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# Chapter 2. Hybrid potato breeding and production systems

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## Abstract

In this chapter, we describe the technical aspects of hybrid potato breeding, the implications for cultural practices, cropping systems, product development and global food security. Diploid hybrid breeding allows the breeders to focus on selecting the right combination of parents instead of selecting the right clone. Combining the most suitable parents results in homogeneous hybrids that can be tested in different environments. It allows to stack resistance genes, stack complex traits, create uniform offspring, makes breeding results more predictable, the production of a new cultivar much faster and the possibilities for innovative products and value creation much more abundant. However, diploid breeding followed by a seed system based on true potato seed may cause disruptive change, for breeders, regulators and policy makers, seed growers, ware growers, traders, and consumers. The biggest bottlenecks are in the agronomy of growing a crop from very tiny true potato seeds (TPS). Options include direct sowing, producing transplants or producing seedling tubers. A paradigm shift in the production system must create the conditions for a successful hybrid TPS value chain. Many companies and research institutes are now developing hybrid breeding programmes in potato, mostly based on diploid breeding. The potential is huge, including potato production in tropical lowlands on the basis of heat and drought tolerant hybrids, resistance against bacterial diseases and viruses, and high-quality, healthy and innovative potato products, thus contributing to a sustainable, food-secure, productive potato production value chain.

**Keywords:** cropping system, production hybrid seeds, logistics

## 2.1 Introduction

Hybrid breeding is an advanced breeding system, whereby inbred lines are generated through repeated selfings and crossed to generate hybrids. The inbred lines allow breeders to better control genetics and this results in more efficient breeding. Many food crops have been adapted to hybrid breeding (Ter Steeg *et al.*, 2022). Potato has been recalcitrant as the tetraploid nature of commercial potato cultivars and inbreeding depression have hampered the development of pure inbred lines. Moreover, potato is traditionally propagated via seed tubers, while the product of hybrid breeding is true seed. This different type of starting material further complicates the application of


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hybrid cultivars in potato tuber production, although it strongly increases the multiplication rate, thereby reducing the number of years between making the cross and producing enough seed for commercial use. The limitations caused by tetrasomic inheritance and inbreeding depression have been overcome and at present, there are hybrid potato breeding programmes in the Netherlands, USA and China (Jansky *et al.*, 2016; Lindhout *et al.*, 2011, 2018; Zhang *et al.*, 2021).

In this chapter, the technical aspects of hybrid potato breeding and the implications for cultivation technologies and product development are briefly outlined. Attention is also paid to additional changes in the potato production systems, when implementing hybrid potato cultivars. Finally the potential impact on the global food security is addressed.

## 2.2 Traditional potato breeding

Traditional potato breeding starts with making crosses between tetraploid cultivars that have four sets of chromosomes (Figure 2.1A). As both parents have a wide genetic variation of genes per sister chromosome (are 'heterozygous'), the offspring will segregate into a very wide collection of genetic recombinations. So, all individuals of the progeny are genetically different. The art of breeding is to identify the best genotype in this progeny, as a potentially new cultivar; such a new genotype is subsequently multiplied clonally.

In a typical breeding programme, some ten to hundred thousands seeds are generated, sown and seedlings are produced to produce first-year tubers, designated 'F1 clones'. These clones are grown in the field to evaluate the plants and tubers in the first year. This is repeated five to ten years, while selections are done in each generation to remove clones with unacceptable quality, low yields or high susceptibilities for diseases. Advanced technologies like marker assisted selection can also be applied, mainly to select for the presence of disease resistance genes. The number of selected clones is gradually diminished to only a few and the numbers of plants per clone that are tested in the field, gradually increase. Finally, the most advanced clones are tested at several locations in repeated field trials, with larger plot sizes (Stockem *et al.*, 2022). When such selected clones have shown added value compared with existing cultivars in the market, they can be considered as a potentially new cultivar that are going to be commercialised. Such a clone is then registered at national seed lists (Chapter 5) and tubers are propagated in the field for five to ten generations to produce sufficient numbers of seed tubers to serve the farmers as starting material for the production of ware potatoes. The reproduction factor of potato tubers is about ten. So, to produce one million seed tubers (enough to plant 20 ha), starting from one single seed tuber, will take six years.

