Am. J. Pot Res (2008) 85:277–285
DOI 10.1007/s12230-008-9030-6

SYMPOSIUM PAPER

Positioning the Potato as a Primary Food Source of Vitamin C

S. L. Love · J. J. Pavek

Published online: 2 July 2008

Abstract Ascorbic acid, better known as vitamin C, is a crucial nutrient in the human diet. It performs many physiological functions in its primary roles as an electron donor and antioxidant. Vitamin C has been directly linked to collagen formation, iron absorption, cancer prevention, immunomodulation, and maintenance of normal nerve function. It is suspected to decrease the likelihood of strokes, cataracts, hypertension, and lead toxicity. Vitamin C deficiency leads to a condition called scurvy, accompanied by a weakening of blood vessels, bones and connective tissues, hair and tooth loss, joint swelling, and eventually death. Intake of vitamin C is considered inadequate, even among some parts of the population in developed countries where diet is not restricted, but more especially for at-risk populations in developing countries. Potatoes are an important worldwide source of vitamin C, contributing about 20% of the dietary intake in Europe. They are a vital source of vitamin C not only because of relatively high content, but because they can be stored, leading to consistent availability. Any improvement in the vitamin C content of potato products will have a beneficial impact on human nutrition. A three-pronged approach can be used to increase the vitamin C content of potatoes involving breeding, improved crop management, and modification of cooking processes. Breeding has tremendous potential for increasing vitamin C content in tubers as evidenced by research results in studies documenting germplasm variability and inheritance patterns. Management research may define practices that will slow the natural decline that occurs near the end of field growth and storage, a response partially conditioned by plant stress. Research into cooking procedures may help reduce the oxidative and enzymatic degradation of vitamin C that results from exposure to moisture, heat, and air.

Resumen El ácido ascórbico, mejor conocido como vitamina C, es un nutriente imprescindible en la dieta humana. Realiza muchas funciones cuyo principal rol es como donante de electrones y antioxidante. La vitamina C ha sido directamente ligada a la formación de colágeno, absorción de hierro, prevención de cáncer, modulación inmunológica y mantenimiento de la función nerviosa. Parece que disminuye la posibilidad de ataques de apoplejía, cataratas, hipertensión y toxicidad por plomo. La deficiencia de vitamina C produce escorbuto, acompañado por un debilitamiento de las venas, huesos y tejido conectivo, pérdida de pelo y dientes, hinchazón de las articulaciones y eventualmente la muerte. El consumo de vitamina C es considerado inadecuado, aún entre parte de la población en los países en desarrollo. La papa es una importante fuente de vitamina C a nivel mundial que contribuye con un 20% del consumo dietético en Europa. Además es una fuente vital de vitamina C no solo por su alto contenido, sino porque puede ser almacenado, contribuyendo a una permanente disponibilidad. Cualquier mejora en el contenido de vitamina C de los productos de papa tiene un impacto benéfico en la nutrición humana. Se puede usar un enfoque de tres puntos para incrementar el contenido de vitamina C en la papa incluyendo el mejoramiento genético, manejo mejorado del cultivo y modificación del proceso de cocción. El proceso de mejoramiento genético tiene un gran potencial para incre-

S. L. Love (✉)
Aberdeen R & E Center, University of Idaho,
Aberdeen, ID 83210, USA
e-mail: slove@uidaho.edu

J. J. Pavek
Aberdeen R & E Center, USDA/ARS,
Aberdeen, ID 83210, USA

mentar el contenido de vitamina C en los tubérculos como ha sido evidenciado en resultados de investigación para documentar la variabilidad del germoplasma y patrones de herencia. La investigación sobre manejo puede definir las practicas que retardan el declive natural que ocurre cerca del final de crecimiento de la planta en el campo y el proceso de almacenaje, respuesta parcialmente acondicionada por el estrés de la planta. La investigación de los procedimientos de cocción pueden ayudar a reducir la degradación oxidativa y enzimática de la vitamina C que resulta de la exposición a la humedad, calor y aire.

Keywords Ascorbic acid · Nutrition

Introduction

Vitamin C, i.e. ascorbic acid, is a critical nutrient in the human diet. Its discovery resulted from efforts to understand and cure scurvy, a disease tightly linked to vitamin C deficiency. In fact, the name "ascorbic acid" is derived from the longer term "antiscorbutic factor" (Hughes 2000). Budd (1840), one of the first researchers to attribute scurvy to poor nutrition, stated that this common disease was due to the "lack of an essential element which it is hardly too sanguine to state will be discovered by organic chemistry or experiments of physiologists in a not too distant future". His prediction came to pass by 1907 when Holst and Frölich (1907) demonstrated that diet manipulation could eliminate scurvy in Guinea pigs. By 1919, Drummond (1919) and other researchers had published strong evidence that a nutriment in citrus, shown to not be citric acid, was responsible for preventing scurvy. He named the factor "water soluble C". In subsequent years, much additional work was done to characterize the chemical nature of vitamin C and, more recently, to define the somewhat debatable extra-antiascorbutic roles attributed to this critical nutrient (Hughes 2000).

