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# Potato in Africa

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## Summary

The potato is a widely used and appreciated food in the world. It is used for human consumption, animal feed, and as a source of starch and alcohol. Potato has a short cropping cycle and a large production per unit area. It provides more nutritious food per land unit in less time and often under more adverse conditions than other food crops due to its efficient water use. It is one of the most efficient crops in converting natural resources, labor, and capital into a high-quality food. Potato is a cash crop for the future of the densely populated sub-Saharan African countries, with a high potential of raising the livelihoods of small-scale farmers and their families. Furthermore, potato could be promoted as a healthy and nutritionally rich food item, primarily due to the presence of various vitamins and minerals, and important phytochemicals, many of which have antioxidant properties.

However, potatoes have long been held back. On the one hand, potatoes are mainly grown using bulky, perishable, contaminated, and degenerated seed-tubers rather than from true seeds like most other crops. On the other hand, due to potatoes' complex genetic structure, breeding new varieties is difficult and potato yields have barely increased compared to other major food crops. Potatoes' high susceptibility and vulnerability to pests and diseases also means they require heavy pesticide use that negatively impacts the environment.

New approaches, including inbred line development of self-compatible diploid potatoes, genetic modification (GM) and gene editing technologies, promise to add more options for crop improvement, particularly to support resource-poor farmers and achieve good yield for improving income and food security.

# Facts and figures

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*Potato is the fourth most important food crop in the world in terms of production with 388 million tons produced in 2017, following rice (770 million tons), wheat (771 million tons) and maize (1.1 billion tons). It is grown in over 158 countries worldwide.*

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*Considering that about 14% of maize production is for food, potato is actually the third most important food crop in terms of human consumption following rice and wheat.*

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*In 2017, potato yielded up to on average 20 tons/ha worldwide, whereas maize, rice and wheat had an average yield of 5.7 tons/ha, 4.7 tons/ha and 3.5 tons/ha, respectively.*

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*Potato is one of the most productive food crops, producing more dry matter (food) per hectare than cereals or any other cultivated plant. As such, it can significantly contribute to food and nutrition security.*

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*A hectare of potatoes provides up to four times the calories of a grain crop and up to 85% of the plant is edible human food, compared to around 50% in cereals.*

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*Potato produces more food per liter of freshwater used through irrigation than cereals and thus is more sustainable to mitigate the effects of climate change.*

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*Over the past 20 years, potato production has significantly increased in developing countries in Asia, Africa and Latin America by 89, 14.5, and 4 million tons, respectively. In Africa, the potato production and harvested areas more than doubled over the last 20 years.*

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*Average potato consumption in East Africa has grown by approximately 300% over the past two decades, yet yields are low.*

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*The major bottlenecks to higher potato yield and reliable supplies in Africa are limited or no access of farmers to high quality seed tubers of improved varieties, poor crop husbandry practices (e.g. disease and soil fertility management), and poor post-harvest management.*

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*A promising alternative to traditional clonal propagation of tetraploid potatoes is the production of hybrid true potato seeds: planting 10 hectares, for instance, takes just 200 grams of easily transported true seeds, compared with 25 tons of perishable seed-tubers.*

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## The potato and its take-off from the Andes

Source: S. Quinn, CIP

### ORIGIN

The potato (*Solanum tuberosum*) belongs to the family Solanaceae which contains several well-known cultivated crops such as tomato (*Lycopersicon esculentum*), eggplant (*Solanum melongena*), tobacco (*Nicotiana tabacum*), and pepper (*Cap-sicum annuum*). The center of diversity for wild species related to potato lies in South America and Mexico. In this area of the world, potato has been used for food for over 10,000 years and it was domesticated during pre-Columbian times over 8,000 years ago (Louderback and Pavlik, 2017). In the 16<sup>th</sup> century, in search of treasures and of the country Eldorado, Spanish conquerors discovered freeze-dried potato - called *chuño* - in the indigenes' native soups. Much as it is still prepared in the Andes today (Woolfe, 1987), harvested potatoes are piled on the ground and repeatedly frozen over several nights. Then, the skin is removed by soaking potatoes in running river water to remove the bitter flavors. The final step involves sun-drying which preserves the *chuño* for up to several years.

Potato was first spread to Europe in the late 1500s by the Spanish (Louderback and Pavlik, 2017). It remained a botanical curiosity and was mostly fed to livestock. Europeans began to actively eat

potato only in the 1800s, during the famines of the Napoleonic Wars. Potato may have been instrumental in preventing scurvy among early consumers, including sailors, due to its relatively high vitamin C content (Buckenhuskes, 2005). Once the potato caught on, there was no turning back. Potato became so widely distributed and important, especially in certain parts of Europe, that it is often referred to as 'European' or 'Irish' potato. It was introduced in Africa at the end of the 17<sup>th</sup> century by Christian missionaries through the formation of small plantations. Soon after, potatoes quickly became part of the feeding habits of both rural and urban populations. As in Europe, potato production could contribute in the fight against food insecurity in the sub-Saharan African countries. Today, potatoes are grown in over 158 countries worldwide (FAOSTAT, 2019). The International Potato Centre CIP - a CGIAR Research Centre - where the most important gene bank for cultivated and wild potato species is found, regularly publishes a World Catalogue of Potato Varieties. The last edition (2009/2010) comprised more than 4500 cultivated potato varieties around the world (<https://cipotato.org/>), adapted to diverse ecologies, ways of utilization, human consumption and industrial transformation (Figure 1.1).



Figure 1.1: Diversity of potato (source: S. Quinn, CIP)

## THE PLANT AND ITS COMPLEXITY

*S. tuberosum* is a dicotyledonous tuberous herbaceous plant, perennial by its tubers but grown as an annual plant (Figure 1.2). The **tuber** is the product for which potatoes are cultivated. Tubers are borne at the end of underground stolons. The flesh is generally white or cream to yellow, the skin color light brownish to red. Tubers can contain high levels of solanine, a toxic alkaloid. After harvesting, some potato tubers can be left in the soil or be dispersed by handling and transportation from the field to the stores. They may then survive over winter, persist in rotation fields (so called volunteers) or outside the field (so called ferals), and finally germinate. Both volunteers and ferals generally constitute a short-term weed problem in areas of commercial potato cultivation and are eliminated by common farming practices.

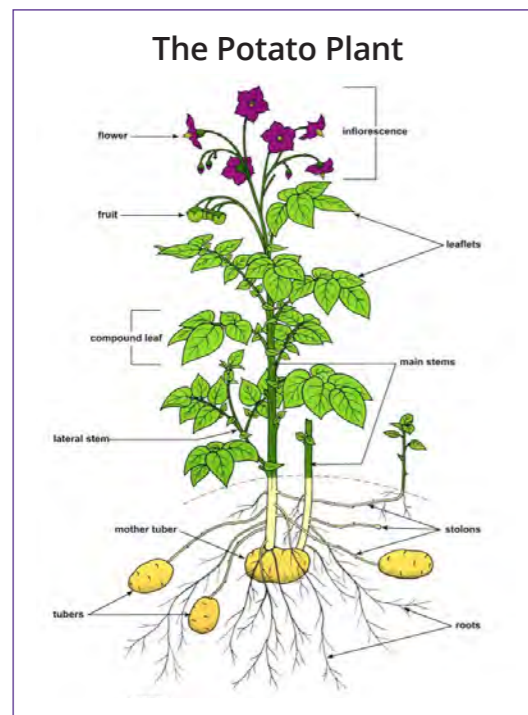


Figure 1.2: Schematic representation of the potato plant (source: CIP)

Potato is characterized by **flowery** plants with white, pink, blue or purple petals. After pollination, flowers often drop to the soil. The result is that few berries with seeds are formed. Moreover, modern potato cultivars flower less profusely than wild potatoes and seldomly produce seeds because of a reduced pollen fertility or even pollen sterility. Amongst them are well known cultivars like **Bintje** and **King Edward**. Several potato cultivars, though, do produce sexual seeds - also termed 'true seeds' to distinguish them from asexual seeds - 'seed tubers' used by potato growers. The number of true seeds produced in commercial fields of fertile modern potato cultivars can be as high as 150–250 million seeds per hectare. True potato seeds can remain viable in the soil from seven to as many as twenty years, regardless of temperature (Arndt *et al.*, 1990).

The basic chromosome number ( $n$ ) in the genus *Solanum* is twelve. The potato gene pool includes **diploid** ( $2n=24$ ), **tetraploid** ( $4n=48$ ) and **hexaploid** ( $6n=72$ ) species, with occasional sterile **triploids** ( $3n=36$ ) and **pentaploids** ( $5n=60$ ). As an example, tetraploid means that there are four sets of chromosomes and thus up to four copies of every gene. The tetraploid *S. tuberosum*, the most commonly cultivated all over the world, is mainly self-pollinating<sup>1</sup>, but cross-pollination of up to 20% may occur (Brown, 1993). Diploid potatoes are mostly self-incompatible and as such must be cross-pollinated by insects. Consequently, diploid potatoes are cross-breeding species (Simmonds, 1995). In particular, bumblebees are better pollinators for potatoes than normal honeybees as the flowers do not produce any nectar (Sanford and Hanneman, 1981). Cultivated tetraploid potatoes contain only a fraction of the potential



Figure 1.3: Harvested potato for seed tubers in Kenya (source: S. Quinn, CIP)

biodiversity that is present in both South American cultivars and sexually-compatible wild species (Bradshaw *et al.*, 2006). Consequently, cultivated potato has a very narrow genetic basis resulting originally from limited germplasm introductions to Europe. In fact, such a **heterozygous<sup>2</sup>, polyploid plant** is difficult to improve by breeding because of difficulties in segregation and purifying genes of interest into a single line. Moreover, due to this complexity, both modern and landrace potato cultivars cannot be maintained through seed propagation. Rather, they are maintained through vegetative propagation, meaning through the planting of tubers or tuber sections (Figure 1.3). Triploid and pentaploid species are fully sterile

and are thus strictly maintained by tuber propagation. The vegetatively propagated varieties consist of clones that enable an indefinite reproduction to produce identical individuals. As potatoes are easily regenerated with the use of *in vitro* tissue culture techniques, they can also be propagated in this way. However, where a callus stage is included, this form of vegetative propagation normally leads to considerable heterogeneity, known as **somaclonal variation**. The drawback of vegetative propagation is that the high diversity of South American potato cultivars and wild species is not sufficiently used for breeding and creating improved varieties.

<sup>1</sup>Self-pollinating means that the plant usually doesn't cross with other plants.

<sup>2</sup>When a gene is present in two alternative forms, the plant is called heterozygous (for more information see VIB Fact Series 'From plant to crop: the past, present and future of plant breeding')

## POTATOES ARE USED IN MANY DIFFERENT WAYS

Potatoes are categorized mainly in three different classes: **seed potatoes**, **consumption or ware potatoes** (for humans and animals), and **starch potatoes**. Cultivation of seed potatoes (i.e. 'true seeds' and 'seed tubers') is necessary for the propagation of plant material. Consumption potatoes are by far the most important in terms of hectarage and production. French fries, mashed potatoes, chips, croquettes or soups: these are only a few of the most popular products derived from potato that we eat on a daily basis

(Figure 1.4). Finally, starch potatoes are cultivated to produce starch for industrial applications (e.g. glues, textile, paper, building materials, adhesives, ethanol biofuel). Potato starch is also used in pre-gelatinized or modified form in the food industry, giving birth to a processing industry with multiple outlets in the agri-food, cosmetics, pharmaceutical and industrial sectors. By-products (peel, trimmings, rejected potatoes, pulp and proteins) are normally used in animal feed (Fauconnier and Delaplace, 2004).



Figure 1.4: Different ways of eating potato in Kenya (source of A: N. Ronoh, CIP; source of B: S. Quinn, CIP)

## NUTRITIONAL VALUE AND CONTRIBUTION TO HUMAN HEALTH

Today, many consumers are still unaware of the potato's contribution to long-term human health, while it has been widely accepted throughout the world as a staple food. **Potato has greater dry matter and protein per unit growing area compared to common cereals** (Bamberg and del Rio, 2005), and as such can contribute significantly to food and nutrition security. The 'nutritional productivity' of potatoes is especially high: for every cubic meter of water applied, 5,600 calories of dietary energy are produced, compared to 3,860, 2,300 and 2,000 in wheat, rice and maize respectively. For the same cubic meter, potato yields 150 g of protein, which is double that of wheat and maize, and 540 mg of calcium, which is double that of wheat and four times that of rice (Nteranya, 2015). Consequently, potato could be further promoted as a healthy food item, primarily due to the presence of vitamins and minerals, as well as important phytochemicals, many of which have antioxidant properties. Antioxidants are important because they may slow the onset of age-related chronic diseases including certain cancers, cardiovascular disease, and diabetes. Despite these benefits, consumers tend to believe that potatoes are high in calories and fat compared to other carbohydrate sources such as rice or pasta. This is not correct since potato has a negligible fat content and a low energy density similar to legumes. Lipids are only a tiny fraction of potato weight, amounting to approximately 0.15 g/150 g fresh weight. This is less than cooked rice (1.95 g) or pasta (0.5 g) (Priestley, 2006).