The ware potato tubers are produced as a fresh product to consumers' markets or as a bulk product to processing plants, where they are processed into fries, chips, or other products. Usually, specialised companies produce the seed tubers. They are experts in avoiding contaminations with seed-borne viruses, bacteria, fungi and other pathogens, as well as seed-borne pests, such as nematodes, to maintain a high quality level of the seed tubers. However, it is unavoidable that some contamination occurs. Many countries have a severe governance system in place that monitors seed tuber quality and provides certification based on strict criteria, on continuous

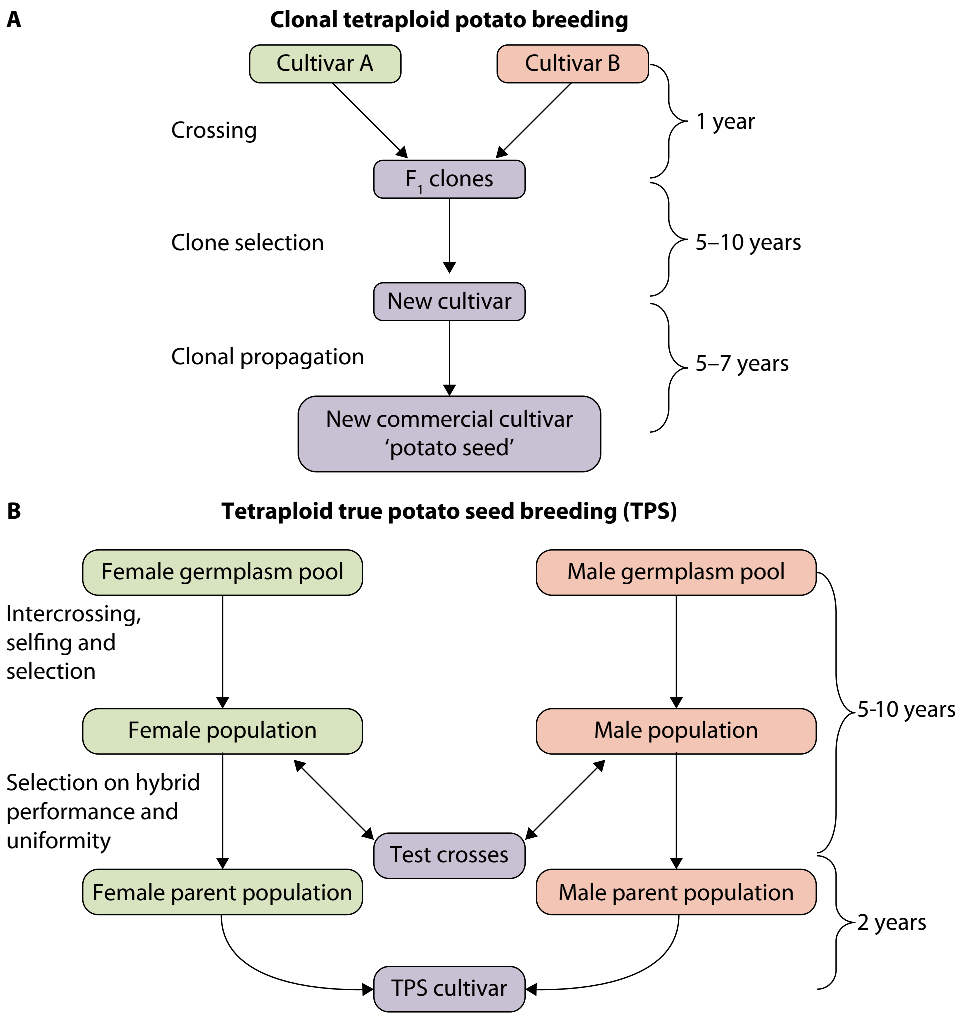


**Figure 2.1. Schematic representation of two contrasting potato breeding systems. (A) traditional potato breeding; (B) hybrid potato breeding.**

degradation to a lower level of certification and on a flush-out scheme. After several generations of seed tuber multiplication, the quality may drop below the level that is required for the lowest grade of certification, and the multiplication of this badge will stop (it will be flushed out). Usually, each year breeding companies start a fresh multiplication round for each cultivar with *in vitro* plantlets that are completely free of any pathogen or pest. Breeding companies may produce large quantities of mini-tubers per plant in the greenhouse, to give a boost to the production of clean seed tubers, that are subsequently multiplied as described above.