In the seventeenth, eighteenth, and nineteenth centuries, scurvy was common among sailors, soldiers, explorers, and other groups of people who did not have easy access to fresh fruits and vegetables. Common symptoms of scurvy include fatigue, increased susceptibility to bruising and bleeding, loss of hair and teeth, and joint swelling and pain (Higdon 2006). Vitamin C was found to be essential for collagen production, an important structural component of connective tissues such as blood vessels, bones, tendons, and ligaments. Symptoms of scurvy are directly related to deterioration of these tissues.

In the USA, Canada, and Europe, current published recommendations for daily intake of vitamin C for an adult range from 45 up to 60 mg (Hughes 2000). These recommendations have their basis in studies whose objectives were to prevent symptoms of scurvy. Modern, but somewhat controversial, thinking by many nutritionists suggests that significantly higher amounts may be beneficial. Surveys of diets in the USA and Europe show that mean vitamin C intake varies from 73 to 86 mg (based on raw produce purchases), an amount that is likely adequate to maintain basic health, if intake is consistent enough to replace the 3% daily loss typical to adults. This intake level may or may not be sufficient to provide all of the advantages of vitamin C's extra-antiascorbutic properties (Higdon 2006; Hughes 2000).

Regardless of socio-economic status, at-risk populations exist in every country and surveys have shown considerable variation in vitamin C intake between low-income and well-to-do groups (FAO 2002). Specific sub-populations in developed countries, including some ethnic groups, those living in poverty, and the elderly are at high risk of vitamin C deficiency. Entire populations in most developing countries are at risk for vitamin C deficiency, with some groups averaging intake as low as 8.2 mg per day, creating a situation wherein scurvy symptoms become common. In developing countries, scarcity of fresh fruits and vegetables creates seasonal instances of near zero vitamin C intake.

Biochemically, vitamin C is categorized as a reducing agent or antioxidant. An FAO (2002) report states that this one characteristic likely accounts for virtually all of its health benefits. Vitamin C is known to act as an electron donor for eight human enzymes, including those involved in collagen synthesis and tyrosine metabolism. It is also in very high concentration in gastric juices where it is thought to prevent the formation of cancer-causing *N*-nitroso compounds. Other physiological functions are to stabilize folate and increase the absorption of iron. Summarily, vitamin C is involved in many aspects of human health and physiology. In addition to preventing scurvy Vitamin C has been directly linked to collagen formation, iron absorption, cancer prevention, immunomodulation, and maintenance of normal nerve function. It is suspected to decrease the likelihood of strokes, cataracts, hypertension, and lead toxicity (Higdon 2006; Hughes 2000). Although evidence does not support the efficacy of mega-dose intake of supplemental vitamin C, it appears that most people in the world could benefit from additional intake as part of a routine diet of fruits and vegetables.

Potatoes as a Dietary Source of Vitamin C

Fruits and vegetables are the major contributors to vitamin C in the human diet. Potatoes are one of the most important sources of vitamin C in those countries where they are produced and consumed. Among vegetables and fruits, concentration of vitamin C in potatoes is moderate to low as listed by Mosure (2004), citing the Dietary Guidelines Advisory Committee. Potatoes provide 25 mg per serving, as compared to 95 mg for red bell pepper, 60 mg for an orange, 60 mg for broccoli, 50 mg for strawberries, and 35 mg for cantaloupe. Pennington and Wilkening (1997) evaluated numerous fruits and vegetables for contribution to recommended daily intake of vitamin C (Table 1).

In spite of moderate content, potatoes may be one of the highest contributors of vitamin C in the diets of people in many parts of the world. A single 148 g serving of baked potato can provides approximately 45% of the recommended daily intake of vitamin C (Pennington and Wilkening 1997). In the USA, consumption of potatoes in 1990 was 180 g per day per person (National Potato Council 2001), meaning that on average, over half of a person's daily requirement for vitamin C may be provided by potatoes. Storey and Davis (1992) cited surveys showing that 15% to 20% of the vitamin C intake among UK citizens was from potatoes, highest among all fruits and vegetables.

Quoting from an FAO (2002) document reviewing worldwide vitamin C status, "... it is important to realize that the amount of vitamin C in a food is usually not the major determinant of a food's importance for the supply, but rather regular intake. For example, in countries where potato is an important staple food and refrigeration facilities are limited, seasonal variations in plasma ascorbate are due to the considerable deterioration in the potato's vitamin C content during storage; the content can decrease from 30 to 8 mg/100 g over 8–9 months. Such data can indicate the important contribution the potato can make to the human vitamin C requirements even though the potato vitamin C concentration is low" (FAO 2002). This statement summarizes the critical role potato plays in human nutrition. It also brings to light the need to improve the potato as a source of vitamin C. Any increase in vitamin C availability in potatoes has the potential to improve worldwide human health and nutrition.

Table 1 Dietary vitamin C contribution of selected raw fruits and vegetables

	Vitamin C (% DV)[a]
Fruits	
Kiwifruit (2 medium)	240
Strawberries (8 medium)	160
Orange (1 medium)	130
Grapes (1 1/2 cups)	25
Apple (1 medium)	8
Vegetables	
Broccoli (1 medium stalk)	220
Bell pepper (1 medium)	190
Cauliflower (1/6 medium head)	100
Potato (1 medium)	45
Tomato (1 medium)	40
Summer squash (1/2 medium)	30
Carrot (1 7 in. long, 1 3/4 in diameter)	10
Sweet corn (1 medium ear)	10
Cucumber (1/3 medium)	10
Leaf lettuce (1 1/2 cups)	6

Values derived from work published by Pennington and Wilkening (1997) in the Journal of the American Dietetic Association.