About 75% of the total dry matter of the potato tuber consists of carbohydrates, with **starch** serving as an energy reserve for the plant

and contributing the major amount of energy obtained through potato consumption. Cooking or processing potatoes greatly improves the digestibility of potato starch. In addition, potato contains some non-starch polysaccharides, which constitute dietary fiber. Potato protein is of superior importance among all the nutrients because of its high biological value (BV)<sup>3</sup>. Potato protein has a BV of 90 - 100 compared with soybean (84) and beans (73) (Buckenhuskes, 2005). Potato also contains valuable minerals, such as potassium (564 mg per 100 g fresh weight), phosphorus (30-60 mg per 100 g fresh weight) and calcium (6-18 mg per 100 g fresh weight), which respectively contribute to the recommended daily intake of human diet up to 22%, 6%, and 6% (White and Broadley, 2005). Moreover, potatoes constitute an important dietary source of essential vitamins such as **vitamin C (ascorbic acid)** (Augustin, 1975). Therefore, potato had a role in the prevention of scurvy ever since it was first adopted by Europeans, partly also due to the fact that tubers can easily be stored for a long time, allowing them to be a regular item in the diet. It is estimated that ascorbic acid from potatoes (ranging in content between 84 to 145 mg per 100 g dry weight) may contribute up to 40 % of the daily recommended intake by humans (Love and Pavek, 2008). Since iron uptake is enhanced by ascorbic acid, vitamin C is also important to iron availability. Iron is often a limiting element in the human diet. Its deficiency is a global health concern for pregnant women and children who are not nursing. Increasing ascorbic acid levels in vegetables such as potato may contribute to alleviating human iron deficiencies (Brown, 2008) (Figure 1.5).

<sup>3</sup> The biological value is a measure of the proportion of absorbed protein from a food which becomes incorporated into the proteins of the organism's body





Equally important is the presence of lipid-soluble pigments such as carotenoids and their derivatives xanthophylls (Brown, 2008). Two of these pigments, present in low concentration in cultivated potato ( $\beta$ -carotene and lutein), have an important role to play in eye health. More than one third of children in need around the world are deficient in vitamin A leading to various diseases, including blindness, and resulting in premature death. The most potent dietary source of vitamin A (pro-vitamin A) is  $\beta$ -carotene. Breeding may increase carotenoid content, as wild species may contain these pigments in greater concentrations (Brown, 2008). It may also be possible to genetically improve potato to increase  $\beta$ -carotene content. To this end, the genetic modification of two cultivars, **Désirée** and **Mayan Gold**, was reported to contain enhanced levels of  $\beta$ -carotene and lutein (Ducruex *et al.*, 2005). Subsequently, enhanced  $\beta$ -carotene content was successfully obtained in potato by RNAi-mediated silencing of the  $\beta$ -carotene hydroxylase gene that converts  $\beta$ -carotene to the less useful zeaxanthin (Van Eck *et al.*, 2007). Similarly, sweet potato (*Ipomoea batatas*) varieties present in Africa and Asia are deficient in  $\beta$ -carotene. The vitamin A-enriched orange-fleshed sweet potato consumption had a significant effect on the household food and nutritional security in these regions. For this contribution, HarvestPlus (<https://www.harvestplus.org/>) and the plant breeders of the SASHA project (Sweetpotato Action for Security and Health in Africa) were honored with the World Food Prize 2016.

However, potato consumption can also lead to health issues: **acrylamide**, a common industrial chemical, can be found in many heated carbohydrate-rich foods (Lineback *et al.*, 2006). The International Agency for Research on Cancer considers acrylamide a 'probable' human carcinogen. French fries and potato chips have some of the highest acrylamide levels reported, fostering numerous studies on the mechanisms of acrylamide formation in foods. Potatoes harvested each fall are cold-stored to ensure a continuous supply throughout the year. During cold storage, reducing sugars can accumulate in potatoes and when cooked at high temperatures, as for French fries, the reducing sugars interact with free amino acids (e.g. asparagine) to form acrylamide (Lineback *et al.*, 2006). Besides acrylamide, potatoes and other members of the Solanaceae family contain natural toxic substances. The most important group of alkaloids in commercial potato varieties are the **steroidal glycoalkaloids (SGAs)**, which can be toxic to animals and humans at high levels (Milner *et al.*, 2011). However, SGAs are also important components of plant resistance against pathogen and pest attacks (Akiyama *et al.*, 2017). Light exposure, heat, wounding, or inappropriate postharvest management can significantly increase the accumulation of SGAs in the tubers of potato beyond the maximum level set by the industry (Petersson *et al.*, 2013). Hence, genetic improvement of potato to prevent toxic levels of SGAs in tubers is highly desirable. At the same time, maintaining high SGA levels in other plant organs may contribute to plant resistance against pathogen and pest attacks.

**Figure 1.5: Potato contributes to human health**  
 (source of A: A. Balaguer, CIP; source of B: H. Rutherford, CIP; source of C: Mayan Gold from Shutterstock)

## 2 Potato: grown and cultivated worldwide



Source: H. Rutherford; CIP

## POTATO, ONE OF THE MOST PRODUCTIVE CROPS

Potato is the **fourth** most important food crop in the world in terms of production with 388 million tons produced in 2017, following rice (770 million tons), wheat (771 million tons) and maize (1.1 billion tons) (FAOSTAT, 2019). Considering that only about 14% of maize production is for food, potato is actually the **third** most important food crop in terms of consumption following rice and wheat (FAOSTAT, 2019). Potatoes grow from sea level up to an altitude of 4,700 meters, and perform best in a temperate climate. The total potato harvested area was estimated at 19 million hectares in 2017, which is substantially lower than the harvested area of rice (167 million hectares), maize (197 million hectares) and wheat (218 million hectares) (FAOSTAT, 2019). Despite this, potato yielded on average 20 tons/ha worldwide in 2017, whereas maize, rice and wheat had an average yield of 5.7 tons/ha, 4.7 tons/ha, and 3.5 tons/ha, respectively (FAOSTAT, 2019). Potato is one of the most productive food crops, producing more dry matter (food) per hectare than cereals or any other cultivated plant, and it has a shorter crop cycle (mostly < 120 days) than major cereal crops like maize (FAOSTAT, 2019). A hectare of potatoes could provide up to four times the calories of a grain crop and up to 85% of the plant is edible

human food, compared to around 50% in cereals. Moreover, potato produces more food per liter of freshwater used through irrigation than cereals and thus is a more sustainable option considering climate change mitigation (Figure 2.1).

In 2017, potato was grown in over 158 countries, with a total production value of around USD 92 billion, making it one of the most profitable crops for the farmer, just behind rice and maize (FAOSTAT, 2019). Potatoes are consumed by more than one billion people worldwide. They have achieved global prominence as a food item, in part due to their tremendous yield per unit area compared with many other food crops. Potatoes are grown and eaten locally, with little significant international trade compared to cereals and therefore are highly recommended by the Food and Agriculture Organization (FAO) for countries seeking to increase their food security (FAO, 2008). Consequently, potato farming is becoming increasingly popular in the developing world. The production levels in the developed nations such as the European Union, Russian Federation and North America have declined over the past 20 years (between 1997 and 2017) by 20.5, 5.5, and 1 million tons, respectively (FAOSTAT, 2019).



Figure 2.1: Potato one of the most productive crops (source A and B: S. Quinn, CIP)



## THE POTENTIAL OF POTATO FOR AFRICA

TABLE 1: TOP TEN AFRICAN COUNTRIES IN POTATO PRODUCTION, AREAS HARVESTED AND YIELDS IN 2017.

Countries	Tons (million)	Countries	Area harvested (ha)	Countries	Yield (tons/ha)
Algeria	4.6	Nigeria	345,246	South Africa	36
Egypt	4.3	Tanzania	211,927	Zambia	31.6
South Africa	2.4	Kenya	192,341	Algeria	31
Morocco	1.9	Angola	180,104	Morocco	30
Tanzania	1.7	Egypt	163,939	Niger	29
Kenya	1.5	Algeria	148,692	Egypt	26.3
Nigeria	1.2	Rwanda	93,991	Senegal	22.5
Malawi	1.2	South Africa	67,746	Mali	21.4
Ethiopia	0.9	Ethiopia	67,591	Mauritius	19.9
Rwanda	0.8	Malawi	66,604	Libya	19.6

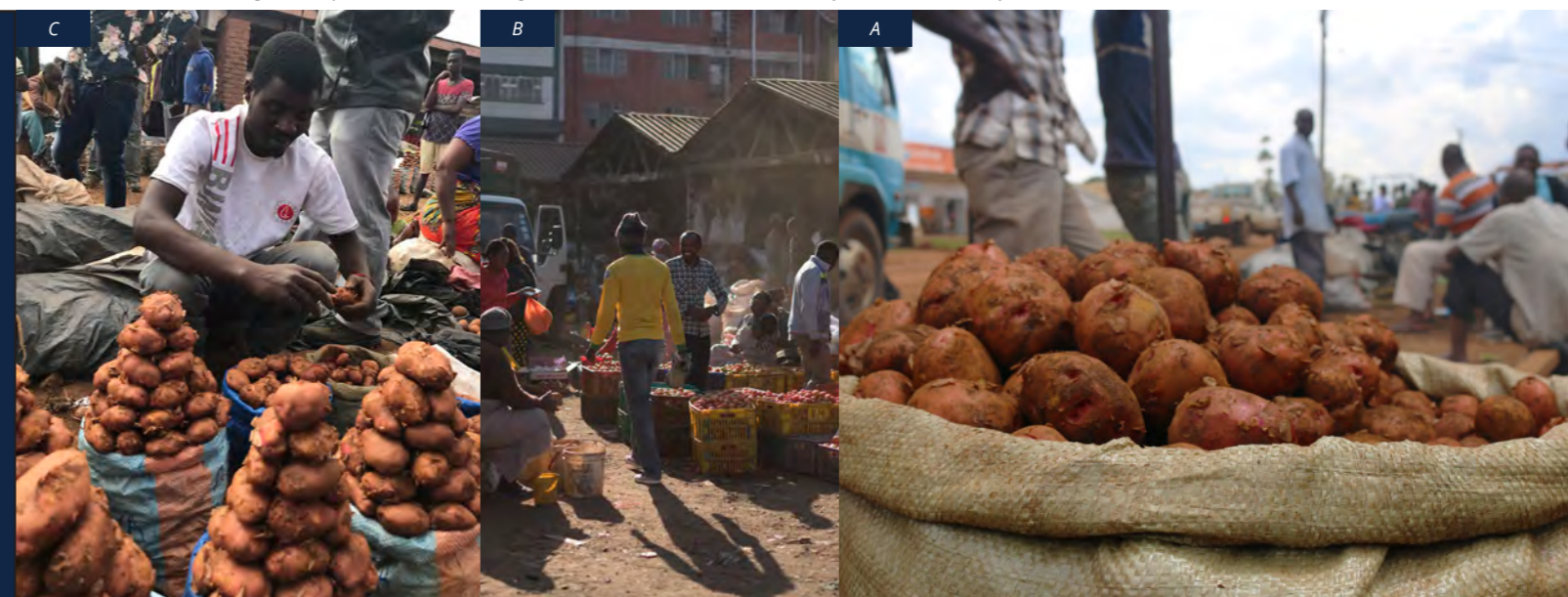
Source: FAOSTAT 2019

It is in Africa where the potato production and harvested areas have more than doubled over the last 20 years (FAOSTAT, 2019). Potato is a main source of revenue in sub-Saharan Africa for both commercial farms and smallholder farmers. In 2017, Africa produced 25 million tons of potatoes on 1.9 million hectares, which accounted for 6.4% and 10% of the world production and area harvested, respectively. Potato yields in Africa ranged from 0.7 to 36 tons/ha with a continent average of 13 tons/ha in 2017, which was below the global average yields of 20 tons/ha and the higher average yields obtained in the USA or in Belgium (48 tons/ha). Higher yields result from many factors, including cool climate with ample rainfall, mechanization and relatively high inputs (fertilizer, pesticides), a long growing season which favors the higher yielding long-season cultivars, and production systems involving rotation with cereals and forages that improve soil structure and discourage disease. Table 1 shows the top ten African countries in potato production, harvested

areas and yields in 2017 (FAOSTAT, 2019).

