INTRODUCTION

Potato is one of the most popular vegetables worldwide and is the most important vegetable crop in the United States, accounting for nearly one-third of per-capita vegetable consumption (Lin and Yen 2004). Potatoes can be prepared in many ways, including baking, boiling, roasting, frying, and microwaving, allowing for a diversity of uses. Most people find potatoes to be an agreeable food, and very few (less than 1%) actually dislike potatoes (Harper 1963). Potato flavor results from the combination of taste, aroma, and texture. Flavor precursors synthesized by the plant are present in raw potatoes and consist mainly of sugars, amino acids, RNA, and lipids (Table 48.1). Plant genotype, production environment, and storage environment influence the levels of these compounds and the enzymes that react with them to produce flavor compounds. During cooking, flavor precursors react to produce the Maillard reaction compounds and the sugar, lipid, and RNA degradation products that contribute to flavor (Duckham et al. 2001).

Domestication has led to a reduction in flavor compounds in fruits such as tomatoes (Goff and Klee 2006) and strawberries (Aharoni et al. 2004). Presumably, selection by breeders for yield, appearance, and disease resistance has resulted in an unintended loss of flavor compounds. Fruits emit volatile compounds in order to attract seed dispersal agents, which seek them out as a source of nutrition (Goff and Klee 2006). Essential nutrients contribute to most volatiles produced by tomato fruits. The volatiles released during fruit ripening act as flavor compounds that signal desirable taste and high nutrient availability. In contrast, potato tubers and other vegetables are not seed dispersal organs. They do not emit volatile flavor compounds at maturity. Instead, elements of flavor develop from compounds in tuber tissues when they are sliced and/or heated. Since flavor compounds per se are not necessary for the function of potato tubers as asexual reproductive structures, it would be interesting to know whether tubers of wild and cultivated potato relatives differ in types and concentrations of flavor compounds. This is an open area for research.
TABLE 48.1. Approximate Levels of Potato Tuber Components

<table>
<thead>
<tr>
<th>Compound</th>
<th>Percent Fresh Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Starch</td>
<td>18.0</td>
</tr>
<tr>
<td>Protein</td>
<td>2.0</td>
</tr>
<tr>
<td>Fiber (suberin, lignin)</td>
<td>1.3</td>
</tr>
<tr>
<td>Sugars (glucose, fructose, and sucrose)</td>
<td>1.0</td>
</tr>
<tr>
<td>Minerals (K, Mg, Ca, P, Na)</td>
<td>1.0</td>
</tr>
<tr>
<td>Free amino acids</td>
<td>0.8</td>
</tr>
<tr>
<td>Non-starch polysaccharides (hemicelluloses and pectins)</td>
<td>0.7</td>
</tr>
<tr>
<td>Organic acids (citric, oxalic, malic, and chlorogenic)</td>
<td>0.2</td>
</tr>
<tr>
<td>Lipids (fatty acids include linoleic, linolenic, and palmitic)</td>
<td>0.1</td>
</tr>
<tr>
<td>Pigments (anthocyanins and carotenoids)</td>
<td>0.01</td>
</tr>
<tr>
<td>Glycoalkaloids (solanine and chaconine)</td>
<td>0.01</td>
</tr>
<tr>
<td>Nucleotides, RNA</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Note: Actual values vary depending on cultivar, production environment, and storage conditions.

Figure 48.1. Chemical structure of α-solanine and α-chaconine, the most common glycoalkaloids in potato tubers. The R group for α-solanine consists of glucose and two moieties of rhamnose. The R group for α-chaconine consists of glucose, galactose, and rhamnose.