These formal systems are in place in the higher income economies. Farmers in low- and middle-income economies in Asia, Africa and South America usually produce their own seed tubers,



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which is considered as an informal system without external quality control or certification. The multiplications of seed tubers may continue for ten to twenty generations or more (Africa: Gildemacher *et al.*, 2009; South America: Navarrete *et al.*, 2022). As these conditions are not optimal, the seed tubers will rapidly accumulate diseases (so-called seed degeneration), which reduces the yield of the crop produced from these seed tubers. The yields in the informal systems are usually about ten tons per ha, about five times lower than the productions in formal systems. This yield gap is caused by low quality seed tubers and low-tech cultivation systems. Globally, 90-95% of seed tubers are produced in the informal system (Thomas-Sharma *et al.*, 2016).

## 2.3 Hybrid true potato seed: hybrid potato breeding, principle and practice

Hybrid potato breeding starts with the generation of inbred lines from the breeders' germplasm. After several rounds of inbreeding all genes on sister chromosomes are identical. Such a parent line is considered 'homozygous' and the genes are 'fixed': the parent line can only pass a unique and fixed composition of genes to the progeny. When both parents are fixed, the genetic make-up of their progeny can reliably be predicted from the characteristics of the parent inbred lines. Each individual plant has an identical chromosome set of both parents and is heterozygous but all progeny plants are genetically identical, which results in a uniform phenotype (Figure 2.1B).

So, in a hybrid breeding programme, most emphasis is on the selection of superior inbred lines that are generated by repeated selfings. This is efficiently done with diploid genotypes that have one pair of each chromosome, as in each selfing generation the frequency of heterozygotes is halved. For some typical pictures, see Figure 2.2. The development of homozygous inbred lines via repeated selfings takes many more generations in a tetraploid genotype with four sets of chromosomes (Lindhout *et al.*, 2018). This is the main reason why hybrid potato breeders prefer to use diploid genotypes.

A hybrid potato breeder can take advantage of genetics by studying the inheritance of the most important traits. For instance, the heritability of crisp frying quality is high. This means that the performance of the hybrids can be predicted from the performance of the parents (Figure 2.3). The heritability of most of the qualitative traits of potato tubers is high (Adams *et al.*, 2022). Inbred lines are thoroughly tested to select parent lines with good combining abilities (i.e. lines that show the ability to combine well with each other during the hybridisation process), thus allowing that desired genes or features are efficiently passed down to their progenies. This selection process is so efficient that the number of hybrids tested can be limited to merely several hundreds per season. So, where in a traditional breeding programme most emphasis is on the selection of clones that are clonally propagated, in a typical hybrid breeding programme, most emphasis is on the selection of the right combination of parent lines. New hybrids are tested in the field and the best ones are repeatedly tested at several locations and environments to eventually select the most robust hybrids for registration and commercialisation (Stockem *et al.*, 2020). However, the hybrid true potato seed technology has certain consequences for breeding and multiplication that need to be described in more detail below.

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**Figure 2.2. Some examples of hybrid potato: (A) The size of true potato seeds compared with the size of a seed tuber and of potato berries; (B) diploid potato growing in the field, the weaker plants at the front are inbred progenies and the vigorous plants at the back are hybrid plants; (C) inbred lines growing in the greenhouse; (D): harvesting a plot with advanced hybrids; (E) tuber yield of a promising hybrid (photos: Solynta, 2019, 2022).**

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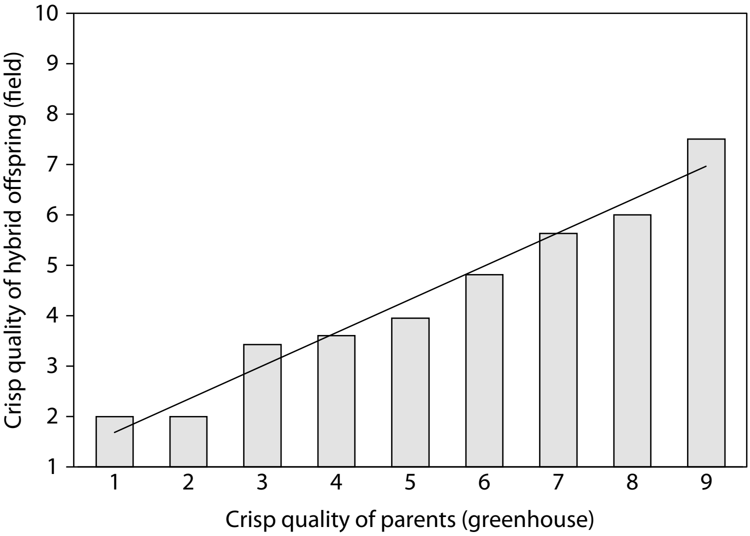