In Africa, increasing demand for potato has been met by increased cultivation area, often by encroachment into forests rather than through increasing productivity and tackling productivity constraints. Demand is fueled by a rising number of potato consumers, interest in processed potato products for a developing food industry, potato use as feed for a growing livestock industry, and export potential to neighboring countries (FAO, 2008). African prosperity gained over the past two decades is compromised by soaring food prices. It is the result of diverting crops from food/feed to biofuels and associated speculation in the commodities markets. This brings a risk of food shortages and social unrest in low-income African countries. Diversification of food production to include new, nutritious and versatile staple crops that are less susceptible to the unpredictability of international markets could help reduce these risks. **Potato is such a crop.**

Figure 2.2: potato markets (A) in Uganda (source: S. Quinn, CIP), (B) in Kenya (source: H. Rutherford, CIP), (C) in Malawi (source: V. Atakos, CIP)



Moreover, with a population doubling every 25 years and urbanization predicted to grow by 13% in the next 10 years, dietary habits in Africa will continue to change in favor of easy-to-prepare foods and street food to facilitate rapid consumption. Processing has the potential of enabling potato to take the status of an industrial crop similar to that of maize and wheat. This would help to create more employment opportunities, improve nutrition, and enhance incomes along the value chain. Rural women provide most of the labor in both small- and large-scale potato production - from conservation and seed tuber selection to planting, harvesting, storing, and marketing (FAO, 2008). By increasing the importance and profitability of the crop, potato can contribute to improve the status of women and provide them and their children access to education for a better future.

The major bottlenecks to higher potato yield and reliable supplies in Africa are, among others,

limited or no access of farmers to high quality seed tubers of improved varieties, poor crop husbandry practices (e.g. disease and soil fertility management) and poor post-harvest management. Farmers' knowledge of good agronomic practices, which could boost potato yields and marketability, is uneven in Africa. This is combined with an ineffective marketing system characterized by a fragmented value chain with too many uncoordinated actors, limited access of smallholder farmers to inputs (fertilizers, pesticides) and financial services (Schulte-Geldermann, 2017) (Figure 2.2). There is also the human and environmental health issue. Due to low literacy levels, it was shown that 91% of Ugandan farmers do not understand the toxicity information labels on their chemical packages (Okonya and Kroschel, 2015). Challenges associated with climate change, as well as an inadequate policy environment and rural development priority, are additional bottlenecks to improved potato yields.

African farmers tend to grow potatoes in very close rotations or even, in some cases, via continuous mono-cropping. As a result, diseases accumulate in crops and soils, yields decline, and farmers are left with little to sell. Another problem is that farmers usually obtain their seed tubers either from untraceable sources, or from their own previous season's production. Such tubers are often diseased and of poor quality, resulting in low yields. Moreover, different varieties of potato can be mixed during harvest or trade, resulting in a product with a lot of variation in cooking and processing qualities. There are also problems in timing the harvest because of differences in maturity between plants. It is common practice of smallholder farmers to save tubers for seed that are too small and inferior to be sold for consumption. However, small-sized tubers may have a delayed emergence and a low sprout number and vigor because of low food reserve (Gildemacher *et al.*, 2007). In addition, these tubers might come from a diseased mother plant and thus be infected by pathogens. Moreover, the African potato value chain is characterized by a lack of on-farm potato storage.



Figure 2.3: Participatory varietal selection of potato clones in Ethiopia (source: V. Atakos, CIP)

## EXAMPLES OF SEED POTATO SYSTEMS IN ETHIOPIA

Seed systems are defined as the ways in which farmers produce, select, save and acquire seeds (Hirpa *et al.*, 2010). In Ethiopia, three seed potato systems co-exist: an informal, an alternative, and a formal seed system. The farmers' informal or local seed systems are dominant and supply 98.7% of the seed tubers required in Ethiopia. It is the seed potato system in which tubers to be used for planting are produced and distributed by local farmers without any regulation. The seed tubers supplied by this system have poor sanitary, physiological, physical and genetic qualities. The alternative seed potato system is a seed potato system that supplies seed tubers which are produced by local farmers but under financial and technical support from breeding centers such as the Ethiopian Institute of Agricultural Research (EIAR). This system supplies about 1.3% of the total supply. There are also farmers' research groups and farmers' field schools in the central and northwestern areas of Ethiopia which are involved in seed potato production (Figure 2.3). The formal seed system covers seed production and supply mechanisms operated by licensed private sector specialists and cooperatives in different aspects of the seed system, ruled by well-defined methodologies, with controlled multiplication, and in most cases regulated by national legislation and international standardization methodologies. The contribution of such a formal seed potato system to the overall seed tuber use in Ethiopia is minimal as both the private sector and the cooperatives are at the incipient stage. There is only one seed potato company working at international standard levels in Ethiopia, i.e. the SolaGrow PLC, established in 2006 by a group of Dutch investors in collaboration with the Dutch potato breeding company HZPC Holland B.V.

## KENYAN POTATO PRODUCERS TURN TO CONTRACT FARMING

Average potato consumption in East Africa has grown by approximately 300% over the past two decades, yet farmers have largely failed to benefit from this with low farm-gate prices due to highly fragmented supply chains and continuing low yields due to lack of access to quality inputs and expertise. Recurring drought and sudden periods of cold weather have affected the quality of potatoes across Kenya, reducing potato yields by over 10% in the past two years (2016 and 2017). To try to fight back, Kenyan potato farmers have increasingly turned to production contracts with food processors in 2018. This is a system known as contract farming through the **East African Potato Consortium**. The consortium, which was set up in 2016 by the National Potato Council, the Alliance for a Green Revolution in Africa and the Grow Africa partnership, aims to increase private investment in agriculture by linking potato farmers with food processing companies across the country. By driving the right partnerships, it will increase farmers' production, improve marketing and increase farmers' income in Kenya, Rwanda and Uganda. Thanks to this consortium, farmers get access to more robust seed, as well as to better fertilizers. They also get a guaranteed price for their crop even when the weather is bad as long as they produce good-quality potatoes on time. Provided with additional support, East African farmers could increase potato production from the current 5 tons/ha to 35-40 tons/ha (Figure 2.4).



Figure 2.4: CIP field visits in Western Kenya (source: S. Quinn, CIP)

## POTATO IS THREATENED BY BOTH ABIOTIC AND BIOTIC STRESSES

The potato crop is subjected to numerous abiotic and biotic risks affecting sustainability of production. Abiotic constraints related to potato production are primarily temperature- and precipitation-related events. Weather-related hazards can result in yield losses over 25% virtually each year (van der Waals *et al.*, 2016). Potato may suffer from low temperatures such as late frosts occurring after winter, early in the planting season and thus damaging crops after emergence. On the contrary, early frosts at the beginning of winter will kill the crop prematurely. Heat waves during the growing season and at the time of tuber bulking may lead to temporarily reduced or halted growth as well as reduced quality of the tubers. Precipitation-related events that pose a risk to potato are excess rain during tuber growth leading to waterlogging, tubers rotting in the soil due to asphyxiation, or too much rain rendering harvest impossible. Too little rain poses risks especially where potatoes are rain-fed whereas elsewhere drought may lead to restrictions on irrigation from dams or rivers affecting potato production as well. Following a period of drought, secondary growth symptoms and tuber malformation could occur when soil moisture is replenished.

The most important air-borne pathogens of potatoes are *Alternaria solani* (early blight), *Alternaria alternata* (brown spot) and *Phytophthora infestans* (late blight), that destroy leaves, stems and tubers (van der Waals *et al.*, 2011). Particularly, late blight was a significant contributor to the historical Irish Potato Famine in the 1840s and, in the 20<sup>th</sup> century, became even the subject of biological weapons research owing to its ability to utterly decimate potato fields. Dominant tuber- and soil-borne fungi and fungus-like organisms are

*Rhizoctonia solani* (black scurf), *Helminthosporium solani* (silver scurf), *Spongospora subterranea* f.sp. *subterranean* (powdery scab), *Fusarium* spp. (*Fusarium* wilt), *Verticillium dahlia* and *V. albo-atrum* (*Verticillium* wilt) (Denner *et al.*, 2012). Potatoes are also susceptible to bacterial diseases, such as bacterial wilt and soft rot that can affect plants in the field and can lead to significant losses for stored potatoes. The incidence and severity of the soft rot/blackleg disease complex in the potato industry has increased substantially in the years, with *Pectobacterium carotovorum* subsp. *Brasiliense* causing tubers to rot in the ground and in storage (van der Merwe *et al.*, 2010). Root knot nematodes are common and destructive pests of potatoes. *Meloidogyne javanica* and *M. incognita* are the most important species attacking potatoes worldwide (Fourie *et al.*, 2001). Nematodes are microscopic roundworms that live in soil, water, and plant tissues. They may cause considerable damage by negatively influencing the water/nutrient transport channels of plants or by damaging their underground vegetative reproductive organs and roots. In South Africa alone, potato production losses associated with plant parasitic nematode species in 2014 were estimated to be 16.7%, accounting for USD 7 million (Onkendi *et al.*, 2014). Potato plant and tuber degeneration is also caused by viral diseases (especially Potato Virus Y (PVY) and Potato Leaf Roll Virus (PLRV)), which are primarily transported to new plants via winged aphid vectors (Radcliffe, 1982) (Figure 3.1). Thus, the presence of aphids in a crop is often an indicator of virus infection. Beside aphids, tuber moths (*Phthorimaea operculella*) and leaf miners (*Liriomyza* spp.) are other important pests affecting planted and stored potatoes in warm and dry areas (Denner *et al.*, 2012).

### 3 Challenges to the sustainability of potato cultivation

Extreme weather conditions, shifts in pest and disease populations, and a lack of affordable fertilizers and pesticides already significantly affect crop yields today, particularly in Africa. By 2050, FAO estimates that food and agriculture systems will need to produce 50% more food to feed the projected global population of close to 10 billion. Climate change is making it harder than ever to grow healthy crops in more and more regions of the world. Not just food quantity, but food quality will be affected. Protein content of crops may be reduced considerably in major staple crops: barley (14.6%), rice (7.6%), and potatoes (6.4%) (FAO, 2017). Studies also pointed out that the zinc and iron content of staple crops will likewise be affected, whereby iron concentrations will drop by as much as 10% in maize for example, putting around 1.4 billion children at risk of major iron deficiencies by 2050 (FAO, 2017). Besides climate change, limited knowledge of good agricultural practices by farmers also leads to low yield, poor quality of potatoes and seasonality in production.



Figure 3.1: Potato diseases diagnosis and training in Limuru, Kenya (source of A, B, and C: S. Quinn, CIP)

Among potato diseases, **late blight**, caused by the fungus-like microorganism *P. infestans* (oomycete), is the most critical problem and threat to global potato production, affecting more than 3 million hectares of cultivated potato globally and causing estimated economic losses of USD 6.7 billion per year (International Potato Center, 2018). In Kenya and Uganda, over 1 million smallholder farmers grow potatoes, and losses due to late blight can be up to 70% of their harvest. In Uganda alone, the losses due to the disease are known to cost more than USD 129 million annually (International Potato Center, 2018). In many parts of Ethiopia, late blight is the cause for the shift of potato production from the long rainy season to off-season production, despite the high potential yield in the long rainy season (Bekele and Eshetu, 2008). When seed tubers become infected by *P. infestans*, they rapidly rot during storage or fail to produce emerging and surviving plants. Towards the end of the 19<sup>th</sup> century, the disease was controlled with 'Bordeaux mixture', an environmentally very unfriendly crop protection agent consisting of

copper sulfate and calcium hydroxide. Similar chemicals are still in use today by organic farming due to the absence of alternative methods of control. Since the mid-20<sup>th</sup> century, chemical products based on manganese and tin became available and farmers commonly resort to spraying their crops with fungicides on a near weekly basis to control the disease. Fungicides are expensive and often not affordable to resource-poor farmers. The few sprays they can afford are never enough to keep the disease off the field. Farmers would benefit from potatoes that do not require extensive spraying, allowing them to use their few resources on other priorities. Due to the resistant nature and hardy lifecycle of *P. infestans*, techniques such as crop rotation have a limited effect in controlling the disease spread. Moreover, the effectiveness of pesticides is limited by the development of fungicide resistance, the emergence of new strains, and concerns for human health and environmental impact. **The control of potato late blight, therefore, remains a major challenge to agriculture.**

## GOOD QUALITY SEED TUBERS

For both increased productivity and area under production, a well-timed availability of good quality seed tubers is vital. This is also a very efficient way to provide further incentives for farmers to adopt high-yielding, disease-resistant potato varieties that have acceptable qualities for both consumption and processing. Increased potato productivity will enhance household income in all the countries where it is grown and consumed, including African ones.