TASTE

Human taste receptors monitor bitter, sour, sweet, salty, and umami flavors. In vegetables, bitterness is considered a deterrent and sweetness is a stimulant for consumption (Dinehart et al. 2006). Unlike fruits, potato tubers have evolved mechanisms to deter consumption. Toxic glycoalkaloids in wild potato tubers produce a strong bitter taste, providing protection against pests and disease (Valkonen et al. 1996). Domestication has selected for low levels of bitterness in potato tubers (Johns and Alonso 1990), but they still contain glycoalkaloids. The major glycoalkaloids in commercial potato cultivars are α-solanine and α-chaconine (Bushway and Ponnampalam 1981). Each is composed of the alkaloid solanidine plus three monosaccharides (Fig. 48.1). Glycoalkaloids are concentrated in the skin of tubers, so when consumed with the skin on, small tubers may taste more bitter than large tubers. Although the upper limit allowed for a new cultivar release is 20mg/100g fresh weight, bitterness can be tasted in tubers with glycoalkaloid levels higher than 14mg/100g (Sinden et al. 1976). At low levels (below 10mg/100g), glycoalkaloids may make a positive contribution to flavor (Ross et al. 1978).

Organic acids determine the acidity of potato tubers. They are produced by the incomplete oxidation of sugars and deamination of amino acids, ascorbic acid, and
polyphenolic acids (Lisinska and Aniolowski 1990). They are generally not considered to be major flavor components (Vainionpaa et al. 2000). However, a positive correlation between levels of phenolic compounds and bitterness/astringency has been reported (Mondy et al. 1971). Sinden and others (1976), on the other hand, did not find a strong relationship between phenolic content and bitterness. They did note that tubers containing 120mg/100g chlorogenic acid tasted slightly sour to some panelists.

Starch is the main carbohydrate in potato tubers. Although starch is tasteless, it influences texture and can also form stable complexes with flavor compounds during cooking (Solms and Wyler 1979). Potato tubers also contain low levels of sugars such as glucose, fructose, and sucrose, which are not typically considered to directly contribute to taste (Solms and Wyler 1979). In fact, sweetness has historically been considered to be an undesirable flavor component in potatoes (Burton 1966). However, the consumption of sugars in developed countries has increased over the past 30 years (Pereira and Simin 2003). Today's consumers are likely to have a strong preference for sweet foods. In fact, we have found that sweetness of baked potatoes is significantly correlated with desirable flavor (Jansky 2008). Similarly, sucrose and reducing sugar levels have been found to be important factors in determining potato flavor attributes (Vainionpaa et al. 2000).

Ribonucleotides act as precursors for flavor potentiators, known as umami compounds, which are associated with desirable flavor. Potato tubers have higher levels of 5′ ribonucleotides than any other plant food (Solms and Wyler 1979). While they are present in low quantities in raw potatoes, 5′ ribonucleotides are liberated by enzymatic hydrolysis of RNA as tubers are heated during cooking. Steamed or boiled tubers of Solanum tuberosum Phureja group cultivars (South American landraces) with higher levels of glutamate and guanosine 5′-monophosphate (GMP) than S. tuberosum cultivars had higher acceptability scores in taste tests (Morris et al. 2007). The most important ribonucleotides for flavor enhancement are inosine 5′-monophosphate (IMP) and GMP. Both levels and types of ribonucleotides vary among potato cultivars (Maga and McNeill 1986). This is probably due to differences in the activities and types of enzymes that break down RNA. A synergistic effect is detected when 5′ ribonucleotides interact with amino acids, especially glutamate. In fact, the products of interactions between amino acids and 5′ ribonucleotides are considered to be mainly responsible for boiled potato flavor (Halpern 2000; Solms 1971). Sugars may also contribute to umami taste characters in the form of glutamate glycoconjugates (Beksan et al. 2003). In addition, potassium salts have been found to enhance umami taste intensity (Ugawa and Kurihara 1994). Significant levels of potassium leach out of potatoes during boiling (Bethke and Jansky 2008). It would be interesting to know whether tuber potassium levels enhance umami flavor intensity more effectively in baked potatoes, which retain potassium, than in boiled potatoes, which lose potassium.

