=221, 2012 and 2013) The starch pasting temperatures were estimated from RVA profiles of 7

The starch pasting temperatures were estimated from RVA profiles of wt.% suspensions of starch isolated from fresh storage roots. ***: significant at p < 0.001.

Table 1. Maltose concentration, beta-amylase activity, starch content and starch pasting temperature of "Beniazuma" and "Beniharuka" harvested in Ibaraki and Hokkaido (Nakamura et al. 2014b)

Variety	Harvest location	Maltose concentration	Beta-amylase activity	Starch content	Starch pasting
		(Wt%)	(Unit)	(%)	temperature (°C)
Beniazuma	Hokkaido	8.55±1.36**	0.108 ± 0.044	18.62±3.36	66.3±2.07***
(n=6)	Ibaraki	6.23±1.18	0.133±0.031	22.67±2.00	73.2±0.71
Beniharuka	Hokkaido	13.4±1.28*	0.228±0.024	20.12±2.67	64.4±0.91***
(n=4)	Ibaraki	10.3±1.28	0.281±0.044	20.87±2.91	69.4±0.54

*, **, *** indicate significant difference between the average values for samples harvested in Hokkaido and Ibaraki at p < 0.05, p < 0.01 and p < 0.001 as determined by Tukey's test, respectively.

 \dagger : unit = mmol maltose min⁻¹ mg⁻¹ protein of enzyme solution

The number of samples examined is enclosed in parentheses below the name of the variety.

harvested in Ibaraki, where the average temperature during the summer season was ca. 5°C higher than in Hokkaido for both varieties. Thus, the gelatinization of intracellular starch in the storage roots harvested in Hokkaido was practically recognized at a lower temperature than in those harvested in Ibaraki for variety 'Beniazuma' (Fig. 4). Sweet potato cultivars containing starch with a lower pasting temperature could have the potential for higher sweetness.

In the 21st century, some new varieties with lower starch pasting temperature have been developed for expanding the usage of sweet potato and its starch. 'Quick Sweet' (released in 2002) was the first of these new varieties (Katayama et al. 2002, 2004), and it possesses the lowest current starch pasting temperature (ca. 53°C determined by RVA) (Katayama et al. 2015). This unique variety was able to produce maltose earlier during heat-cooking than other traditional popular varieties with higher pasting temperatures (70-75°C) because the gelatinization of its starch occurred at a lower temperature. In addition, Nakamura et al. (2014a) reported that the activity of betaamylase isolated from 'Quick Sweet' storage roots heated at 80°C almost maintained its original level in the fresh roots, whereas the activity of 'Beniazuma' (with a starch pasting temperature of about 75°C) was severely inhibited at the same temperature (Fig. 5). Takahata et al. (1994) indicated the importance of beta-amylase stability during heat-cooking as well as starch gelatinization for maltose generation in sweet potato. 'Quick Sweet' has an advantage for maltose

generation during heating because beta-amylase in its storage roots could maintain its activity at a higher temperature than the enzyme in 'Beniazuma' storage roots. However, the activity of the enzyme isolated from the fresh roots of both varieties exhibited similar responses to temperature. This indicated that beta-amylase in the heated storage roots of 'Quick Sweet' remained stable due to starch-gelatinization at lower temperatures before its inactivation during heating. Therefore, maltose generation in 'Quick Sweet' storage roots started at lower temperatures and continued at higher temperatures than that in 'Beniazuma' during heating. In addition, such varieties as "Quick Sweet" and "Hoshikirari" that contain starch with lower pasting temperatures in their storage roots exhibited another useful function of being able to maintain a larger percentage of total ascorbic acid content in the fresh roots after heat-cooking than other older varieties (Nakamura et al. 2016). The earlier generation of maltose in heated storage roots of 'Quick Sweet' and 'Hoshikirari' containing starch with lower pasting temperature may also have a protective effect against the heat breakdown of ascorbic acid - a well-known antioxidant compound.

Although maltose is one of the key elements for the sweetness of steamed sweet potato storage roots as described above, it becomes less important for the sweetness of roots stored for long periods (3-6 months) after harvesting. The storage of sweet potato induces an increase in the concentration of sucrose, the sweetness of which was

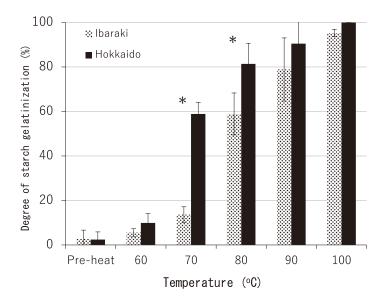


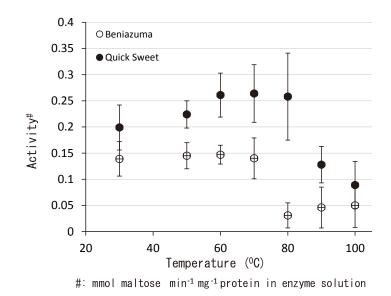
Fig. 4. Degree of intracellular starch gelatinization in heated storage roots of "Beniazuma" harvested in Ibaraki and Hokkaido (modified from Nakamura et al. 2014b).