[a] Reported as percent of daily recommended intake (Daily Value) for a healthy adult

Role of Vitamin C in Plants

Understanding the possibilities and processes of improving vitamin C concentration in potatoes requires, to some degree, knowledge of its role and function in plants. Although details of function are uncertain, it is an area of active investigation and there is convincing evidence of its biochemical function. Smirnoff (1996) and Smirnoff and Wheeler (2000) reviewed the state current knowledge on vitamin C in plants.

The simplest evidence of the importance of vitamin C in plants, is that it is found in all chlorophyll containing eukaryotes. In plants, it serves as an antioxidant, an enzyme cofactor, and as a substrate for other compounds. Evidence suggests it is a critical component of photosystem protection (Grace and Logan 1996). Vitamin C also participates in cell division, cell wall expansion, enhancement of resistance to stresses, and assistance in the synthesis of ethylene, gibberellins, anthocyanins, and hydroxyproline. It appears to be an essential compound for the development and survival of plants, including potatoes.

Increases in vitamin C in plant tissues can be the result of either new synthesis or regeneration of the oxidized (used) form via the action of dehydroascorbate reductase. The vitamin C pool is enhanced by exposure to a number of triggering mechanisms. Exposure to light enhances the production of vitamin C. Leaves that have adapted to high light intensity have much higher levels than leaves that have not. Exposure to dark results in a decrease in vitamin C in plant tissues. This is not unexpected given the role of vitamin C in photoprotection and active growth.

Exposure to environmental stresses, particularly atmospheric ozone, sulfur dioxide, and UV-B radiation, triggers up-regulation of dehydoascorbate reductase, resulting in more rapid recycling of dehydroascorbate to vitamin C (Chen et al. 2003; Conklin et al. 1996; Yoshida et al. 2006). Other biotic and abiotic stresses that result in the development of molecules known as reactive oxygen species (free radicals) may also trigger increases of protective vitamin C through either synthesis or recycling.

It is not clear whether the presence of high levels of vitamin C is causal or secondary to rapid cell division and

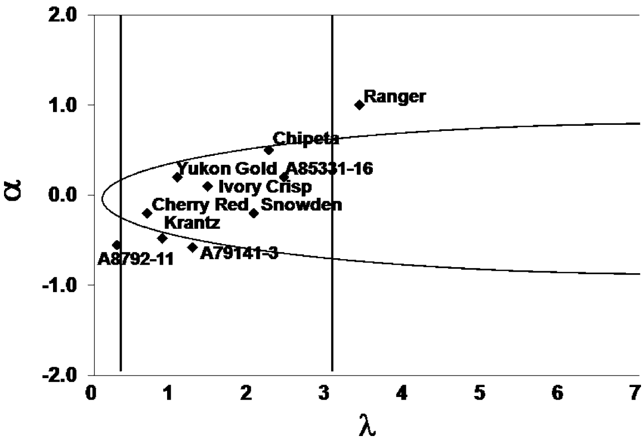

Fig. 1 Stability of vitamin C expression for potato clones across growing environments, based on Tai's stability statistic. Clones contained within the two vertical lines and the parabola are considered to be stable. Potatoes were grown in Washington, Oregon, and Idaho during 1999 and 2000. Adapted from Love et al. (2004)

growth. However, there is strong evidence that it is involved in the growth process and that rapidly developing tissues contain very high levels of vitamin C (Chen and Gallie 2006). Once growth slows, without the presence of additional triggers, the concentration of vitamin C in tissues begins to decline as the existing pool is used for protective and physiological functions under conditions of reduced synthesis or recycling.

Increasing the Vitamin C Contribution of Potatoes

Improving potatoes as a source of vitamin C will involve increasing the concentration in tubers throughout the processes of production, harvest, storage, marketing, and food preparation. Improvement strategies will require research involving breeding and genetics, agronomy and handling, and food processing. A review of completed research suggests that significant progress has been made in understanding the vitamin C availability and retention in potato-based foods. However, much work is needed to define the principles and practices that can be utilized successfully to improve the nutritional value of the potato and deliver that value to the consumer. This paper will summarize completed research on improving vitamin C content in potatoes and define future research needs.

Improvement Via Breeding and Genetics

Breeding varieties with superior levels of vitamin C is a primary and logical step in increasing the availability of vitamin C in the human diet. One essential factor for the success of traditional breeding is access to genetic variability. Many studies, conducted as far back as 1945, have shown cultivar differences for tuber vitamin C content (Hyde 1962; Kemp and Kemp 1982; Lampitt et al. 1945; Mullin et al. 1991; Murphy and Dove 1945; Okeyo and Kushad 1995; Perkins 1993). In 2004, Love et al. further explored the potential for genetic improvement by documenting the variability among breeding parents from North American breeding programs. They found a four-fold difference in tuber vitamin C concentration among parental clones (Table 2). Clones expressed tuber concentrations as high as 29.8 and as low as 11.5 mg/100 g FW. Interestingly, there was not only a significant range of concentration, but large differences in stability of vitamin C expression across environments (Fig. 1). It would appear, based on evidence from this and past work that adequate variability exists within adapted, high-quality potato germplasm to make feasible rapid breeding progress for tuber vitamin C concentration.