AROMA

Cooked potatoes contain a complex array of aroma compounds. In one study, 228 volatile compounds were found to contribute to baked potato flavor (Coleman et al. 1981). The most important aroma compounds are produced by lipid
degradation and by the Maillard reaction and/or sugar degradation during the heating of potato tubers (Oruna-Concha et al. 2002). In the nonenzymatic Maillard reaction, reducing sugars (glucose and fructose) interact with amino acids at high temperature.

During baking, the surface temperature of the tuber increases first and water evaporates from the skin. As the temperature of the skin rises over 100°C, a crust develops and the tuber gradually warms from the outside toward the interior. At these high temperatures, baked potatoes produce a complex array of volatile compounds including lipid degradation products, Maillard reaction products, sulfur compounds, and methoxypyrazines (Oruna-Concha et al. 2001). Pyrazines are considered to be among the most important and characteristic components of baked potato flavor (Buttery et al. 1973). There is a strong positive relationship between pyrazines and organoleptic quality in both baked potatoes (Maga and Holm 1992) (Fig. 48.2) and potato chips (Maga and Sizer 1973). Pyrazines are produced by the Maillard reaction, which is the same reaction that causes dark fries and chips. It is interesting that industry standards require light-colored chips. While there is some visual preference for light-colored chips, blindfolded taste panelists clearly prefer the taste and odor of dark-colored chips (Maga 1973).

In contrast to baked potatoes, water loss in boiled potatoes is minimal and the interior warms quickly. However, the tuber temperature never rises above 100°C, as it does during baking. The major aroma components of boiled potatoes include methional, aliphatic alcohols and aldehydes, thiols and sulfides, and methoxypyrazines (Maga 1994; Mutti and Grosch 1999; Ulrich et al. 2000). Boiled tubers contain higher levels of lipid degradation products than do baked potatoes (Oruna-Concha et al. 2002). The disruption of tissues during slicing in preparation for boiling

![Figure 48.2](image_url)

**Figure 48.2.** Relationship between sensory score (1 = positive, 5 = negative) and total pyrazines in baked potatoes of 13 cultivars and breeding clones. Derived from Maga and Holm (1992).
provides more opportunities for lipoxygenase to come into contact with its substrates. In addition, during boiling, tuber tissues heat up more gradually, allowing time for lipoxygenase to oxidize lipids. Lipid-derived flavor components in boiled tubers, then, are expected to include both products of enzymatic oxidation and thermal degradation, while those from baking are primarily products of thermal degradation. Fatty acids degrade to produce aldehydes and ketones, which contribute to fatty, fruity, and floral flavor notes (Duckham et al. 2002). Another major contributor to boiled potato aroma is the lipid oxidation product c4-heptanal (Josephson and Lindsay 1987). It produces an earthy aroma at low levels. However, the higher levels found in dehydrated potatoes following storage result in stale flavors. The aldehydes produced by lipid oxidation have been implicated in the off-flavor of boiled potatoes after they are refrigerated (Peterson and Poll 1999).

During microwave baking, the tuber temperature increases relatively uniformly, with all parts reaching 100°C within a few minutes of each other (Oruna-Concha et al. 2002). In contrast to oven baking, though, the skin remains cooler than the interior of the tuber due to evaporative cooling, and a crust does not develop. Because there is no crust, the rate of water loss is higher. Microwave-baked potatoes have lower levels of volatiles than oven-baked or boiled potatoes, probably due to evaporative cooling at the tuber surface and the loss of volatile compounds through co-distillation as water evaporates.

Methional is a major aroma compound that is formed by the Strecker degradation reaction, in which intermediates in the Maillard reaction interact with the amino acid methionine. “Russet Burbank” plants transformed with a gene to enhance methionine biosynthesis produced tubers with two to four times more methional than those of untransformed plants (Di et al. 2003). Levels of methional vary among cultivars and production environments (Duckham et al. 2002; Oruna-Concha et al. 2001). It is interesting that this compound is not detectable in all potato cultivars. In fact, in one study, it was found in only 5 out of 11 cultivars evaluated (Duckham et al. 2001).