**Figure 2.3. Illustration of the high heritability of quality traits in hybrid breeding. Diploid potato inbred lines were grown in the greenhouse and crossed to produce hybrid progeny seeds. The seeds were sown, seedlings raised and transplanted into the field and cultivated as a crop to produce ware potato tubers. The tubers of the parent lines and of the hybrid progenies were assessed for crisp quality. There is a close association between the crisp quality of the offspring and the crisp quality of the parents. Similar associations for conventional tetraploid cultivars would demonstrate a much poorer relationship between crisp quality of the offspring and that of the parents.**

## 2.4 Specific aspects of the hybrid true potato seed technology

As stated above, hybrid breeding takes advantage of knowledge on the inheritance of traits, by efficiently selecting parent lines and combining or stacking desirable (either monogenic or polygenic) traits in uniform offspring. Moreover, hybrid true potato seed (HTPS) allows rapid multiplication of desirable genotypes without degeneration of the planting material and with low costs of storage and transport. Some relevant aspects are explained below.

### 2.4.1 Uniformity

Hybrids are generated by crosses between inbred parents. Molecular markers may be helpful to select the most homozygous parent lines (Zhang *et al.*, 2021). When inbred parents are not completely homozygous, this may result in genetically not completely uniform hybrid seeds. As it takes much more generations to generate homozygous tetraploid lines, usually hybrids generated from tetraploid inbred plants or populations lack uniformity (Lindhout *et al.*, 2018). The initial TPS cultivars generated by the International Potato Center (CIP) were tetraploid and hence lacked good uniformity (Table 2.1). The present trend is to generate fully homozygous diploid lines and hence the hybrids generated from these lines are uniform (Stockem *et al.*, 2020).

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**Table 2.1. Main potato breeding systems.[1,2]**

| | Vegetative system | TPS (CIP system) | HTPS |
|---|---|---|---|
| Ploidy level | tetraploid | tetraploid | diploid |
| MAB introduction one gene | 10-20 years | 10-20 years | 2-3 years |
| MAB introduction two genes | >25 years | >25 years | 3-4 years |
| Multiplication | tubers (5-10 years) | seeds (one season) | seeds (one season) |
| Seed health | high chance of contamination | clean | clean |
| Uniformity | high | low | high |
| Commercial interest | proven | limited | growing |
| Conclusion | Dominant system: Russet Burbank is leading cultivar for >140 years | CIP introductions: mainly in developing world, area is declining | Potential: dynamic introductions of innovative products, value creation, disruptive change |

[1] For comparison, traditional TPS is included that is not further outlined in this chapter, as it is hardly used anymore.

[2] CIP = International Potato Center; HTPS = hybrid true potato seed; MAB = marker assisted backcrossing; TPS = true potato seed.

## 2.4.2 Qualitative tuber traits

In traditional breeding, most emphasis is on the selection of qualitative tuber traits, as these traits segregate in the progeny populations (see above). In contrast, due to the fixation of genes in homozygous potato inbreds, the genes for qualitative traits in diploid inbred parents are fixed and the quality traits of hybrids can well be predicted from the performance of the parent lines (Adams *et al.*, 2022). So, the majority of the tuber traits is selected in the inbred parents and the hybrids are just checked to guarantee that the high tuber quality is maintained.

## 2.4.3 Plant vigour and tuber yield

The growth and tuber yield of potato plants are very sensitive to (fluctuations in) the environmental conditions. Moreover, there is a large genotype by environment (G×E) interaction. In general, the conditions in a greenhouse, where potato plants of the parents are grown in pots, are very different from the natural field conditions where the offspring is selected. Therefore, the growth and tuber yield of the offspring plants are not well predicted by growth and tuber yield of the parents. This requires that these traits are evaluated in the natural conditions of a potato field. So, the growth and tuber yield of potato hybrids are assessed in the field, preferably in randomised, repeated trials under different conditions, locations and years (Stockem *et al.*, 2020).