Although variability has been adequately documented, very little has been done to determine the inheritance of vitamin C content in potatoes. Pavek and Corsini (unpublished data), at the 2003 meeting of the Potato Association of America, reported preliminary results of an inheritance study using low and high concentration parents. Although no computations for heritability were given, distributions of progeny within crosses were generally distributed across the parental range with the progeny mean near the midparent (Fig. 2). They suggested that vitamin C concentration in tubers is highly heritable and likely additive in nature. From these results, it appears that traditional breeding could be successfully employed to rapidly create new cultivars with increased levels of vitamin C. Unfortunately, no modern breeding programs consider vitamin C concentration to be a make-or-break trait in

Table 2 Vitamin C concentration in tubers of select potato parental germplasm

Cultivar	Concentration (mg/100 g)[a]
Ranger Russet	29.4
Yukon Gold	29.3
Shepody	25.5
NY112	25.3
Eva	23.0
Dakota Pearl	21.6
Durango Red	19.2
Snowden	18.8
Dakota Rose	17.6
NorDonna	16.5
Cherry Red	14.9
A8792-11	11.5

Adapted from Love et al., published in HortScience in 2004

[a] Vitamin C concentration determined within a few weeks of harvest on tubers grown at the University of Idaho's Aberdeen Research and Extension Center.

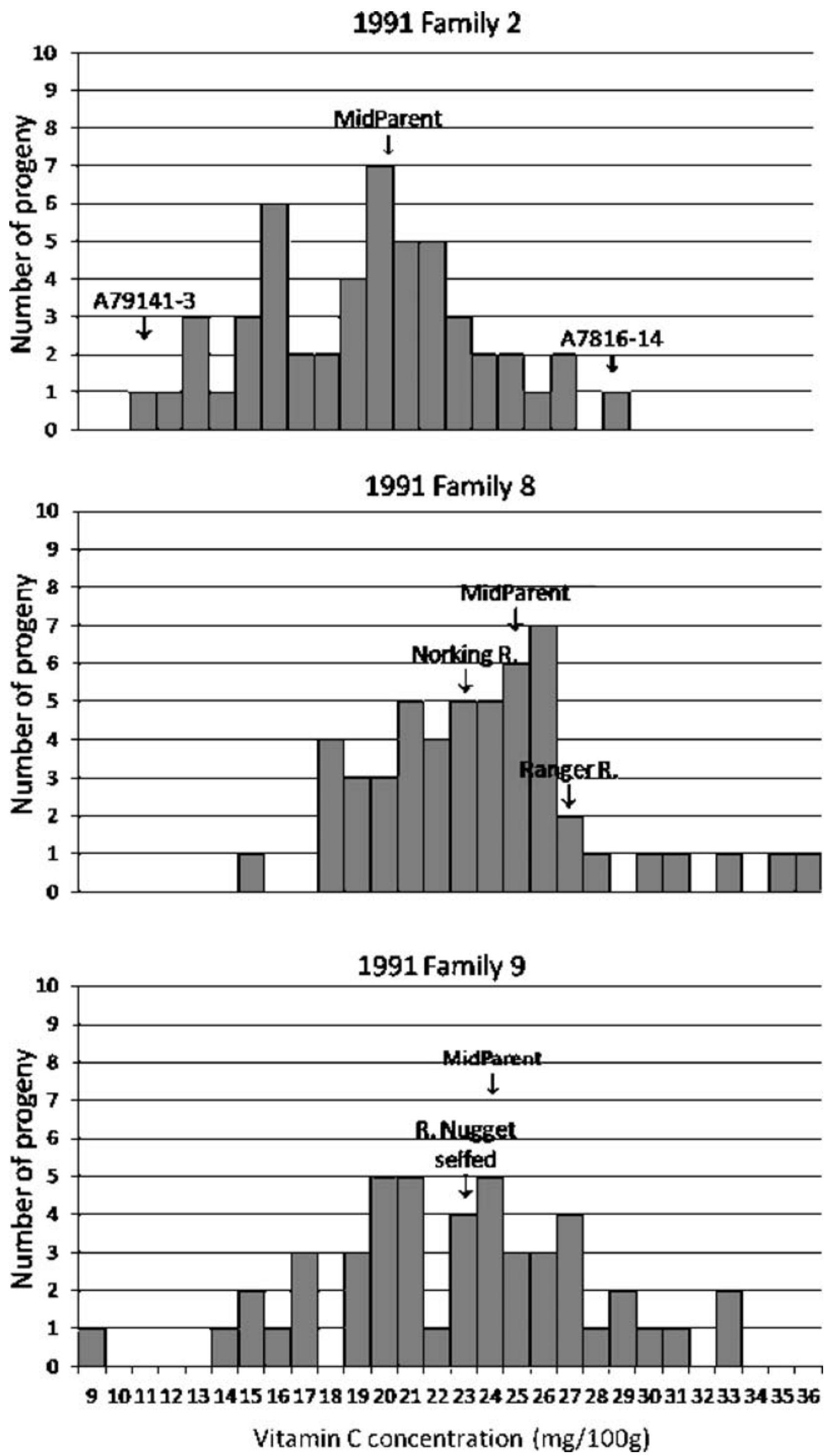

Fig. 2 Vitamin C concentration histogram for progeny of **a** cross between low (A79141-3) and high concentration (A7816-14) parents, **b** between medium (Norking Russet) and high (Ranger Russet) parents, and **c** selfed family for a high (Russet Nugget) concentration parent. Unpublished data reported by Pavek and Corsini (2004)

variety release decisions. For progress to be apparent, this will need to change.