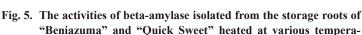
(n=4, 2012)

Error bars represent standard deviations (n=4).

* indicates a significant difference (p < 0.05) between the average value for the storage roots harvested in Ibaraki and Hokkaido.

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tures (modified from Nakamura et al. 2014a). The plots and vertical bars represent the means and standard devia-

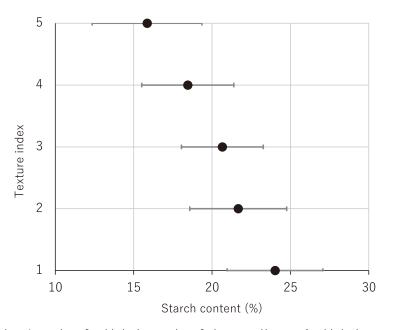
tions of 10 individual experiments, respectively.

2-3 times higher than that of maltose, in the fresh roots. Conversely, maltose concentration in its steamed roots did not increase, but actually decreased during storage. Thus, sucrose instead of maltose played an important role in the sweetness of steamed sweet potato root after long-term storage. Takahata et al. (1995) demonstrated that changes in such sucrose-synthetic enzymes as sucrose synthase and sucrose-phosphate-synthase were possibly associated with sucrose accumulation in fresh sweet potato roots during storage. It was also reported that storage at low temperature promoted the changes accompanying the decreased beta-amylase activity in 'Kokei 14' (Masuda et al. 2007).

Starch hydrolysis by beta-amylase and its association with the texture of steamed storage roots of sweet potato

The texture of heat-cooked storage roots is another important factor for the eating quality of sweet potato (Nara 1957). In the Japanese breeding system of sweet potato for food, breeding resources and lines were evaluated for texture as well as sweetness (Kitahara et al. 2017). The texture was classified based on a comparison with that of the standard variety ('Kokei 14') steamed together into five texture groups: mealy, slightly mealy, intermediate, slightly soggy, and soggy. The "intermediate" category indicated that the texture of the tested sample was substantially equal to that of the standard variety. The same five texture indices were used for statistical analyses (Nakamura et al. 2010, 2015). Figure 6 shows the relationship between the texture indices of steamed roots and the starch content of fresh roots for the cultivars investigated. It was recognized that fresh storage roots with higher starch content tended to exhibit a mealy texture in its steamed roots. However, the starch content in the fresh roots was not the only determinant factor of texture, because the five groups of cultivars sorted on the basis of texture of steamed roots were classified into three or four groups based on the starch content of their fresh roots with significant (p < 0.05) differences (Nakamura et al. 2015).

The starch content in fresh roots could change somewhat after steaming due to the digestion of starch into maltose by beta-amylase during heating. The amount of starch digested into maltose was calculated from the maltose concentration in steamed roots, with the starch content in both fresh and steamed roots also being quantified from the content of glucose produced by the complete enzymatic digestion of starch (Nakamura et al. 2017). The differences in starch content between the fresh and steamed roots were very $(r = 0.94^{***}, n = 40)$ consistent with the amount of digested starch for the six varieties of sweet potato with three different levels of beta-amylase (Fig. 7). The starch digestion rate in steamed roots (i.e. ratio of starch content in steamed roots against that in fresh roots) was practically correlated to beta-amylase activity in the fresh roots (Fig. 8). Table 2 summarizes the maltose concentration and the degradation rate of starch in steamed storage roots of three different groups for the levels of beta-amylase activ-



Texture index:1;mealy, 2;slightly mealy, 3;intermediate, 4;slightly soggy, 5;soggy

Fig. 6. The relationship between the starch content in fresh storage roots and the texture index of steamed storage roots in sweet potato cultivars (Nakamura et al. 2015).

(n=312) Bars represent standard deviations in the starch content of the roots (n=60-65) having the each texture index.

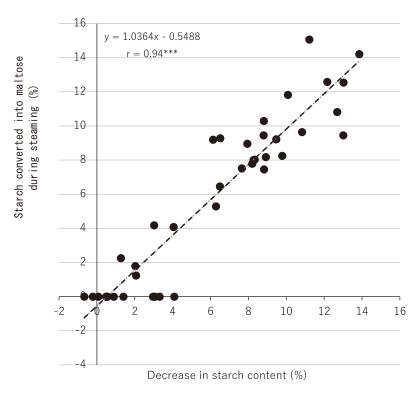


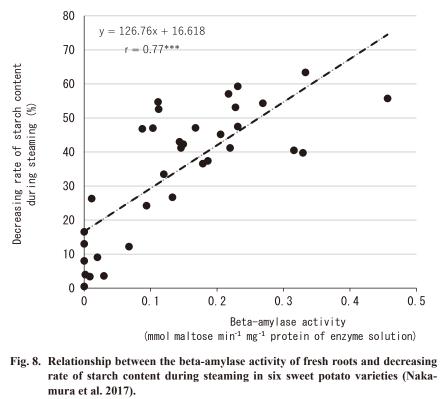
Fig. 7. Relationship between the decrease in starch content of storage roots and the amount of starch converted into maltose in steamed storage roots of six sweet potato varieties.