## 2.4.4 Trait stacking

In potato, there are many traits, that inherit as one locus or gene. Good examples are resistances and genes involved in the synthesis of pigments, like anthocyanins and carotenoids (Haynes *et al.*, 2011; Van Eck *et al.*, 1994). These genes can relatively easily be mapped on the potato genome

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by genetic studies using molecular markers (Korontzis *et al.*, 2020; Meijer *et al.*, 2018). These genes, often identified in wild species, can be introduced into potato parent lines by a process designated 'marker assisted backcrossings'. This is done by crossing the resistant donor with one of the inbred parent lines of the hybrid), followed by two backcrosses to the same inbred parent line and finally the cross with both original parent lines to reconstitute the hybrid, but now with one or two additional resistance genes. In this way, a susceptible hybrid can be converted into a resistant hybrid with maintenance of the genetic composition, but with an additional resistance gene (Figure 2.4; Su *et al.*, 2020).

## 2.5 Hybrid true potato seed: seed production

The multiplication of hybrid seeds is very fast: a female inbred line is manually pollinated with pollen from a male parent and each berry may contain hundred seeds, while a female plant may produce dozens of berries and, thus, thousands of seeds. This can be done in a greenhouse, allowing two cycles per year. Like with vegetable seeds, this can also be done in remote locations, where the conditions for the production of clean hybrid seeds are favourable, like at high altitudes


**Figure 2.4. Trait stacking in hybrid potato. Note that R1, Susceptible, R1 + R2 and R2 refer to the resistance levels of the rows in which these codes appear. Field trial of potato hybrids with one or two resistance genes to late blight (caused by *Phytophthora infestans*) and the susceptible control. Wild potato species carrying a single resistance gene were crossed in 2015 with the parent plants of a susceptible hybrid. In 2016, the F1s were backcrossed to the recurrent parent plants and the two parent lines with resistance genes were crossed to reconstitute the hybrids with one (R1 or R2) or two resistance genes (R1 + R2). The susceptible original hybrid was added as control. The susceptible control shows a high frequency of diseased plants, some hybrids with one resistance gene (R1 or R2) show some diseased plants, while nearly all plants of the double stack resistant hybrids (R1 + R2) are healthy at the end of the season (photo Solynta, 2017).**

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in tropical regions. There are only ten true-seedborne pathogens known in potato (Chapter 5, Table 5.3). This is in great contrast to tuber-borne diseases as over 200 pathogens are listed as tuber-borne (Gildemacher *et al.*, 2009). Hybrid potato seeds are produced in greenhouses with high phytosanitation conditions, principally hybrid potato seeds are devoid of any pathogen. These greenhouses are usually existing facilities and the technology of producing these hybrid potato seeds is comparable to common production techniques. In this way, millions of clean hybrid seeds can be produced in one year. The shipment to the regions where the seeds are grown is technically simple as one kg may contain two million seeds. The most important limitations are the legal restrictions for import and export of potato seeds (Chapter 5).

## 2.6 Hybrid true potato seed: agronomy of potato cultivation from true seeds

True potato seeds are very small: there are about 2,000 seeds in one gram. Upon sowing, the seed germinates into a seedling that grows into a plant that is similar to plants raised from seed tubers. A farmer may start with true seeds and sow them in the field. Sowing needs to be done shallow, followed by delicate construction of the ridges. However, direct sowing is risky as the young, delicate seedlings have a low early vigour, have difficulty in acquiring the necessary resources (such as light, water and nutrients), may not be competitive enough against weeds, may suffer from pathogens (dying off) or may suffer from extreme conditions: heat, frost, drought, wind erosion, etc. Alternatively, a farmer may sow the seeds in a protected environment like in a greenhouse or nursery, where the conditions are favourable: no weeds and conducive environmental conditions. At five to six weeks after sowing, the seedling is transplanted into the field. This is another risky step as the seedling has to cope with a transplant shock and has to compete with weeds and deal with different field conditions (van Dijk *et al.*, 2021, 2022a,b). When established, the seedling grows into a plant that is similar to a tuber raised plant (Kacheyo *et al.*, 2021). In conclusion, the technical systems to implement HTPS are in place, but the seed and ware potato growers, the packers and processors, as well as the retailers will have to adopt these technologies.