Although still suffering from a poor public image, gene engineering and plant transformation appears to be a viable alternative for increasing the vitamin C in potatoes. Foyer et al. (1995) reported increased vitamin C in plant tissues by overexpressing glutathione reductase. Theoretically, if a potato variety was transformed using tuber-specific promoter attached to an unregulated gene coding for this enzyme, it could result in continuous recycling of vitamin C and associated increase in nutritional value. Manipulation of vitamin C synthesis genes is not yet feasible due to lack of knowledge concerning biosynthetic pathways. Research is needed to resolve this informational shortfall.

Improvement Via Agronomy and Handling

Mullin et al. (1991) found that potatoes varied in vitamin C content when grown at different locations in Canada. Some of this variation may be due to uncontrollable environmental factors, but part may be due to crop management. Many factors reportedly influence the amount of vitamin C in tubers. These include length of storage period, storage temperature, reconditioning, soil fertility, irrigation, and disease infection. The impact of these factors varies from high to inconsequential. For those that have sufficient impact, appropriate changes in management may improve vitamin C nutrition.

Length of Storage Period Shekhar et al. (1978) found that Vitamin C is fairly low in newly initiated tubers, that it increased throughout the active growing phase, and reached its highest level sometime during the last month before vine death. From that point, potatoes experienced a continuous decline in vitamin C for as long as they remained in storage. Shekhar et al. (1978) showed the decline to initially be rapid, resulting in a two-fold reduction in vitamin C during the first 4 weeks of storage. This same trend was reported by Perkins (1993) who showed rapid decline in stored potatoes for the first 10 weeks, after which the decline continued but the rate lessened. Over a period of 35 weeks in storage, tubers decreased in vitamin C content from about 30 mg/100 g to less than 10, a three-fold change (Fig. 3). Of all management factors previously studied, length of storage period appears to have the greatest impact on vitamin C nutrition. Because long-term availability requires that potatoes be stored for up to 10 months, modification of other storage management factors may be necessary to minimize losses.

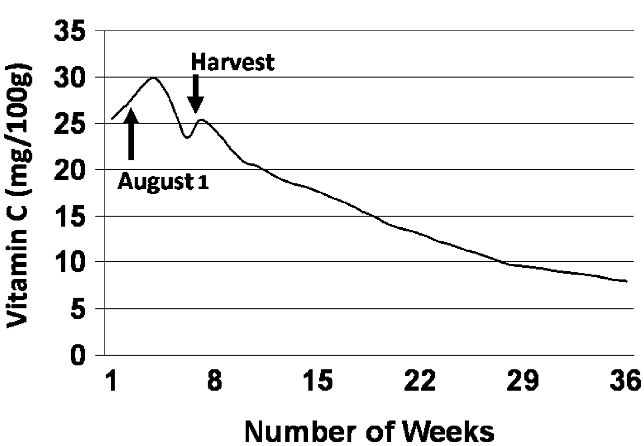

Fig. 3 Typical response of vitamin C concentration in tubers during the late growth stages, at harvest, and through extended storage. Adapted from Perkins (1993)

Storage Temperature Research showing the impact of storage temperature on tuber vitamin C content has given mixed results. Among unrelated studies, Augustin et al. (1978a) and Arkoudilos and Crean (1978) found no significant differences in vitamin C for potatoes stored for 6 or 8 months at temperatures ranging from 2.9°C to 12.7°C. Linnemann et al. (1985), on the other hand, found that after storage vitamin C content increased approximately 20% in tubers stored for 12 weeks at 16°C or 28°C, but declined about 15% in tubers stored at 7°C. The increase at the higher temperatures may have been an artifact caused by greater moisture loss in the tubers stored at warmer temperatures. Barker and Mapson (1950) also found that vitamin C declined faster in association with colder storage temperatures.

Storage Reconditioning Results of research on the impact of reconditioning on vitamin C is in conflict. Arkoudilos and Crean (1978) reported that after 6 months storage at 4.4°C to 12.7°C, five cultivars universally increased in vitamin C during reconditioning at 21°C, with the increase ranging from 10% to 49%. The longer the reconditioning period, up to 20 days, the larger the increase. In contrast, Okeyo and Kushad (1995) found that tubers stored for 6 weeks at 3°C then reconditioned at 25°C for 1 week continued to decline in vitamin C, but at a reduced rate compared to tubers left in cold storage.

Soil Type Augustin (1975) reported that potatoes grown in sandy soil had higher levels of vitamin C at harvest than tubers grown in a loam soil. No plausible explanation was given.

Nitrogen Fertilizer Augustin (1975) reported a 15% to 20% decrease in vitamin C associated with increasing N application rates. Mondy et al. (1979) reported the opposite, a 28% increase in vitamin C with higher N application rates. Shekhar et al. (1978) reported a delay in vitamin C increase when plants were fertilized at a higher rate and subsequently hypothesized that impact on ascorbic acid may be a secondary effect of changes in rate of maturation.