Unlike most flavor compounds, methoxypyrazines are present in raw tubers, so heating is not required for their production. They are products of free amino acids and are responsible for subtle earthy flavor notes. They may be produced by the tuber and have been found in higher amounts in boiled potatoes than in baked potatoes (Oruna-Concha et al. 2002). The production of methoxypyrazines may be increased by the cell damage that results from peeling tubers in preparation for boiling. Alternatively, methoxypyrazines may be produced by soil bacteria (Pseudomonas taetrolens) and then absorbed by the tuber (Buttery et al. 1973). Consequently, the production environment may make an important contribution to this flavor component. The odor threshold of these compounds is very low. For example, the odor threshold of a common methoxypyrazine, 2-methoxy-3-isopropylpyrazine, in water is two parts in 10^{12}. Consequently, methoxypyrazines are said to have a high aroma impact value (Duckham et al. 2002). 2-Methoxy-3-isopropylpyrazine has been found in tubers at one part in 10^{10} (Buttery et al. 1973). Therefore, even though it is present at very low levels, it is detectable when a potato is eaten. In biochemical analyses, methoxypyrazines are not detectable in many cultivars and are present at very low levels in others. Because of their high aroma impact values, though, small changes in methoxypyrazine levels are expected to have large effects on flavor.
TEXTURE

Texture is one of the most important quality attributes of potato tubers. It is determined mainly by cultivar, but with effects of production environment and storage. This component of flavor is easily recognizable by consumers, who tend to have distinct preferences. While potato texture is a complex trait, much variation can be explained by determining the degree of a tuber’s mealliness or, at the opposite end of the spectrum, waxiness (Faulks and Griffiths 1983; van Marle et al. 1997a). A mealy potato is dry and granular, while a waxy potato is moist and gummy. Mealliness has been found to be associated with high dry matter content (Jansky 2008; Leung et al. 1983; van Dijk et al. 2002). As a result of selection by breeders for market class qualities, red-skinned potatoes are typically waxy, while white and russet processing potatoes are mealy. Mealliness is one of the readily described components of flavor for taste panelists. In fact, detection thresholds for mealliness by taste panelists have been identified (Murphy et al. 1967). However, dry matter content does not always explain mealliness. In one sensory analysis study, the cultivar “Ontario” was judged to be less mealy than other cultivars in the trial, but its total solids content was similar to some of those cultivars (True and Work 1981).

Another component of texture is the size and structure of starch grains in raw tuber tissue (Thybo and Martens 1999). Starch gelatinizes during cooking and creates pressure in cells as it expands. The proportion of each tuber cell occupied by gelatinized starch influences the moistness components of texture (Martens and Thybo 2000). A large volume of gelatinized starch is associated with a mealy texture, while cells that contain less starch and more loosely held water produce a waxy texture (Martens and Thybo 2000; McComber et al. 1994). The loosely held water in the latter cell type is released upon chewing, producing a moist mouthfeel in sensory analyses. The gelatinized starch in the mealy types retains water, creating a dry mouthfeel. Cell size has also been found to be associated with mealliness (Barrios et al. 1963). Tubers with high mealliness scores by taste panelists were found to contain more starch and have larger cells than less mealy tubers.