## 2.7 Hybrid true potato seed: paradigm shift in the potato production system

The entire potato production system consists of a chain of activities from research and breeding to the final consumption of the fresh or processed products (Figure 2.5). Upon the implementation of HTPS, many technologies have to be adapted. This goes for the breeding, production of true hybrid seeds, sowing seeds, raising seedlings and transplanting into the field to produce seed tubers or ware potatoes. For all these steps, the present stakeholders in the potato systems will have to adopt these technologies and new stakeholders may take their positions in these steps. The HTPS system is very similar to the systems of field grown vegetables, where also hybrid seeds and transplanting technologies are used. It is expected that growers and seed companies, who and which are experts in these technologies will easily adopt HTPS as it is just a new crop in their portfolio of vegetables.

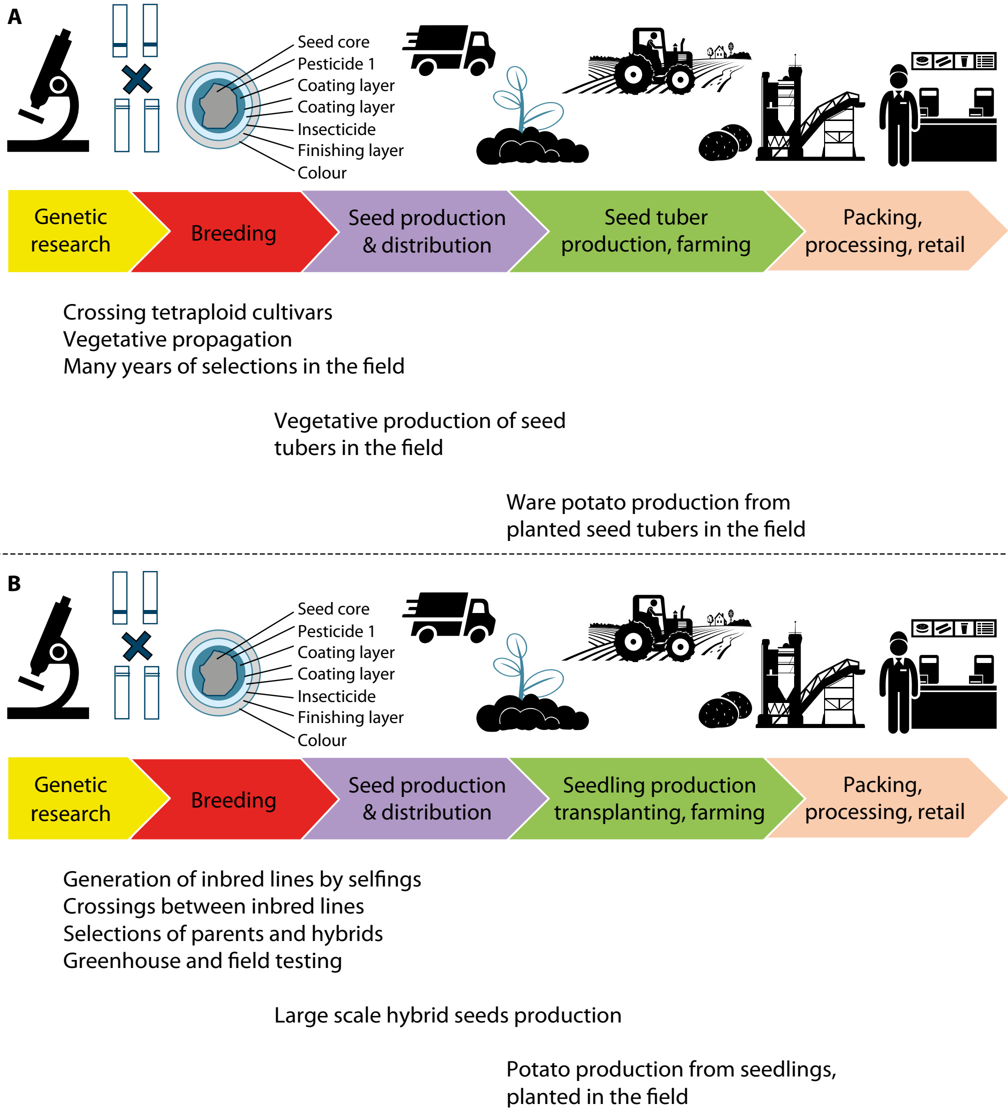


**Figure 2.5. Schematic representation of potato systems with the main technologies used: (A) the traditional potato system; (B) the hybrid potato system.**