Although potato production in Africa has more than doubled since 1997, potato yields of small-scale farmers fall far short of their potential due mostly to a combination of inadequate supplies of high-quality seed and smallholders' limited awareness of better seed management practices. Having good varieties is not enough when the supply of planting material is limited, or when conventional multiplication has low multiplication rates (about 10 seed tubers per plant). This multiplication rate implies that it typically takes up to seven seasons of seed production (i.e. seven generations) to produce sufficient high-quality seed tubers. To increase the availability of high-grade seed tuber potato for farmers, the International Potato Center (CIP) together with its national partners, has developed an innovative seed strategy between 2008 and 2011 that dramatically lowers the cost of seed tuber

production and couples this with extension-based interventions to train smallholders in better on-farm management of their own seed tubers. Engagement with the private sector all along the seed value chain as a means to widen the supply base and satisfy the demand for quality seed was also a key component of the strategy. The centerpiece of this effort is **the three-generation '3G' seed multiplication strategy** that can reduce the number of seed multiplications from the conventional seven generations to just three (International Potato Center, 2011). Implemented in Kenya, Rwanda and Uganda, the '3G' strategy increased access to, and production of, basic seed tuber potato in both public and private sectors. It successfully introduced the aeroponics technology and supported its adoption, and significantly increased production of minitubers at the national and regional scales. More than 15,000 smallholder growers gained knowledge and skills on potato production technologies and best practices, and saw average yields increase by 20% (Figure 3.2). This is expected to raise incomes of smallholder farmers by 15%, improve food security through a 10% increase in potato production, and develop more business opportunities for at least 240,000 households of smallholder potato growers in the region (International Potato Center, 2011).



Figure 3.2: Smallholder growers gaining knowledge and skills on potato production technologies and best practices (A) in Rwanda (source: K. Sindi, CIP) and (B and C) in Malawi (source of B: V. Atakos, CIP; source of C: H. Rutherford, CIP)

## THE '3G' SEED STRATEGY

The '3G' seed strategy relies on producing large numbers of minitubers through one generation of a very rapid multiplication technology (RMT), allowing bulking of sufficient seed in only three field generations rather than the conventional seven. This reduces both the cost of production and prevents the buildup of damaging diseases in the field. The main RMT method is **aeroponics**, which achieves multiplication rates of over 50:1 compared with the normal 5:1. Aeroponics involves producing minitubers from in-vitro cuttings in a totally enclosed darkened box into which water and nutrient are sprayed as a mist. Minitubers are harvested from the suspended roots (Figure 3.3).

In 2011, 11 aeroponics units were established which produced 1.4 million minitubers in Kenya alone. Economic analysis showed that minitubers in aeroponics can be produced for about 20-50% of the cost of minitubers from conventional pot production systems. The aeroponics technology attracted private sector involvement in the seed potato business. This helped to increase minituber production from 30,000 to 1,000,000 within 3.5 years.



Figure 3.3: Aeroponics rapid multiplication technology (RMT) for minitubers production (source of A: H. Rutherford, CIP; source of B, C and D: S. Quinn, CIP)

## ADEQUATE SEED TUBER STORAGE



Figure 3.4: Seed tuber storage in Africa (source of A: R. Jumah, CIP; source of B and C: S. Quinn, CIP; source of D: H. Rutherford, CIP)

Potato tubers harvested at full maturity can be conserved for 10-12 months. The live tubers with high levels of water undergo the phenomena of respiration and transpiration. They are also subjected to weight loss with time, wilting and development of germs. Potato tubers are thus highly perishable and can be infected with pests and diseases. They must also be safeguarded from freezing. Seed tuber storage is a common practice in all potato-producing areas in Africa but this still uses rudimentary techniques. Farmers often store potatoes by leaving the tubers un-harvested in the soil. This postponed harvesting method is mainly used to extend piecemeal consumption and also to wait for a better price. There are other traditional storage methods like storing seed from the previous harvests in piles on the floor of the houses or in sacks or baskets stacked on the floor in untidy places where there is no ventilation, heaped loosely or put on a bed-like structure. Such storage practices result in poor and usually long sprouts that break easily during transportation and/or planting, leading to low yields. Post-harvest losses due to mishandling can be as high as 30-50% (Hirpa *et al.*, 2010). Diffused light storage (DLS) is another storage

method that uses a low-cost rustic structure to store seed tubers. It maintains seed tuber quality by allowing diffusion of light and free ventilation which suppress sprout elongation and thereby slow down the aging of the sprout (Hirpa *et al.*, 2010) (Figure 3.4).

At harvest time, there is the problem of glut, which leads to very low prices (discouraging farmers) during times of abundance, and very high prices (discouraging consumers) during times of scarcity. Data from Ethiopia shows that farm gate prices fluctuate by more than 25% within 2 months before and after harvest (Schulte-Geldermann, 2013). Improvement in post-harvest management would expand the period of potato availability for household consumption and increase marketing opportunities. Technologies for reducing postharvest losses include reduction of physiological deterioration (due to damage or disease), increased knowledge on appropriate transport techniques, storage facilities, and market information for timely delivery and use. The adoption of such technologies and practices would enhance the potential of potato processing that could largely extend shelf life.

# 4 Potato improvement strategies

The main goals of potato improvement strategies are to develop cultivars with resistance to biotic and abiotic stresses, with improved yield stability and nutrient content, with black spot bruising tolerance, non-browning, and reduced acrylamide potential. Germplasm from all over the world have been used to improve potato varieties. However, creating a new improved potato variety is slow and difficult. Unlike other major crops, potato has not had a breeding breakthrough of the kind that helped dramatically boost yields during the Green Revolution of the 1950s and 1960s. Commercial varieties are out-crossing tetraploid, which force breeders to create and test hundreds of thousands of seedlings to find just one with the desired combination of traits. Many countries continue to plant popular potato varieties that have remained essentially unchanged for decades. New approaches, including inbred line development of self-compatible diploid potato, genetic modification (GM) and gene editing technologies, promise to add more options for crop improvement, particularly to support resource-poor farmers and achieve good yield for improving income and food security.

Source: S. Quinn, CIP

## WILD POTATO SPECIES CAN BRING SOLUTIONS

The key to develop a robust and resilient potato may reside in the wild species that grow from southwestern North America through Central and South America. These species can bring more genetic diversity to improve cultivated potatoes (Figure 4.1). Wild potato varieties from Mexico, for example, evolved in the presence of *P. infestans* and can resist many strains of the pathogen. Many other wild species have yet to be thoroughly collected and studied. The **Crop Trust's**<sup>4</sup> effort to collect, conserve, and breed the wild relatives of 29 crops began in 2011. In Lima, the Crop Trust has funded the International Potato Center (CIP) in 2013 to test wild varieties for promising traits such as drought tolerance and bacterial wilt resistance. The international effort to collect wild potatoes has yielded samples representing 39 species from six nations: Peru, Brazil, Ecuador, Guatemala, Costa Rica, and Chile. The plants are stored in each nation's gene bank, at CIP and at the Millennium Seed Bank at the Royal Kew Botanic Gardens in the United Kingdom. The stored seeds are available to potato breeders worldwide.



Figure 4.1: Feed the Future accelerated value chain development program in Kenya (source: V. Atakos, CIP)

However, getting desirable genes from wild species into cultivated potatoes is the hardest

part of a breeding effort. In the past, breeders acquired traits such as disease resistance from a dozen wild species. Those victories were hard-won, some taking decades to achieve. That is largely because wild relatives also carry many unwanted traits (e.g. low yield or bad taste) which combined with those of cultivated potatoes vastly lower breeders' chances of finding a good variety that can satisfy farmer, consumer and processor. Even without wild species, potato breeding is an adventure. Traditional potato breeding is based on crossings between highly heterozygous tetraploid cultivars. Because tetraploid varieties carry four copies of each chromosome, the traits of the two parents show up in the next generation in largely unpredictable combinations. As a result of the traditional way of potato breeding, unfavorable alleles easily remain 'hidden' in the tetraploid genome and become manifest at each breeding cycle. It takes extensive selection programs on progeny plants derived from crosses between tetraploid potato cultivars to select a plant that has the right balance between unfavorable and desired favorable traits. Typically, a potato breeder must screen up to 100,000 offspring potatoes per year to generate one new variety (Figure 4.2). And still, such a variety may contain numerous 'masked' or 'hidden' unfavorable traits. Consequently, the genetic gain in breeding is very limited. Therefore, developing a new variety can take 15 years or longer to find one with the right trait, fully test it, and generate enough seed tubers to distribute to farmers. Compounding the headache, breeders usually select for many traits at once, further lowering the probability of finding a winner improved cultivar.

<sup>4</sup>Crop Trust is an intergovernmental organization based in Bonn, Germany



Figure 4.2: Potato breeding program at IITA 'Transforming African Agriculture' in Nigeria (source of A, B and C: S. Quinn, CIP)

Genetic markers linked to specific genes have successfully sped up the process. To find out whether seedlings have inherited a trait such as disease resistance, breeders can quickly test for the marker rather than wait for the plants to mature and then expose them to the disease. However, even with this tool, variety development takes a long time. Another frustration is that potato breeders can't easily improve existing varieties. Once a potato variety is established, introducing new traits while retaining all of its favored characteristics is practically impossible. That's why classic, widely grown varieties, such as the **Russet Burbank** and **Bintje**, still dominate the market many decades after their debuts. Russet Burbank was released in 1902 (Bethke *et al.*, 2014) and Bintje was bred in 1904 (Sree Ramulu *et al.*, 1983). Patient breeders using traditional methods can nevertheless achieve impressive results. In 2017, for example, CIP released four new varieties in Kenya, the result of crosses from established breeding lines. In field trials, the new potato plants maintained yields even with 20% less rainfall and temperatures higher by 3°C (Stokstad, 2019) (Figure 4.3). Such successes show that there is still genetic diversity to be tapped into in existing breeding lines. But researchers fear that the potato gene pool may not be deep enough to adapt to future climates or enable other improvements. Wild potatoes, however, hold valuable, untapped genetic diversity.



Figure 4.3: Harvesting potato for seed tuber in Kenya (source: S. Quinn, CIP)

## GENETICALLY IMPROVED POTATO

Potato was one of the first crops to be genetically modified (GM) in the early 80's (Shahin and Simpson, 1986). Since then, more efficient transformation systems have been developed (Han *et al.*, 2015) and *Agrobacterium*-mediated transformation is the most commonly used technique to obtain GM potatoes (for more information on *Agrobacterium*-mediated transformation, see VIB Facts Series issue 'Bananas, the Green Gold of the South'). The GM traits researched to date mainly include insect-, nematode-, and disease resistance (in particular late blight and virus resistance), altered starch content and composition, tolerance to abiotic stresses, anti-bruising, anti-browning,

and biofortification (e.g. enhanced protein, beta-carotene content). Field trials of GM potatoes have been conducted in several regions worldwide. In Africa, Uganda is currently conducting multi-location trials in preparation for general release of late blight resistant GM potato (Figure 4.4). GM potato varieties have been recently commercialized in the United States and Canada. In 2012, the cultivation of the GM potato varieties developed by the BASF company (GM variety **Amflora** with modified starch composition and GM variety **Fortuna** with late blight resistance) were discontinued because of the European public hostility towards GM crops. Consequently, BASF shifted its research activities to the US.



Figure 4.4: Yield evaluation trial of GM and non-GM potato varieties in Uganda (source A and B: E. Magembe, CIP)

A 110-fold increase in global GM acreage has been recorded in just 21 years of commercialization (from 1.7 million hectares in 1996 to 185.1 million hectares in 2016) making GM technology the fastest adopted crop technology in recent times and reflecting farmer satisfaction with GM crops (ISAAA, 2017). The adoption of GM crops has reduced CO<sub>2</sub> emissions equal to removing approximately 16.7 million cars from the road annually in recent years, has conserved

biodiversity by saving 183 million hectares of land from cultivation, and has decreased the environmental impact from herbicide and insecticide use by 18.4% (ISAAA, 2017). With the commercial approvals in the US and Canada and plantings of new varieties of GM potatoes in 2016 and 2017, consumers will begin to enjoy direct benefits of biotechnology with products that have the added potential to substantially reduce food waste and consumer grocery costs.