Cell wall characteristics can also affect texture (Jarvis and Duncan 1992; Jarvis et al. 1992; Martens and Thybo 2000; McComber et al. 1994; van Marle et al. 1997a). Pectin methyl esterase activity is important for creating firm tissue during cooking by cross-linking pectin in the middle lamella, which binds cells together (Faulks and Griffiths 1983; Thybo and Martens 1999). Cultivars vary in cell wall density and in the degree of solubilization of the middle lamella and cell walls, which are believed to influence texture (van Marle et al. 1997a). The mealy cultivar “Irene” was found to have more cell wall material per unit cell surface area than the non-mealy cultivar “Nicola.” The cell wall and middle lamella were also found to be thicker in the mealy cultivar “Russet Burbank” than in the waxy cultivar “Red Pontiac” (McComber et al. 1994 [#362]). The thicker cell walls and middle lamellae, along with stronger pectic substances, may result in more resistance to shearing and a hard, particulate mouthfeel. Both cohesiveness and adhesiveness of cells in tuber tissue influence texture. In one study, while either factor alone did not correlate with mealliness of boiled potatoes, a strong negative correlation (−0.87) was detected between mealliness and the product of the two parameters (Leung et al. 1983).
EFFECT OF PRODUCTION ENVIRONMENT ON FLAVOR

Production environment may affect sensory quality. Levels of methional vary among tubers harvested from different production environments (Duckham et al. 2002; Oruna-Concha et al. 2001). Because methionine contains sulfur, it has been suggested that sulfur application rates in the field may account for some differences in methional levels (Duckham et al. 2002). Similarly, potassium application in the field may influence umami flavor intensity (Morris et al. 2007). Methoxypyrazines may be produced by soil bacteria (*P. taetrolens*) and then absorbed by the tuber, so soil microbe populations may influence flavor (Buttery et al. 1973). In a study involving three U.K. cultivars, the influence of production site on texture (as measured by physical properties and sensory analyses) was stronger than that of cultivar (Faulks and Griffiths 1983).

The levels of off-flavors may be influenced by the production environment as well. As nitrogen levels increase, sensory quality decreases, probably due to the production of acrid-tasting amides and amines (Cieslik 1997; Jansky 2008; Thybo et al. 2006). Differences in production environment were found to influence the development of off-flavor in precooked vacuum-packed potatoes, but specific environmental parameters influencing off-flavor were not determined (Jensen et al. 1999). A musty off-flavor detected in cooked potatoes was found to be due to the presence of 2,4,6-trichloroanisole (TCA). While TCA is not a known metabolite of potato, it was found in tubers harvested from pesticide-treated soils after an exceptionally warm production year (Daniels-Lake et al. 2007). Glycoalkaloid levels and, consequently, bitter flavor may increase in tubers grown under stressful conditions and in tubers that are exposed to light during harvest, storage, and/or marketing (Percival et al. 1994; Sinden and Webb 1972; Uppal 1987; Valkonen et al. 1996). In addition, bruising during harvest can result in significant increases in levels of glycoalkaloids and chlorogenic acid (Dale et al. 1998), both of which may contribute to bitterness.

Some studies have evaluated the effects of organic versus conventional production systems on sensory attributes. Using triangle tests, Wszelaki and others (2005) found that taste panelists were able to distinguish between conventionally and organically grown boiled red potatoes if the skin was left on the tubers while boiling. If the skin was removed during boiling, then differences could not be detected. Hajislova and others (2005) determined that cultivar and production year are important influences on the sensory quality of boiled potatoes, but organic production systems are not consistently superior or inferior to conventional. Jansky (2008) also reported that no flavor differences were detected between organic and conventionally grown potatoes. Minor effects of organic fertilizer treatments have been reported to influence moistness, mealiness, color, and odor (Thybo et al. 2002). However, a comprehensive review of studies conducted to evaluate organoleptic quality in organic versus conventional systems found that no clear statements could be made regarding the superiority of one type over the other (Woese et al. 1997).