***: significant at *p* < 0.001

(n=40, 2015)

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ity in sweet potato varieties, with each group consisting of two varieties. The starch content in fresh storage roots of 'Beniharuka' and 'Himeayaka' having higher beta-amylase activity decreased remarkably to less than 50% during steaming. In contrast, older varieties such as 'Kokei 14' and 'Tamayutaka' having 50-60% of the beta-amylase activity in the former varieties, maintained approximately 60% of the starch content existing in their fresh roots after steaming due to lower starch digestion. Furthermore, in such varieties as 'Okikogane' and 'Satsumahikari' that lack or have extremely low levels of beta-amylase activity, the starch content of their fresh roots hardly decreased during steaming. The steamed roots of these two varieties consequently contained the highest content of starch among the six



***: significant at p < 0.001.

(n=40, 2015)

Table 2. Beta-amylase-activity, maltose concentration, starch degradation rate in three groups of sweet potato varieties with different levels of beta-amylase activity (modified from Nakamura et al. 2017).

Activity level of sample*	Beta-amylase [†] activity (mmol maltose min ⁻¹ mg ⁻¹)	Maltose concentration [†] (%)	Degradation rate of starch** † (%)
High (n=12)	0.283 ± 0.073^{a}	11.29±2.70ª	51.19±8.45ª
Middle (n=11)	0.139 ± 0.037^{b}	7.25±2.20 ^b	41.31±8.89 ^b
Extremely low (n=11)	0.0126±0.022°	0.13±0.037°	0.92±2.43°

*: High activity varieties: "Beniharuka" (n=7), "Himeayaka" (n=5)

Middle activity varieties: "Kokei 14" (n=6), "Tamayutaka" (n=5)

Extremely low activity varieties: "Okikogane" (n=7), "Satsumahikari" (n=4)

The number of samples examined is enclosed in parentheses.

**: Maltose content in steamed root \times 0.95 / Starch content in fresh root \times 100

[†]: Different letters in a column indicate significant differences at p < 0.05 as determined by Tukey's HSD test among the three sample groups.

varieties described above, and thus showed a mealy texture even though their fresh roots had the lowest starch content. The texture of the steamed roots of sweet potato could be closely correlated with the remaining content of starch after steaming rather than that prior to steaming. The starch content in steamed roots could be predicted by the starch content and beta-amylase activity of fresh roots before steaming; therefore, beta-amylase activity was thought to be an important factor in determining texture as well as the sweetness of steamed sweet potato.

Conclusions

Maltose generation by beta-amylase relative to the sweetness and texture of steamed storage roots, which are the major determinant factors for eating quality, was investigated in current Japanese cultivars of sweet potato, including new varieties developed in the 21st century. The sweetness of storage roots stored for no more than three months after harvesting was largely dependent on the concentration of maltose produced by beta-amylase during steaming. The concentration of maltose increased with the activity of the enzyme, increasing up to about 0.2 mmol maltose min⁻¹ mg⁻¹ protein of enzyme solution; however, the increase stopped even if the activity increased over this level. The concentration also correlated negatively (r = -0.53, n = 221) to the pasting temperature of starch contained in the storage root. Such new varieties as 'Quick Sweet' and 'Beniharuka' having higher beta-amylase activity and/or lower starch pasting temperature possess great advantages in producing much higher amounts of maltose than traditional varieties such as 'Beniazuma' and 'Kokei 14'. Maltose generation also remarkably influenced the texture of steamed roots relative to the remaining content of starch in steamed roots after the digestion of starch into maltose by beta-amylase during steaming. The difference in starch content between fresh and steamed storage roots was closely correlated with the amount of starch digested into maltose by beta-amylase in the six varieties of sweet potato with different levels of enzyme activity. The rate of remaining starch content after steaming was revealed to be highly correlated to the activity of beta-amylase in the fresh root in the six varieties of sweet potato. Varieties such as 'Beniharuka' with higher beta-amylase activity showed a moist texture due to its higher degradation rate of starch during steaming, whereas varieties such as 'Okikogane' with extremely low activity exhibited a mealy texture in its steamed roots as the starch content of the fresh root hardly decreased due to extremely low beta-amylase activity. From these results, maltose generation by beta-amylase was found to be significantly associated with the eating quality of steamed sweet potato.

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