Soil Amendments Organic matter added in the form of manure or compost had no significant influence on vitamin C content of tubers (Zhang et al. 1997).

Irrigation Zhang et al. (1997) reported a 15% to 20% decrease in vitamin C content of tubers as a result of supplemental irrigation. Using Guinea pig feeding methods, Thiessen (1936) reported a slight advantage in vitamin C content for dryland potatoes as compared to irrigated potatoes.

Disease Infection Murphy and Dove (1945) reported no relationship between genetic disease resistance and vitamin

C content of potato cultivars. However, they referenced a study conducted by Smith and Patterson wherein infection with some diseases, specifically potato virus Y and potato leafroll virus caused a significant rise in vitamin C content. Studies on potatoes infected with common scab showed greater storage losses in vitamin C for diseased tubers (Thiessen 1936).

A review of potato management studies reveals that length of storage period is the single major factor in determining vitamin C concentration in fresh tubers (Table 3). Other controllable crop management factors influence vitamin C but in many cases conflicting results cloud understanding of true impact. This suggests that we do not yet understand enough about the role of crop management on vitamin C concentration in tubers. Additional research is needed to separate causal factors from those that are associative. Recent research results indicate that vitamin C increases as a result of specific stresses on the growing crop. Potentially, investigating methods for applying selective stresses could yield interesting results.

Improvement Via Food Preparation Techniques

The process of cooking destroys a portion of vitamin C present in raw potato tubers. Quantification of vitamin C losses has been the object of numerous researchers, including Artz et al. (1983); Augustin et al. (1978b, 1979), Fillion and Henry (1998); Kincal and Giray (1987); Pelletier et al. (1977), Sumner et al. (1983), Wang et al. (1992); Watt and Merrill (1963). The results of every study by these scientists provided evidence that cooking method has a large influence on the amount vitamin C available for consumption. The range of reported losses is summarized in Table 4.

Three external factors are involved in the destruction of vitamin C during cooking, including heat, leaching, and exposure to air (oxidation). Cooking and processing methods that provide more exposure to these factors result in greater losses. Food preparation methods that maintain tuber skin intact, minimize shredding or cutting, utilize limited water, and/or involve reduced cooking times or temperatures appear to result in greater vitamin C retention.

Table 3 Range of documented Vitamin C % response to various management variables

Management factor	Range of response
Length of storage (pre→post harvest)	−70% to −56%
Storage temperature (cold→warm)	+33% to +50%
Storage reconditioning (pre→post conditioning)	−42% to +49%
Soil type (lighter→heavy)	−17% to −2%
N fertilizer (less→more)	−20% to +15%
Soil amendment (none→added)	No change
Irrigation (less→more)	Slight decrease to +20%
Disease infection (none→infected)	Moderate decrease to slight increase

Table 4 Range of Vitamin C losses in potatoes exposed to various cooking methods

Cooking method	Range of loss (%)
Baked	15–28
Microwaved	12–27
Boiled unpeeled	16–21
Boiled peeled	23–34
Fried	15–49
Pan-fried/frozen/heated	41–55
Mashed	20–67
Dehydrated	50–81

Based on published studies. Cooking procedures and initial Vitamin C content of raw tubers varied among experiments

Although much work has gone into documenting nutrient loss during cooking processes, little research has been completed with intent to modify cooking conditions. Modification of cooking parameters for existing products may reduce vitamin C breakdown. Such modifications could include increasing the dimensions of sliced products, reducing cooking time or temperature, steaming rather than boiling, or preparing products with the skin left intact. As another option, research could include the development of new products that retain more vitamin C.

It is logical to assume that precooked products offer the potential to solve the problem of storage losses in fresh potatoes. Precooked products can be stored under a variety of conditions, unlike storing fresh potatoes where options are limited. Research by Wang et al. (1992) and Sumner et al. (1983) show that storing potatoes as processed products may not provide a significant advantage in vitamin C preservation over storing fresh tubers. Potatoes processed and stored for 12 months as dehydrated flakes lost 66% of vitamin C content when stored at 25°C. Frozen baked potatoes, stored for only 1 week at −20°C, declined from 5.8 to 4.8 mg/100 g (Sumner et al. 1983). These losses are in line with those reported for fresh-stored potatoes. On the other hand, Linnemann et al. (1985) found a strong relationship between vitamin C loss and storage temperature of fried potato chips. When stored at 2°C, stored chips showed very little loss. Considerable work is needed to resolve the conflicting findings and allow development of recommendations for storing processed products.

Potato processing provides the opportunity to add supplemental nutrients, including vitamin C. Wang et al. (1992) found that fortified dehydrated potato flakes retained about the same percentage of vitamin C as unfortified flakes. However, because the fortified flakes started the process with a higher concentration, they retained higher levels through the entire processing and reconstitution procedure. Many potato food products offer excellent opportunity for fortification to make up for storage and cooking losses.