EFFECT OF STORAGE ENVIRONMENT ON FLAVOR

Changes in sensory quality have been reported following the storage of potato tubers. In a sensory analysis study, tubers for 6 months at 5.5°C were found to be mealier,
sweeter, and more flavorful than fresh tubers (Jansky 2008). In addition, levels of off-flavors have been reported to decrease during storage (Jansky 2008; Thybo et al. 2006). True and Work (1981) noted that “Russet Burbank” ranked high and “Ontario” ranked low for flavor preference in fresh baked potatoes, but differences were not detected in tubers stored at 8.2°C for 6 months. In a study of pre-peeled boiled potatoes, cultivar and storage time (0, 1.5, and 6.0 months at 4°C) explained a major portion (68%) of taste, color, and texture attributes (Thybo et al. 2006). Interestingly, in another study, while taste panelists were not able to detect the sprout inhibitor isopropyl-N-chlorophenyl carbamate (CIPC), they were able to taste residual levels of the alternative sprout inhibitor 1,8-cineole (Boylston et al. 2001).

When potato tubers are cooked, fatty acids degrade to produce aldehydes and ketones, which contribute to flavor (Duckham et al. 2002). The total levels of fatty acids and their flavor products increase during storage (Duckham et al. 2002). It is interesting to note that tubers alter their fatty acid profiles as they acclimate to cold storage temperatures. Consequently, both levels and types of fatty acids change. Cultivars vary in the way they change their fatty acid profiles during cold storage (Mondy et al. 1963). However, levels of linoleic acid typically decrease and α-linolenic acid increases (Dobson et al. 2004). Variation exists among cultivars in levels of fatty acids at harvest and after storage.

Lipoxygenase activity in potato tubers increases during cold storage, but the concentrations of off-flavor products, such as aldehydes, were found to decrease when these tubers were boiled and then chilled (Peterson et al. 2003). Since an increase in lipoxygenase activity does not necessarily result in a corresponding increase in aldehydes, further research is needed to determine the availability of substrates in the pathways leading to the production of aroma compounds, including those leading to off-flavor.

The types and levels of Maillard reaction components of flavor also change during storage, presumably due to changes in enzyme activities and levels of flavor precursors, such as sugars (Duckham et al. 2002). Levels of reducing sugars and free amino acids increase during cold storage (Blenkinsop et al. 2002; Fitzpatrick and Porter 1966; Sowokinos 2001). Consequently, aroma intensity due to pyrazines increases during cold storage (Duckham et al. 2002). In addition, Maillard-derived glutamate glycoconjugates, which act as umami compounds, are expected to increase with the accumulation of sugars during storage.

Cultivar-dependent effects of storage on texture have been reported (Faulks and Griffiths 1983; Martens and Thybo 2000; Thybo and Martens 1999). In general, though, tuber mealiiness decreases during storage (Ridley and Lindsay 1984; Shetty et al. 1992; van Marle et al. 1997b). Starch is broken down during storage, leading to pitted starch granules (Cottrell et al. 1993). The degradation of starch and the breakdown of the middle lamella during storage may lead to less mealy tubers (Martens and Thybo 2000). In addition, potato tubers lose water during storage and become less turgid. As a result, cells lose their elasticity and are ruptured during cooking, resulting in a less mealy texture (Shetty et al. 1992).

CONCLUSIONS

Flavor is an important marketing trait for any vegetable crop, but potato breeders have not historically focused on selection for superior flavor. The development of
potato varieties with enhanced flavor has the potential to increase consumer interest in fresh market potatoes and to boost consumption. Breeding progress for improved flavor requires both genetic diversity for the trait and an effective way to identify superior clones. The first requirement is not a problem because tremendous diversity is found in cultivated and wild relatives of potato. The second requirement is more problematic because flavor evaluation based on sensory panels is extremely time-consuming and can be carried out on only a few samples at a time. Breeders must be able to characterize specific components of flavor to allow them to identify superior clones in their programs. In addition, the effects of production environment and storage environment on flavor must be understood. While the biochemical components of potato flavor are well characterized, the connection to taste panel data is often missing. As we increase our knowledge base, our goal is to reach a point where growers can optimize growing, harvest, and storage conditions, while breeders can select for varieties with appropriate levels of flavor compounds, resulting in a highly desirable, nutritious food crop.

REFERENCES