## CONVENTIONAL BREEDING VERSUS GENETICALLY MODIFIED PLANTS

Since the origins of agriculture, people have sought to produce plants that are more productive, stronger, and have commercial appeal. These new and improved plants are obtained by continuous selection every harvest time. By crossbreeding two parent plants differing in traits, their offspring may display new trait combinations. Subsequently, the offspring that contains the advantageous combination of the traits of the two parent plants is used. When plants are crossbred, large sections of DNA are exchanged, by way of which half the DNA of parent plant 1 is united with half the DNA of parent plant 2. This produces offspring each with a unique combination of the desirable and undesirable traits of the parent plants. To purify the new cultivar, the progeny is backcrossed with the original (commercially appealing) parent plant 2. Backcrossing is repeated several times to obtain a new plant with as many traits as possible from the original beneficial parent plant 2, but with only the new trait from parent plant 1. This process can take from several years to several decades.

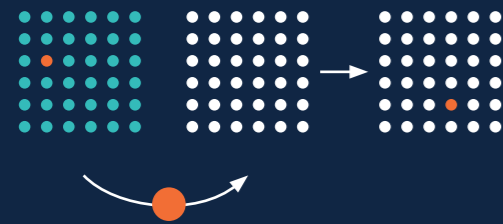
### CONVENTIONAL BREEDING

 Trait from plant 1 that is sought to be incorporated into plant 2



### BIOTECHNOLOGY

8 to 10 crosses with plant 2



Source: VIB Facts Series 'Bananas, the green gold of the South'.

Biotechnology and genetic modification (GM) of plants have the same goal as conventional breeding: create new varieties with traits that are beneficial for the farmer, industry, or consumer. The great advantage of genetic modification is that one or more desirable traits can be incorporated into a plant in a targeted way. The GM plant will, as a result, be genetically identical to the beneficial parent plant 2, except for the trait that was added. As a result, the new beneficial plant is obtained much more rapidly than with conventional breeding.

### GM potato can reduce fungicide use by 90%

Researchers from the Irish agricultural research agency (Teagasc) and Wageningen University (The Netherlands) have developed a GM potato carrying late blight resistance genes that could help farmers reduce fungicide sprays (Kessel *et al.*, 2018). Consequently, both the environmental burden of agro-chemical sprays as well as costs to farmers are reduced. The commercial susceptible potato *Désirée* received individual or multiple late blight resistance genes *Rpi-sto1*, *Rpi-vnt1.1*, and *Rpi-blb3* through the technique called **cisgenesis** (Haesaert *et al.*, 2015). This means that the resistance genes were transferred using crossable species; in this case, from the wild potato relatives, *S. stoloniferum*, *S. venturii*, and *S. bulbocastanum* respectively, to the commercial variety *Désirée*, and thus within a breeding pool of crossable species (for more information on cisgenesis versus transgenesis, see VIB Facts Series issue 'A late blight resistant potato for Europe'). Three years of field trials in the two countries have been conducted to examine the effectiveness of these genes to confer resistance to late blight disease. Alongside both susceptible and GM resistant *Désirée* potatoes, the conventionally-bred resistant potato variety **Sarpo Mira** was also included in the trials. The conventionally-bred Sarpo Mira was confirmed to be 'highly late blight resistant'. However, being conventionally-bred, it has a very limited market share due to a number of sub-optimal agronomic and commercial traits. In contrast, cisgenesis allows an acceleration of the breeding process that does not modify the basic characteristics of the potato. It transfers only the late blight resistance genes into an established commercial potato variety. Moreover, by using 'integrated pest management', so-called IPM2.0, fungicide use could be reduced by as much as

80-90 %, compared to the conventionally-grown potato (Kessel *et al.*, 2018). The IPM2.0 approach adds three extra components to the current control strategy for potato late blight: the use of resistant varieties, the monitoring of naturally occurring genetic adaptations in the pathogen and a 'do not spray unless' strategy, which dictates that a grower only needs to apply fungicides when a resistant variety is at risk of infection due to pathogen adaptation. As well as helping the environment, late blight-resistant potatoes could help farmers with limited access to inputs in developing countries where potato is an important part of the diet. Both Uganda and Bangladesh could benefit in the near future, as potato trials are ongoing in both countries. Inspired by the success of Bangladesh's first commercially released GM crop - insect resistant eggplant, the country may soon plant another GM crop, a late blight resistant potato, as potato scientists have field trials going on with a possible release in few years from now.

### Potato late blight resistance in Africa

Durable resistance to late blight disease would contribute significantly to food and economic security of African farmers. Scientists in Uganda under the National Agricultural Research Organisation (NARO) in close collaboration with the International Potato Centre CIP in Kenya conducted and analyzed field trials during three seasons (2015, 2016 and 2017) of farmer-preferred varieties of potato that have been engineered for durable late blight resistance (Ghislain *et al.*, 2018). These plants contain three resistance genes, so called stacked genes, that were isolated from wild potato relatives (*Rpi-blb1* and *Rpi-blb2* from *S. bulbocastanum*; and *Rpi-vnt1.1* from *S. venturii*) and transferred by *Agrobacterium* mediated transformation into four susceptible but popular farmer-preferred varieties in East



Africa: **Désirée, Victoria, Tigoni** and **Shangi** (Figure 4.5). GM plants were highly resistant to a variety of late blight isolates. The yield of the so-called, **3R Victoria.1** variety was estimated to be as high as 40 tons/ha. Moreover, the GM plants showed no alterations in morphology, dormancy and maturity - an approach not possible with traditional breeding. Genetic modification was chosen over conventional breeding because of its precision and its ability to keep the farmer-preferred variety qualities intact. The next phase of the project is the ongoing testing of the GM

potato variety in three different areas in Uganda to investigate whether it will thrive in different environmental conditions. When it comes to GM plants, people tend to focus more on the harm it may cause to the environment rather than on how the crop may improve the environment and be of great benefit to African farmers. Ugandan scientists are positive that GM potatoes will be commercially available in their country in 2020. GM potatoes that resist late blight have already been commercialized in the United States and Canada.



Figure 4.5: CIP staff at work in Nairobi, Kenya (source: S. Quinn, CIP)

### GM potato Innate® Generations 1 and 2

Innate® 1<sup>st</sup> and 2<sup>nd</sup> Generations potato GM varieties were developed by the J. R. Simplot Company in the US. Four Innate® 1<sup>st</sup> Generation potato varieties (**Russet Burbank, Ranger Russet, Atlantic, and Snowden**) that are non-browning, black spot bruising tolerant, and with less asparagine were deregulated successively

since 2014 and planted in the US (in 2015, 2016 and 2017) and in Canada (in 2017). Having less asparagine in potatoes was found to reduce formation of acrylamide by 58-72% when exposed to high temperatures during cooking (Zhu *et al.*, 2014). Innate® potatoes are currently branded as “White Russet™” potatoes and are available in supermarkets in both countries.

Consumers prefer these potatoes due to its reduced browning benefits: they can be prepared ahead of time because off-site peeling or dicing is possible, and they look fresher for longer.

Innate® 2<sup>nd</sup> Generation potato varieties contain four beneficial traits of relevance to potato growers, processors and consumers. They have a late blight resistance gene and an additional gene which further lowers sugars in addition to 1<sup>st</sup> generation traits. The decrease in reducing sugars further contributes to the reduction in acrylamide while enhancing cold-storage capability. The resistance to late blight trait originates from an Argentinian potato wild relative that naturally exhibits defense against the pathogen. The late blight resistance trait in these potatoes addresses the major disease of potato, protects farmers’ fields and reduces fungicide spray by up to 45%. In 2017, the three 2<sup>nd</sup> Generation potato varieties (Russet Burbank, Ranger Russet, Atlantic) were given approvals for planting in the US and for import, planting, and commercialization in Canada. In 2017, Australia also approved Innate® 1<sup>st</sup> and 2<sup>nd</sup> Generations potato for food.

The increasing acceptance and adoption of GM potatoes coincides well with the global concern for food waste. A study conducted in Canada indicated that if all fresh potatoes had Innate® 2<sup>nd</sup> Generation traits, potato waste (infield, during storage, packing, retail, and food service for fresh potatoes) could annually be reduced by 93 million kilograms; CO<sub>2</sub> emissions by 14 million kilograms; water usage by 13 billion liters; and a total of 154,000 fewer pesticide hectare-applications would be needed (ISAAA, 2017).

### The TSL Potato Partnership Project (UK-US, 2015-2019)

In 2017, Defra (UK’s Department for Environment, Food and Rural Affairs) has approved The Sainsbury Laboratory/s (TSL) application to conduct field trials of GM potato crops between 2017 and 2021. The field trials are part of TSL’s Potato Partnership Project to develop a **Maris Piper** potato variety that is late blight and nematode resistant, bruises less, and produces less acrylamide when cooked at high temperatures. The project is funded by the Biotechnology and Biological Sciences Research Council (BBSRC) with additional funding from BioPotatoes (UK) and J.R. Simplot Company (US). First introduced in 1966, the Maris Piper variety was the result of a potato breeding program based in Cambridge. The key benefit of this ‘new’ potato was its resistance to potato cyst nematodes. Today fairly common in UK supermarkets, Maris Piper is considered a good ‘all-rounder’ and it is particularly popular for making chips and crisps. In addition to late blight resistance, the Partnership has tested the ability of the *EFR* gene, a broad-spectrum immune receptor that recognizes bacteria (bacterial wilt and soft rot) to protect potatoes (Boschi *et al.*, 2017). *EFR* has already been demonstrated to confer resistance against bacterial diseases in tomato and tobacco (Lacombe *et al.*, 2010), and in monocotyledonous crop species such as wheat and rice (Schoonbeek *et al.*, 2015; Schwessinger *et al.*, 2015).

## GENOME-EDITING: A POTENTIAL GAME CHANGER FOR POTATO IMPROVEMENT

Genome or gene-editing technologies have revolutionized genetic engineering for crop improvement. They provide unprecedented precision in altering existing DNA sequences in crop genomes. The result is a plant with one or more mutations in a specific gene that is no longer distinguishable from a plant developed through conventional mutation breeding. The potential benefits of gene-editing technology are vast, and scientists are continuously improving the technology and uncovering new applications to resolve some of agriculture's greatest challenges. Genome or gene-editing involves the precise cutting and pasting of DNA by specialized proteins, adapted from existing bacterial systems in nature. These proteins come in three varieties, all known by their acronyms: ZFN (Zinc Finger Nucleases), TALEN (Transcriptional Activator-Like Effector Nucleases), and CRISPR (Clustered Regulatory Interspaced Short Palindromic Repeat).

Genome-editing presents tremendous opportunities for trait improvement of complex genomes such as that of the potato (Nadakuduti *et al.*, 2018). These new techniques allow the addition, removal, or alteration/silencing of genes at pre-selected locations in the genome with a level of precision never reached before, and without impacting optimal allele combinations in current varieties. Furthermore, the function of one or more specific genes can be disrupted, existing sequenc-