The Future

Potatoes already have a prominent place in human vitamin C nutrition. Because they are a staple food in many countries, potatoes can become even more vital through increasing initial concentration and managing the crop to maximize retention of nutrients. This future will be guided by geneticists, plant physiologists, agronomists, and food scientists with interest in the nutritional value of potatoes. A three-pronged approach can be applied to the problem. (1) Increase Vitamin C supplied by potatoes through careful application of traditional or modern molecular genetics. One question yet to be answered is whether there is exploitable genetic variation for limiting storage losses or retention during cooking. (2) Manipulate production and storage conditions to maximize and retain high levels of vitamin C through the events associated with crop growth, storage, and marketing. Certain stresses trigger vitamin C production in plants. One important question is whether managed stress can be used to induce higher levels of vitamin C without negatively affecting yield and quality. For example, it has been shown that ozone will induce vitamin C synthesis in plant leaves. Will it do the same for tubers in storage? Another question is whether it is possible to increase vitamin C in potatoes through exposure to non-greening wavelengths of light. (3) Develop products and cooking procedures that limit vitamin C losses in foods. A viable question is whether or not conditions exist to store partially or wholly processed foods without the losses in vitamin C typical of stored fresh potatoes.

Improvement of nutritive value in potato foods and products has the potential to improve the health of people in both developed and developing countries. Attention to nutrition, including vitamin C, needs greater attention by researchers with interest in potatoes.

References

Arkoudilos, I.S., and D.E. Crean. 1978. Effect of reconditioning on the ascorbic acid content of potato cultivars. *Research Circular* 240: 46–48. Ohio Agricultural Research and Development Center, Wooster, Ohio.

Artz, W.E., C.A. Pettibone, J. Augustin, and B.G. Swanson. 1983. Vitamin C retention of potato fries blanched in water. *Journal of Food Science* 48: 272–273.

Augustin, J. 1975. Variations in the nutritional composition of fresh potatoes. *Journal of Food Science* 40: 1259–1299.

Augustin, J., S.R. Johnson, C. Teitzel, R.B. Toma, R.L. Shaw, R.H. True, J.M. Hogan, and R.M. Deutsch. 1978a. Vitamin composition of freshly harvested and stored potatoes. *Journal of Food Science* 43: 1566–1574.

Augustin, J., S.R. Johnson, C. Teitzel, R.H. True, J.M. Hogan, R.B. Toma, R.L. Shaw, and R.M. Deutsch. 1978b. Changes in nutrient composition of potatoes during home preparation: II. Vitamins. *American Potato Journal* 55: 653–662.

Augustin, J., B.G. Swanson, C. Teitzel, S.R. Johnson, S.F. Pometto, W.E. Artz, C.P. Huang, and C. Schomaker. 1979. Changes in nutrient composition during commercial processing of frozen potato products. *Journal of Food Science* 44: 807–809.

Barker, J., and L.W. Mapson. 1950. The ascorbic acid content of potato tubers II. The influence of temperature of storage. *New Phytologist* 49: 283–303.

Budd, G. 1840. Scurvy. In *The Library of Medicine. Practical medicine*, ed. A. Tweedie, 58–95. London: Whittaker.

Chen, Z., and D.R. Gallie. 2006. Dehydroascorbate reductase affects leaf growth, development, and function. *Plant Physiology* 142: 775–787.

Chen, Z., T.E. Young, J. Ling, S. Chang, and D.R. Gallie. 2003. Increasing vitamin C content of plants through enhanced ascorbate recycling. *Proceedings of the National Academy of Sciences of the United States of America* 100: 3525–3530.

Conklin, P.L., E.H. Williams, and R.L. Last. 1996. Environmental stress tolerance of an ascorbic acid-deficient *Arabidopsis* mutant. *Proceedings of the National Academy of Sciences of the United States of America* 93: 9970–9974.

Drummond, J.C. 1919. Note on the role of the antiscorbutic factor in nutrition. *Biochemical Journal* 13: 77–88.

FAO. 2002. Vitamin C. Chapter 6 in: Human Nutrition and Mineral Requirements. Report of a joint FAO/WHO expert consultation, Bangkok, Thailand.

Fillion, L., and C.J.K. Henry. 1998. Nutrient losses and gains during frying: a review. *International Journal of Food Sciences and Nutrition* 49: 157–168.

Foyer, C.H., N. Souriau, S. Perret, M. Lelandais, K.J. Kunert, C. Pruvost, and L. Jouanin. 1995. Overexpression of glutathione reductase but not glutathione synthetase leads to increase in antioxidant capacity and resistance to photoinhibition in poplar trees. *Plant Physiology* 109: 1047–1057.

Grace, S.C., and B.A. Logan. 1996. Acclimation of foliar antioxidant systems to growth irradiance in three broadleaved evergreen species. *Plant Physiology* 112: 1631–1640.

Higdon, J. 2006. Vitamin C. http://lpi.oregonstate.edu/infocenter/vitamins/vitaminC/. Reviewed web document of the Linus Pauling Institute, Oregon State University, Corvallis, Oregon.

Holst, A., and T. Frölich. 1907. Experimental studies relating to ship beri-beri and scurvy. II. On the etiology of scurvy. *Journal of Hygiene* 7: 634–671.

Hughes, R.E. 2000. Vitamin C. In *The Cambridge world history of food*, Vol 2, pp 754–762 eds. Kiple, K.F., K.C. Ornelas, Cambridge: Cambridge University Press.