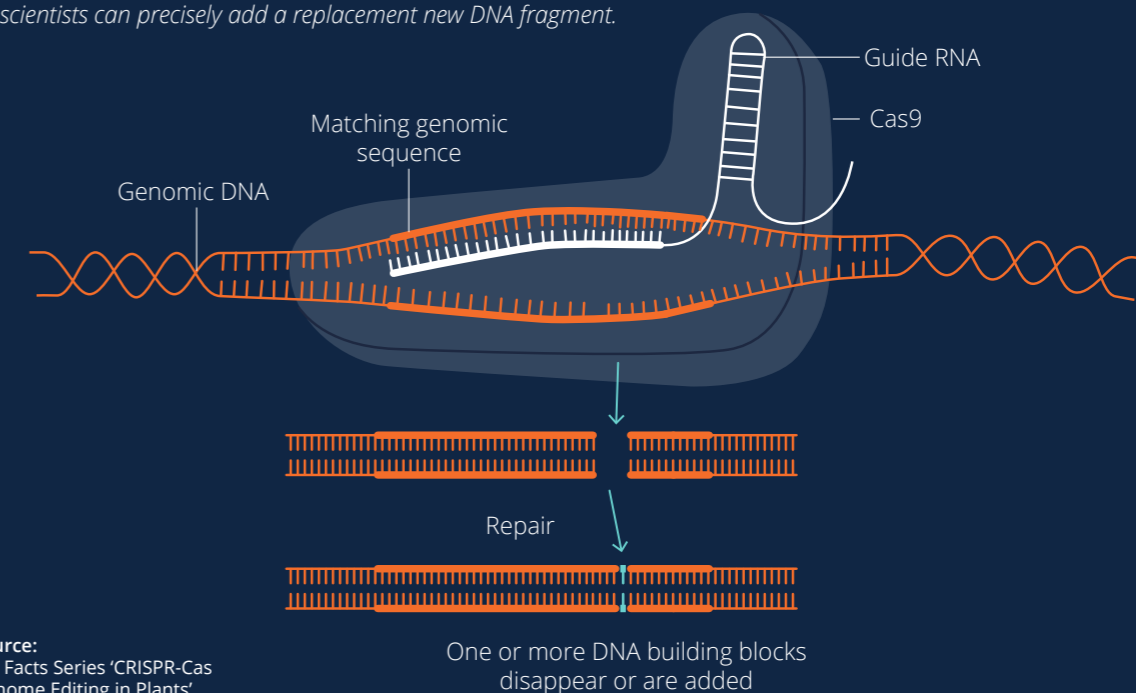
es can be edited to reproduce ancient alleles, and new beneficial alleles or new genetic material can be introduced (Rani *et al.*, 2016). Thanks to the ability to simultaneously target multiple genomic loci and to modulate the gene expression, these new breeding techniques are a more viable approach for inserting resistance genes into plants and for knocking-out whole gene families (Lowder *et al.*, 2015). The first successful demonstration of the use of TALEN in a tetraploid potato cultivar was by knocking out all four alleles of *Sterol side chain reductase 2 (StSSR2)* gene involved in **anti-nutritional sterol glycoalkaloid (SGA) synthesis** (Sawai *et al.*, 2014). Interestingly, the potato SGAs are important components of plant resistance against pests and diseases. They have been shown to accumulate in different plant organs and developmental stages (Eltayeb *et al.*, 1997). Therefore, precisely manipulating SGA biosynthesis and degradation to exploit tissue-specific expression rather than whole-plant suppression of SGA production, could produce potato cultivars with SGA content enriched in the foliage but diminished in the edible tubers. The ultimate goal would be to develop new potato cultivars with low SGA levels in tubers while still maintaining high levels in above ground tissues for crop protection. Research on factors that regulate SGA biosynthesis and catabolism as well as searches for genetic markers linked to total and specific SGA levels have only recently been pursued.

<sup>5</sup> A palindromic sequence is a DNA sequence that is the same when read from 5' to 3' on one strand and 5' to 3' on the other, complementary strand.

## HOW GENE EDITING WORKS? THE EXAMPLE OF CRISPR-CAS9

CRISPR-Cas9 is a complex of an enzyme and RNA guides that together find and edit DNA. CRISPR technology is inspired by an ancient bacterial defense system against viral invasions. In order to replicate, viruses use the cell's inner machinery. Certain bacteria evolved a way to fight this attack. They deploy DNA-cutting proteins to cut up any viral genes floating around. If the bacteria survive the attack, they incorporate these small fragments of virus DNA into their own genomes. They position each bit of viral code at regular intervals (so-called 'guide RNAs') with repetitive, palindromic sequences<sup>5</sup> in between. The next time a virus returns, the bacteria can equip Cas9 - a DNA cutting protein - with a copy of that guide RNA. Like a molecular killer, it then goes out and snips anything that matches the genetic code.

In the laboratory, scientists have adapted this ancient bacterial system. The first step is the design of a guide RNA that can recognize a particular DNA sequence in a cell, i.e. a genetic defect or an undesirable plant trait. If that gene consists of a string of the bases AATGC, scientists make a complementary strand of RNA: GCAUU. Then, this short sequence of RNA is injected, along with Cas9, into the cell to edit. The guide RNA forms a complex with Cas9; one end of the RNA forms a hairpin curve that keeps it stuck in the protein, while the other end hangs out to interact with any DNA it comes across. Once in the cell's nucleus, the CRISPR -Cas9 complex attaches every time it comes across a small sequence called PAM. This Protospacer Adjacent Motif is made of a few base pairs, and Cas9 needs PAM to grab onto the DNA. By grabbing it, the protein is able to destabilize the adjacent sequence, unzipping a bit of the double helix. That allows the guide RNA to slip in and see if it has a match. If every base pair lines up to the target sequence, the guide RNA triggers Cas9 to produce two pincer-like appendages, which cut the DNA in two. The process can stop here, simply knock out a gene and rely on cellular repair mechanisms to correct the breaks. Or, scientists can precisely add a replacement new DNA fragment.



Source:  
VIB Facts Series 'CRISPR-Cas  
Genome Editing in Plants'

Similarly, using CRISPR/Cas9 and TALENs in both diploid and tetraploid potato varieties, the mutation of the *endogenous Acetolactate synthase1 (StALS1)* gene led to **herbicide tolerant plants** (Butler *et al.*, 2016). The *ALS* gene was also targeted using a new CRISPR-Cas9 tool - Cytidine Base Editor (CBE). This new tool was used to direct cytosine to thymine base substitution, which led to chlorsulfuron-resistant plants with precise base editing efficiency of up to 71% (Veillet *et al.*, 2019). **Improvement in tuber cold storage quality** of a commercial tetraploid cultivar, Ranger Russet, was achieved by targeting *Vacuolar invertase (StVlnv)* gene using TALEN (Clasen *et al.*, 2016). The *Vlnv* enzyme breaks down sucrose to the reducing sugars glucose and fructose in cold-stored potato tubers which form dark-pigmented bitter tasting products when processed at high temperatures (Matsuura-Endo *et al.*, 2006). Tubers from *StVlnv* knock-out lines had undetectable levels of reducing sugars, low acrylamide, and made light colored

chips. They bring additional benefits to the consumers of French fries and potato chips. The first field trials of this cold storable and reduced acrylamide content potato were completed in 2015<sup>6</sup> and certified seed production is underway to facilitate a commercial launch. **A waxy potato with altered tuber starch quality** was also developed by knocking out all four alleles of *Granule-bound starch synthase (GBSS)* gene in a tetraploid potato cultivar via CRISPR/Cas9. Gene-edited lines in all four alleles had the desired high amylopectin starch (Andersson *et al.*, 2017 and 2018). Being non-transgenic, these gene-edited potatoes do not have to go through the cumbersome GM regulation and products will not be labelled in the US and few other countries. Unfortunately, Europe has again taken the stand of restricting the use of these new breeding technologies by imposing the GM regulation even on these non-transgenic crops.

## WHAT IS IN THE PIPELINE TO ENHANCE POTATO BREEDING USING GENOME-EDITING?

An alternative breeding strategy for durable and broad-spectrum resistance is based on the loss-of-function of **plant disease susceptibility genes (S-genes)** (Pavan *et al.*, 2009). By using the RNAi (RNA interference)<sup>7</sup> technique, silencing of six susceptibility genes (S-genes) resulted in late blight resistance in potato (Sun *et al.*, 2016). However, RNAi does not always result in a complete gene knockout. Genome-editing could potentially be used to simultaneously knockout susceptibility genes. An extracellular surface protein called receptor-like **protein ELR (elicitor response)** from the wild potato species, *S. microdonum*, has been reported to recognize an elicitor that is highly conserved in *Phytophthora* species offering a broad-spectrum durable resistance to this pathogen (Du *et al.*, 2015). Introducing both extracellular and intracellular receptors in potato cultivars by genome-editing could aid in getting durable broad-spectrum resistance for late blight. **Reduced bruising** is another trait that could be improved using genome-editing. In this case, RNAi silencing of the Polyphenol oxidase (PPO) gene was shown to reduce the browning in tubers due to mechanical damage (Arican and Gozukirmizi, 2003). Finally, breeders are working **toward converting** asexually propagated **tetraploid** potato into a seed propagated **diploid crop** (Jansky *et al.*, 2016). Moving to diploid potatoes would allow to take full advantage of the modern genetics and genomics tools available for crop improvement. Genome-editing combined with re-domestication of potato into an inbred line-based diploid crop propagated by seed would represent a promising alternative to traditional clonal propagation of tetraploid potato.

## HYBRID TRUE SEED POTATO

Hybrid breeding revolutionized maize production in the 20<sup>th</sup> century by enabling breeders to create high-yielding varieties that have what is known as **'hybrid vigor'**. A prerequisite for hybrid potato breeding is the development of homozygous lines, preferably at the diploid level. Homozygous lines (or inbred potato lines) are created through self-pollination: the pollen of one plant is applied to its own pistil. As a result, traits are fixed in homogenous genetic material, also called the homozygous form. However, attempts to develop homozygous diploid potato lines were blocked by self-incompatibility in diploid germplasm (prohibiting selfing, which is needed to generate and maintain homozygous lines) and severe inbreeding depression<sup>8</sup>. Solynta, a Dutch startup company founded in 2006 (<https://solynta.com/>), has lifted these barriers by introgressing the *Sli*-gene from the wild species *S. chacoense* into diploid potato, and by dedicated breeding, consisting of many generations of crossings, selections and selfings (Lindhout *et al.*, 2011). The result is a self-compatible diploid potato. Moving to diploid inbred potatoes enabled to create healthy hybrids from true-breeding parent lines (de Vries *et al.*, 2016). Diploid inbred potatoes and sexual seed propagation are at the heart of Solynta's strategy. In this way, it is easier for breeders to combine complex traits in one variety, and for farmers to plant true-seeds instead of bulky chunks of tuber. Hybrid breeding could cut the time required to create new varieties by more than half. Moreover, basic research could benefit from this technique since having diploid potatoes will drastically facilitate the understanding of the potato genome (Figure 4.6).



Figure 4.6: Potato varieties at the Bvumbwe Research Station in Malawi (source: H. Rutherford, CIP)

Moreover, an additional important benefit of hybrid true potato seeds is logistical: planting 10 hectares, for instance, takes just 200 grams of easily transported true-seeds, compared with 25 tons of perishable seed-tubers. Traditionally, when a new variety is selected, seed-tuber potatoes are vegetatively multiplied by specialized farmers as the starting material for the next season of commercial potato production. It takes 5 to 7 years of clonal propagation to get sufficient seed-tuber potatoes to fulfill the market need of a successful cultivar. Another problem is that during this clonal (asexual) multiplication, seed-tuber potatoes are continuously at risk of contamination with pathogens and insects during each multiplication round. True potato seeds are easier to ship and to store, and they are non-perishable. Therefore, waste in the supply chain, transport costs and carbon emissions will be considerably reduced. By providing excellent and healthy starting material, hybrid potato seeds can produce significantly higher yields (thanks to the hybrid vigor) than the seed-tubers.

<sup>6</sup><https://www.potatopro.com/news/2015/calixt-completes-first-field-trials-its-cold-storable-potatoes>

<sup>7</sup>RNA interference is based on sequence-specific RNA degradation that follows the formation of double-stranded RNA (dsRNA) homologous in sequence to the targeted gene.

<sup>8</sup>Inbreeding depression is defined as the reduction or loss in vigor and fertility as a result of inbreeding

In 2015, the first parental lines were crossed in such a way that a hybrid potato was created. In 2016, Solynta conducted its first field trials of hybrid potato seedlings in the Democratic Republic of the Congo and in 17 locations across Europe (de Vries *et al.*, 2016). The plants performed well, yielding large tubers over a typical growing season. The company has not yet commercialized a variety. Within a few years, it hopes to create customized potatoes for European and African markets. Other firms, including large seed companies, are also working to develop hybrid potatoes. HZPC in Joure, the Netherlands, has begun field trials in Tanzania and in several countries in Asia.

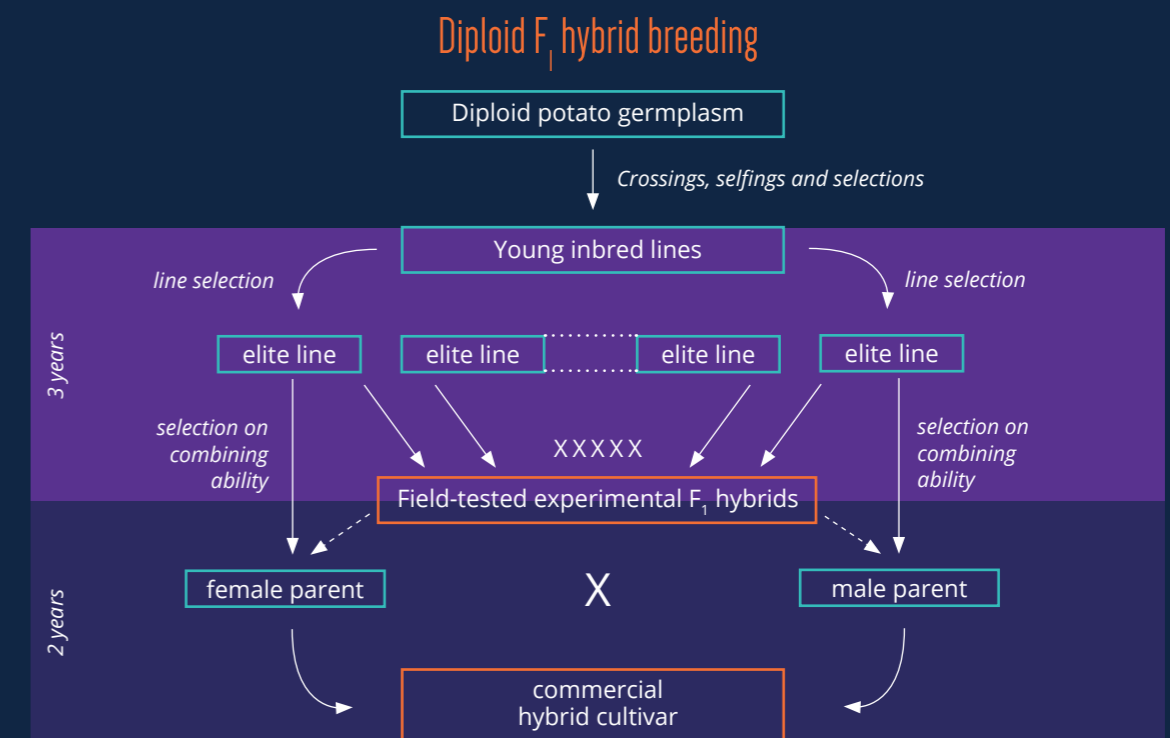
However, hybrid potato seeds aren't a panacea. Young plants grow more quickly and vigorously from tubers than from seeds, putting seeds at a disadvantage in some climates. And depending on how complete the inbreeding is, hybrid potatoes could have less uniformly shaped tubers than those of traditional plants, a problem for farmers who supply food-processing companies. Such complexities have prompted the Dutch government to commission a study of the potential socioeconomic impacts of hybrid potatoes, which will be published soon.



Source: S. Quinn, CIP

## HOW DOES HYBRID POTATO BREEDING WORK?

Solynta breeding technology works by sexual propagation of diploid homozygous lines. New traits can be introduced from any germplasm as long as it is crossable with diploid elite lines. Crossing two elite parents (male and female) generates  $F_1$  hybrid offspring which shares the best features of both parents. The performance of the parent is gradually improved by crossing and selection, and experimental  $F_1$  hybrids are field-tested to evaluate their performance and commercialize the best products. In two series of backcrossing followed by two generations of selfing, and by using diagnostic molecular markers for the trait of interest and random markers for the recurrent parent genome, an existing parent line can be enriched with a trait in 2 to 3 years. Both parents can be used for backcrossing and this process can be repeated. In this way, a series of derivatives of an existing  $F_1$  hybrid cultivar can be generated that all have the same basic genetic composition except for the introduced traits. This process can easily be upgraded to a high-throughput seed production system. As one plant can produce over 10,000 seeds and the parent lines are propagated by selfings, any quantity of  $F_1$  hybrid seeds can be produced in one season to fulfill the market needs.



# 5 Conclusion

Potato increasingly contributes to world food and economic security and has a critical role to play in developing nations facing hunger and rural poverty, including Africa. Potatoes supplement or replace cereals-based diets where rice, wheat, or maize availability has lessened, or price has become unaffordable. The harvested area and production of potato in sub-Saharan Africa has greatly increased over the last decades. However, yields are still low due to harsh climates, large numbers of pests and diseases, a lack of affordable fertilizers and pesticides, as well as due to various agronomic, institutional and marketing problems. Improvement of the potato production system, especially in sub-Saharan Africa, where potato is an important cash and food crop, can be a pathway out of poverty with a high potential to raise the livelihoods of small-scale farmers and their families.



Source: S. Quinn, CIP

Creating a new potato variety by conventional breeding is slow and difficult, but there are new approaches, including hybrid diploid breeding, genetic modification and gene-editing techniques. Potato breeders are particularly excited about hybrid diploid potato breeding, a method that could cut the time required to create new varieties by more than half, make it easier for breeders to combine traits in one variety, and allow farmers to plant seeds instead of bulky chunks of tuber. In addition, breeders will soon have more genetic diversity available to improve cultivated potatoes. Through breeding, there exists enormous capacity to advance the potato towards an increasingly healthier food item, with stable or improved yields under more sustainable growing conditions (primarily lower fuel and fertilizer inputs), environmental stresses, and disease and pest pressures. In countries where the daily per capita availability of nutritious food is below recommended dietary intake, diet diversification and improved preparation and processing to increase micronutrient bioavailability is needed. Where food security is not an overwhelming issue, consumer demand focuses more on convenience foods, with improved nutritional and health properties, or better flavor.



Source: H. Rutherford, CIP

# References

- 1 Akiyama R, Nakayasu M, Umemoto N, Muranaka T, Mizutani M (2017). Molecular breeding of SGA-free potatoes accumulating pharmaceutically useful saponins. *Regulation of Plant Growth & Development* 52 (2):92-98.
- 2 Andersson M, Turesson H, Nicolai A, Fält A-S, Samuelsson M, Hofvander P (2017). Efficient targeted multiallelic mutagenesis in tetraploid potato (*Solanum tuberosum*) by transient CRISPR-Cas9 expression in protoplasts. *Plant Cell Rep.* 36 (1):117-128.
- 3 Andersson M, Turesson H, Olsson N, Fält A-S, Ohlsson P, Gonzalez MN, Samuelsson M, Hofvander P (2018). Genome editing in potato via CRISPR-Cas9 ribonucleoprotein delivery. *Physiol. Plantarum* 164 (4):378-384.
- 4 Arican E, Gozukirmizi N (2003). Reduced polyphenol oxidase activity in transgenic potato plants associated with reduced wound-inducible browning phenotypes. *Biotechnol. & Biotechnological Equip.* 17 (2):15-21.
- 5 Arndt GC, Rueda JL, Kidane-Mariam HM, Peloquin SJ (1990). Pollen fertility in relation to open pollinated true seed production in potatoes. *Am. Potato J.* 67: 499-505.
- 6 Augustin J (1975). Variations in the nutritional composition of fresh potatoes. *J. Food Sci.* 40:1295-1299.
- 7 Bamberg J, del Rio A (2005). Conservation of potato genetic resources. In: *Genetic improvement of Solanaceous crops Vol. 1: Potato*. Chap. 1, 1-38. Razdan, J.K. and Mattoo, A.K., Eds. Science Pub. Inc.
- 8 Bekele K, Eshetu B (2008). Potato disease management. In *Root and tuber crops: The untapped resources*, ed. W. Gebremedhin, G. Endale, and B. Lemaga, 79-96. Addis Abeba: Ethiopian Institute of Agricultural Research.
- 9 Bethke PC, Nassar AMK, Kubow S, Leclerc YN, Li X-Q, Haroon M, Molen T, Bamberg J, Martin M, Donnelly DJ (2014). History and origin of Russet Burbank (Netted Gem) a sport of Burbank. *Am. J. Potato Res.* 91 (6):594-609.
- 10 Boschi F, Schwartzman C, Murchio S, Ferreira V, Siri MI, Galván GA, Smoker M, Stransfeld L, Zipfel C, Vilaró FL, Dalla-Rizza M (2017). Enhanced bacterial wilt resistance in potato through expression of Arabidopsis EFR and introgression of quantitative resistance from *Solanum commersonii*. *Front. Plant Sci.* 8:1642-1642.
- 11 Bradshaw JE, Bryan GJ, Ramsay G (2006). Genetic resources (including wild and cultivated *Solanum* species) and progress in their utilisation in potato breeding. *Potato Res.* 49: 49-65.
- 12 Brown CR (1993). Outcrossing rate in cultivated autotetraploid potato. *Am. Potato J.* 70: 725-734.
- 13 Brown CR (2008). Breeding for phytonutrient enhancement of potato. *Am. J. Potato Res.* 85:298-307.
- 14 Buckenhüskes H J (2005). Nutritionally relevant aspects of potatoes and potato constituents. In: *Potato in Progress: Science Meets Practice*. Ch. 1: 17-45.
- 15 Butler NM, Baltés NJ, Voytas DF, Douches DS (2016). Geminivirus-mediated genome editing in potato (*Solanum tuberosum* L.) using sequence-specific nucleases. *Front. Plant Sci.* 7 (1045).
- 16 Clasen BM, Stoddard TJ, Luo S, Demorest ZL, Li J, Cedrone F, Tibebu R, Davison S, Ray EE, Daulhac A, Coffman A, Yabandith A, Retterath A, Haun W, Baltés NJ, Mathis L, Voytas DF, Zhang F (2016). Improving cold storage and processing traits in potato through targeted gene knockout. *Plant Biotechnol. J.* 14 (1):169-176.
- 17 Denner FDN, Venter SL, Niederwieser JG (2012). Guide to potato production in South Africa. Agricultural Research Council - Vegetable and Ornamental Plant Institute, Pretoria.
- 18 De Vries M, ter Maat M, Lindhout P (2016). The potential of hybrid potato for East-Africa. *Open Agricult.* 1: 151-156.
- 19 Du J, Verzaux E, Chaparro-García A, Bijsterbosch G, Keizer LCP, Zhou J, Liebrand TWH, Xie C, Govers F, Robatzek S, van der Vossen EAG, Jacobsen E, Visser RGF, Kamoun S, Vleeshouwers VGAA (2015). Elicitin recognition confers enhanced resistance to *Phytophthora infestans* in potato. *Nature Plants* 1:15034.
- 20 Ducreux LJM, Morris WL, Hedley PE, Shepherd T, Davies HV, Millam S, Taylor MA (2005). Metabolic engineering of high-carotenoid potato tubers containing enhanced levels of  $\beta$ -carotene and lutein. *J. Exp. Bot.* 56:81-89.
- 21 Eltayeb EA, Al-Ansari AS, Roddick JG (1997). Changes in the steroidal alkaloid solasodine during development of *Solanum nigrum* and *Solanum incanum*. *Phytochem.* 46 (3):489-494.
- 22 FAO (2008). Why potato? International Year of the Potato 2008. <http://www.fao.org/potato-2008/en/aboutiyp/index.html>.
- 23 FAO (2017). The future of food and agriculture – Trends and challenges. Rome.
- 24 FAOSTAT (2019). Available at <http://www.fao.org/faostat/en/#data>.
- 25 Fauconnier ML, Delaplace P (2004). Valorisation industrielle de la pomme. *Troupeaux et Cultures des Tropiques.* 51 – 56.
- 26 Fourie H, Zijlstra C, McDonald AH (2001). Identification of root-knot nematode species occurring in South Africa using the SCAR-PCR technique. *Nematologica* 3: 675-680.
- 27 Gildemacher P, Demo P, Kinyae P, Nyongesa M, Mundia P (2007). Selecting the best plants to improve seed potato. *LEISA Magazine* 23(2): 10-11.
- 28 Ghislain M, Byarugaba A, Magembe E, Njoroge A, Rivera C, Roman ML, Tovar JC, Gamboa S, Forbes G, Kreuze J, Barekye A, Kiggundu A (2018). Stacking three late blight resistance genes from wild species directly into African highland potato varieties confers complete field resistance to local blight races. *Plant Biotech J.* 1-11.
- 29 Haesaert G, Vossen JH, Custers R, De Loose M, Haverkort A, Heremans B, Hutten R, Kessel G, Landschoot S, Van Droogenbroeck B, Visser RGF, Gheysen G (2015). Transformation of the potato variety Désirée with single or multiple resistance genes increases resistance to late blight under field conditions. *Crop Protect.* 77:163-175.
- 30 Han EH, Goo YM, Lee MK, Lee SW (2015). An efficient transformation method for a potato (*Solanum tuberosum* L. var. Atlantic). *J Plant Biotechnol.* 42: 77-82.
- 31 Hirpa A, Meuwissen MPM, Tesfaye A, Lommen WJM, Oude Lansink A, Tsegaye A, Struik PC (2010). Analysis of seed potato systems in Ethiopia. *Am. J. of Potato Res.* 87 (6):537-552.
- 32 International Potato Center (CIP) (2011). Roadmap for investment in the seed potato value chain in eastern Africa. Lima, Peru, 27 pp.
- 33 International Potato Center (CIP) (2018). CIP Annual Report 2017. Harnessing potato and sweetpotato's power for food security, nutrition and climate resilience. Lima, Peru. International Potato Center. 47 p.