Hyde, R.B. 1962. Variety and location effects on ascorbic acid in potatoes. *Journal of Food Science* 27: 373–375.

Kemp, P., and T.C. Kemp. 1982. The ascorbic acid content of thirteen varieties of potato. *Proceedings of the Nutrition Society* 41: 6A.

Kincal, N.S., and Ç. Gìray. 1987. Kinetics of ascorbic acid degradation in potato blanching. *International Journal of Food Science & Technology* 22: 249–254.

Lampitt, L.H., L.C. Barker, and T.L. Parkinson. 1945. Vitamin C content of potatoes: the effect of variety, soil, and storage. *Journal of the Society of Chemical Industry* 64: 22–26.

Linnemann, A.R., A. van Es, and K.J. Hartmans. 1985. Changes in the content of L-ascorbic acid, glucose, fructose, sucrose and total glycoalkaloids in potatoes (cv. Bintje) stored at 7, 16 and 28°C. *Potato Research* 28: 271–278.

Love, S.L., T. Salaiz, B. Shafii, W.J. Price, A.R. Mosley, and R.E. Thornton. 2004. Stability of expression and concentration of ascorbic acid in North American potato germplasm. *HortScience* 39: 156–160.

Mondy, N.I., R.L. Koch, and S. Chandra. 1979. Influence of nitrogen fertilization on potato discolouration in relation to chemical composition. 2. Phenols and ascorbic acid. *Journal of Agricultural and Food Chemistry* 27: 418–420.

Mosure, J. 2004. Vitamin C (Ascorbic Acid). Ohio State University Fact Sheet No. HYG-5552-05. Columbus, Ohio.

Mullin, W.J., P.Y. Jui, L. Nadeau, and T.G. Smyrl. 1991. The vitamin C content of seven cultivars of potatoes grown across Canada. *Canadian Institute of Food Science and Technology Journal* 24: 169–171.

Murphy, E.F., and W.F. Dove. 1945. Observations on genetic, physiological, and environmental factors affecting the vitamin C content of Maine-grown potatoes. *American Potato Journal* 22: 62–83.

National Potato Council. 2001. *Potato statistical yearbook*. Greenwood Village, Colorado: National Potato Council.

Okeyo, J.A., and M.M. Kushad. 1995. Composition of four potato cultivars in relation to cold storage and reconditioning. *HortTechnology* 5: 250–253.

Pavek, J.J., and D.L. Corsini. 2004. Inheritance of vitamin C content in several 4x potato crosses. *American Journal of Potato Research* 81: 80.

Pelletier, O., C. Nantel, R. Leduc, L. Tremblay, and R. Brassard. 1977. Vitamin C in potatoes prepared in various ways. *Journal de I' Institut Canadien de Technologie Alimentaire* 10: 138–142.

Pennington, J.A.T., and V.L. Wilkening. 1997. Final regulations for the nutrition labeling of raw fruits, vegetables, and fish. *Journal of the American Dietetic Association* 97: 1299–1305.

Perkins, L.B. 1993. Comparisons of sugars, glycoalkaloids, vitamin C, and organic acids in six potato cultivars from tuber formation throughout storage. Master's Thesis, University of Maine, Orono, Maine.

Shekhar, V.C., W.M. Iritani, and R. Arteca. 1978. Changes in ascorbic acid content during growth and short-term storage of potato tubers (*Solanum tuberosum* L.). *American Potato Journal* 55: 663–670.

Smirnoff, N. 1996. The function and metabolism of ascorbic acid in plants. *Annals of Botany* 78: 661–669.

Smirnoff, N., and G.L. Wheeler. 2000. Ascorbic acid in plants: biosynthesis and function. *Critical Reviews in Plant Sciences* 19: 267–290.

Storey, R.M.J., and H.V. Davis. 1992. Tuber quality. In *The potato crop: the scientific basis for improvement*, ed. P.M. Harris, 507–568. London: Chapman and Hall.

Sumner, J.L., S.L. Eu, and A.S. Dhillon. 1983. Ascorbic acid retention in foods. *Journal of Food and Nutrition* 40: 43–47.

Thiessen, E.J. 1936. Effect of storage upon the vitamin C content of Wyoming potatoes. Wyoming Agric. Exp. Sta. Bull. No. 213.

Wang, X.Y., M.G. Kozempel, K.B. Hicks, and P.A. Seib. 1992. Vitamin C stability during preparation and storage of potato flakes and reconstituted mashed potatoes. *Journal of Food Science* 57: 1136–1139.

Watt, B.K., and A.L. Merrill. 1963. Composition of foods. Agric. Handbook No. 8. U.S. Department of Agriculture.

Yoshida, S., M. Tamaoki, T. Shikano, N. Nakajima, D. Ogawa, M. Ioki, M. Aono, A. Kubo, H. Kamada, Y. Inoue, and H. Saji. 2006. Cytosolic dehydroascorbate reductase is important for ozone tolerance in *Arabidopsis thaliana*. *Plant and Cell Physiology* 47: 304–308.

Zhang, L., G.A. Porter, and R.J. Bushway. 1997. Ascorbic acid and glycoalkaloid content of Atlantic and Superior potato tubers as affected by supplemental irrigation and soil amendments. *American Potato Journal* 74: 285–304.