- 34 ISAAA (2017). Global status of commercialized biotech/GM crops in 2017: Biotech crop adoption surges as economic benefits accumulate in 22 years. ISAAA Brief No. 53. ISAAA: Ithaca, NY.
- 35 Jansky SH, Charkowski AO, Douches DS, Gusmini G *et al.* (2016). Reinventing potato as a diploid inbred line-based crop. *Crop sci.* 56 (4): 1412-1422.
- 36 Kessel GJT, Mullins E, Evenhuis A, Stellingwerf J, Cortes VO, Phelan S, van den Bosch T, Förch MG, Goedhart P, van der Voet H, Lotz LAP (2018). Development and validation of IPM strategies for the cultivation of cisgenically modified late blight resistant potato. *Eur. J. Agron.* 96:146-155.
- 37 Lacombe S, Rougon-Cardoso A, Sherwood E, Peeters N, Dahlbeck D, van Esse HP, Smoker M, Rallapalli G, Thomma BPHJ, Staskawicz B, Jones JDG, Zipfel C (2010). Interfamily transfer of a plant pattern-recognition receptor confers broad-spectrum bacterial resistance. *Nat. Biotechnol.* 28:365.
- 38 Lindhout P, Meijer D, Schotte T, Hutten RCB, Visser RGF, van Eck HJ (2011). Towards F1 hybrid seed potato breeding. *Potato Res.* 54 (4):301-312.
- 39 Lineback D, Pariza MW, Coughlin J, Davies C, Kettlitz B, Robin LP, Schmidt D, Scimeca J, Stadler R (2006). Acrylamide in food. Issue Paper No. 32, 16 pp. Council for Agricultural Science and Technology, Ames, IA.
- 40 Louderback LA, Pavlik BM (2017). Starch granule evidence for the earliest potato use in North America. *Proc. Natl. Acad. Sci.* 114 (29):7606-7610.
- 41 Love SL, Pavek JJ (2008). Positioning the potato as a primary food source of vitamin C. *Am. J. Potato Res.*, 85:277-285.
- 42 Lowder LG, Zhang D, Baltus NJ, Paul JW, Tang X, Zheng X, Voytas DF, Hsieh T-F., Zhang Y, Qi Y (2015). A CRISPR/Cas9 toolbox for multiplexed plant genome editing and transcriptional regulation. *Plant Physiol.* 169(10): 971-985.
- 43 Matsuura-Endo C, Ohara-Takada A, Chuda Y, Ono H, Yada H, Yoshida M, Kobayashi A, Tsuda S, Takigawa S, Noda T, Yamauchi H, Mori M (2006). Effects of storage temperature on the contents of sugars and free amino acids in tubers from different potato cultivars and acrylamide in chips. *Biosci. Biotechnol. & Biochem.* 70 (5):1173-1180.
- 44 Milner SE, Brunton NP, Jones PW, O' Brien NM, Collins SG, Maguire AR (2011). Bioactivities of glycoalkaloids and their aglycones from *Solanum* species. *J. Agric. & Food Chem.* 59 (8):3454-3484.
- 45 Nadakuduti SS, Buell CR, Voytas DF, Starker CG, Douches DS (2018). Genome editing for crop improvement – Applications in clonally propagated polyploids with a focus on potato (*Solanum tuberosum* L.). *Frontiers in Plant Science* 9 (1607).
- 46 Nteranya S (2015). Root and tuber crops (cassava, yam, potato and sweet potato). Background paper: An action plan for African agricultural transformation. United Nations Commission for Africa. Feeding Africa held at Abdou Diouf International Conference Centre, Dahar Senegal.
- 47 Okonya JS, Kroschel J (2015). A cross-sectional study of pesticide use and knowledge of smallholder potato farmers in Uganda. *BioMed Res. Intern.* 2015:9.
- 48 Onkendi EM, Kariuki GM, Marais M, Moleleki LN (2014). The threat of root-knot nematodes (*Meloidogyne* spp.) in Africa: a review. *Plant Pathol.* 63 (4):727-737.
- 49 Pavan S, Jacobsen E, Visser RGF, Bai Y (2009). Loss of susceptibility as a novel breeding strategy for durable and broad-spectrum resistance. *Mol. Breed.* 25 (1):1.
- 50 Petersson EV, Arif U, Schulzova V, Krtková V, Hajšlová J, Meijer J, Andersson HC, Jonsson L, Sitbon F (2013). Glycoalkaloid and calystegine levels in table potato cultivars subjected to wounding, light, and heat treatments. *J. Agric. Food Chem.* 61:5893-5902.
- 51 Priestley H (2006). How to think like consumers and win! In: Potato developments in a changing Europe. Chap. 20 pp. 189-198. Haase, N.U. and Haverkort, A.J. Eds. Wageningen Academic Pub.
- 52 Radcliffe EB (1982). Insect pests of potato. *Annu. Rev. Entomol.* 27 (1):173-204.
- 53 Rani R, Yadav P, Barbadikar KM, Baliyan N, Malhotra EV, Singh BK, Kumar A, Singh D (2016). CRISPR/Cas9: a promising way to exploit genetic variation in plants. *Biotechnol. Letters* 38(12): 1991-2006.
- 54 Sanford JC, Hanneman RE (1981). The use of bees for the purpose of inter-mating in potato. *Am. Potato J.* 58: 481-485.
- 55 Sawai S, Ohyama K, Yasumoto S, Seki H, Sakuma T, Yamamoto T, Takebayashi Y, Kojima M, Sakakibara H, Aoki T, Muranaka T, Saito K, Umemoto N (2014). Sterol side chain reductase 2 is a key enzyme in the biosynthesis of cholesterol, the common precursor of toxic steroidal glycoalkaloids in potato. *Plant Cell* 26 (9):3763-3774.
- 56 Schoonbeek H-j, Wang H-H, Stefanato FL, Craze M, Bowden S, Wallington E, Zipfel C, Ridout CJ (2015). Arabidopsis EF-Tu receptor enhances bacterial disease resistance in transgenic wheat. *New Phytol.* 206 (2):606-613.
- 57 Schulte-Geldermann E (2017.) Potato research in Africa to improve farmers' livelihoods: Priorities in crop improvement, seed system, crop management, nutritional value, policies and marketing. *Potato Res.* 60 (3):287-289.
- 58 Schulte-Geldermann E (2013). Tackling low potato yields in Eastern Africa: an overview of constraints and potential strategies. In: Woldegiorgis, G.; Schulz, S.; Berihun, B. (eds.). Seed potato tuber production and dissemination, experiences, challenges and prospects: Proceedings. National Workshop on Seed Potato Tuber Production and Dissemination. Bahir Dar (Ethiopia). 12-14 Mar 2012. (Ethiopia). Ethiopian Institute of Agricultural Research (EIAR); Amhara Regional Agricultural Research Institute (ARARI); International Potato Center ISBN 978-99944-53-87-x. pp. 72-80.
- 59 Schwessinger B, Bahar O, Thomas N, Holton N, Nekrasov V, Ruan D, Canlas PE, Daudi A, Petzold CJ, Singan VR, Kuo R, Chovatia M, Daum C, Heazlewood JL, Zipfel C, Ronald PC (2015). Transgenic expression of the dicotyledonous pattern recognition receptor EFR in rice leads to ligand-dependent activation of defense responses. *PLOS Pathogens* 11 (4): e1004872.
- 60 Shahin EA, Simpson RB (1986). Gene transfer system for potato. *Hort. Sci.* 21: 1199-1201.
- 61 Simmonds NW (1995). Potatoes. In: Simmonds S and Smartt J (eds.) Evolution of crop plants, 2<sup>nd</sup> edn. (Longman Scientific and Technical: Harlow, UK). pp. 466-471.
- 62 Sree Ramulu K, Dijkhuis P, Roest S (1983). Phenotypic variation and ploidy level of plants regenerated from protoplasts of tetraploid potato (*Solanum tuberosum* L. cv. 'Bintje'). *Theor. Appl. Genet.* 65 (4):329-338.

- 63 Stokstad E (2019). The new potato. *Science* 363: 574-577.
- 64 Sun K, Wolters A-MA, Vossen JH, Rouwet ME, Loonen AEHM, Jacobsen E, Visser RGF, Bai Y (2016). Silencing of six susceptibility genes results in potato late blight resistance. *Transgenic Res.* 25 (5):731-742.
- 65 Van der Merwe JJ, Coutinho TA, Korsten L, van der Waals JE (2010). *Pectobacterium carotovorum* subsp. *brasiliensis* causing blackleg on potatoes in South Africa. *European Journal of Plant Pathol.* 126 (2):175-185.
- 66 Van der Waals JE, Pitsi BE, Marais C, Wairuri CK, (2011). First report of *Alternaria alternata* causing leaf blight of potatoes in South Africa. *Plant Dis.* 95: 363.
- 67 Van der Waals JE, Steyn JM, Franke AC, Haverkort AJ (2016). Grower perceptions of biotic and abiotic risks of potato production in South Africa. *Crop Prot.* 84:44-55.
- 68 Van Eck J, Conlin B, Garvin DF, Mason H, Navarre DA, Brown CR (2007). Enhancing beta-carotene content in potato by RNAi-mediated silencing of the beta-carotene hydroxylase gene. *Am. J. Potato Res.*, 84:331–342.
- 69 Veillet F, Perrot L, Chauvin L, Kermarrec M-P, Guyon-Debast A, Chauvin J-E, Nogué F, Mazier M (2019). Transgene-free genome editing in tomato and potato plants using *Agrobacterium*-mediated delivery of a CRISPR/Cas9 cytidine base editor. *Int. J. Mol. Sci.* 20 (2):402.
- 70 VIB Facts Series (2019). CRISPR-Cas Genome Editing in Plants.
- 71 VIB Facts Series (2016). From plant to crop: the past, present and future of plant breeding.
- 72 VIB Facts Series (2016). Bananas, the Green Gold of the South.
- 73 VIB Facts Series (2014). A late blight resistant potato for Europe.
- 74 White PJ, Broadley MR (2005). Biofortifying crops with essential mineral elements. *Trends Plant Sci.* 10:586–593.
- 75 Woolfe JA (1987). *The potato in the human diet.* Cambridge University Press. p. 143–149.
- 76 Zhu X, Richael C, Chamberlain P, Busse JS, Bussan AJ, *et al.* (2014). Vacuolar invertase gene silencing in potato (*Solanum tuberosum* L.) improves processing quality by decreasing the frequency of sugar-end defects. *PLoS ONE* 9(4): e93381.



**IPBO** (International Plant Biotechnology Outreach), which forms part of the VIB, was set up in 2000 by Prof. Em. Marc Van Montagu and Ghent University. IPBO's mission is to promote knowledge and technology transfer in the area of plant biotechnology to developing countries, with a focus on a green and sustainable agriculture and agro-industry. To accomplish this mission, IPBO focuses on communication, training in plant breeding, green biotechnology and related biosafety, and fosters networking and project development to implement cooperation between developing countries and Flanders. More information: [www.ipbo.vib-ugent.be](http://www.ipbo.vib-ugent.be)

Basic research in life sciences is **VIB's** raison d'être. VIB is an independent research institute where some 1,500 top scientists from Belgium and abroad conduct pioneering basic research. As such, they are pushing the boundaries of what we know about molecular mechanisms and how they rule living organisms such as human beings, animals, plants and microorganisms. Based on a close partnership with five Flemish universities – Ghent University, KU Leuven, University of Antwerp, Vrije Universiteit Brussel and Hasselt University – and supported by a solid funding program, VIB unites the expertise of all its collaborators and research groups in a single institute. The VIB-UGent Center for Plant Systems Biology wants to gain insight into how plants grow and respond to the environment. Scientists study how leaves and roots are formed, which micro-organisms live on and around the plant and which substances the plant makes. This knowledge can lead to sustainable innovations in agriculture and food. More information: [www.vib.be](http://www.vib.be)

**Ghent University** After more than twenty years of uninterrupted growth, Ghent University is now one of the most important institutions of higher education and research in the Low Countries. Ghent University yearly attracts over 41,000 students, with a foreign student population of over 2,200 EU and non-EU citizens. Ghent University offers a broad range of study programs in all academic and scientific fields. With a view to cooperation in research and community service, numerous research groups, centers and institutes have been founded over the years. More information: [www.UGent.be](http://www.UGent.be).

**The International Potato Center** (known by its Spanish acronym CIP) is a research-for-development organization with a focus on potato, sweetpotato, and Andean roots and tubers. CIP is dedicated to delivering sustainable science-based solutions to the pressing world issues of hunger, poverty, gender equity, climate change and the preservation of our Earth's fragile biodiversity and natural resources. CIP is truly a global center, with headquarters in Lima, Peru and offices in 30 developing countries across Asia, Africa, and Latin America. Working closely with its partners, CIP seeks to achieve food security, increased well-being, and gender equity for poor people in the developing world. More information: [www.cipotato.org](http://www.cipotato.org)

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