In addition, where nowadays seed tubers are stored and transported over the globe, in future hybrid seeds may be distributed over the globe, where local players will produce seed tubers and distribute them over the farmers. The storage, transport and handling of HTPS is much more efficient than those of bulky seed tubers. So, the initial steps in the potato systems will change but as soon as seed tubers are produced from HTPS, the farmers' practices will largely remain the same. If farmers see the advantages of HTPS and become familiar with the new technologies, more farmers may follow this route. Still, farmers may have a mixed system whereby they regularly purchase fresh seed tubers from the formal system, followed by a small number of saved seed



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generations. These systems may go hand in hand and differ dependent on the geographies, agronomic and economic conditions, and farmers' communities and skills.

The driver for these changes is the added value of HTPS. As stated above, the advantages of HTPS are the faster development of new cultivars with new traits that are desired by farmers and by other stakeholders in the potato systems.

In conclusion: HTPS is a new technology with great potential, but the implementation is challenging as it affects many steps in the potato systems.

## 2.8 Hybrid true potato seed: state of the art in the context of developing countries

The first publication about the development of HTPS appeared in 2011 (Lindhout *et al.,* 2011). The first hybrid field trials were done in 2015 and repeated in 2016 in the Democratic Republic of Congo (DRC), Africa (De Vries *et al.*, 2016; Figure 2.6). These field trials in the DRC were caried out in an international context of developing countries with often a dominance of an informal seed potato system and a high rate of seed degeneration of traditional seed potato production. Although the genetic composition of the potato hybrids at that time did not meet the market demands (e.g. in terms of uniformity of the hybrids and their produce), the added value of clean true potato seeds was already so high that local farmers wanted to use these HTPS cultivars. Still, legal regulations did not permit to use these hybrid cultivars and some more breeding was needed to further improve these cultivars genetically. Similarly, already in 2017, a hybrid potato cultivar was generated with two resistance genes against *Phytophthora infestans*. These 'double stack' cultivars showed a strong resistance during the entire growing season (Su *et al.*, 2020). But these cultivars were meant for demonstration and were not genetically good enough for commercialisation.

One of the main challenges is the regulation of HTPS (see also Chapter 5). The breeding pipelines of the HTPS breeding companies are very promising, but it takes some years before the added value is proven in the field and in demonstration plots and before all regulations are in place to transport and import HTPS over the globe, certify the quality of seeds and the progeny seed tubers, and register the hybrid cultivars.

## 2.9 Hybrid true potato seed: global food security

HTPS has great potential to contribute to the global food and nutrient security (Global Development Goal II: zero hunger; FAO, IFAD, UNIUCEF, WFP and WHO, 2019; FAO, 2021). At present, all HTPS breeding programmes are executed in the northern hemisphere at mild climatic conditions (Aardevo[1]; HZPC[2]; Solynta[3]; Jansky *et al.*, 2016; Zhang *et al.*, 2021). The HTPS products are well suited for these mild climates and at high altitudes in tropical regions,

[1] https://www.aardevo.com/en/.
[2] https://tinyurl.com/yckv742w.
[3] https://www.solynta.com/about-solynta/.


**Figure 2.6. First hybrid potato cultivation in Africa: (A) raising seedlings; (B) seedlings two weeks after transplanting in the field; (C) harvested potato tubers; (D) relative yields of nine hybrids (S1…S10) compared to a local control (photos: Solynta, 2016).**

the centre of origin of potato. Implementation of HTPS requires technical adaptations that can only successfully be implemented when this is supported by training and capacity building programmes of the main stakeholders in the potato systems. This is a great challenge that is only achievable by cooperations and coalitions: breeding companies will develop new HTPS cultivars that are tested in the target markets over the globe, where local users can participate in selecting the best adapted cultivars. These activities have to be embedded in the local potato systems with active involvement of these stakeholders. Government bodies should implement the new rules and regulations on HTPS. When these systems around HTPS are well organised and function well, all stakeholders will benefit. This is crucial for the sustainability of this system. This means that additional funding, including public funding, is required to set up the HTPS potato system, but when it is established, no more funding is needed.

The long-term aim of this new technology is to develop HTPS cultivars that are adapted to cultivation in the tropical lowlands. As no cultivated potato is adapted to tropical lowland conditions, a completely new breeding programme – and in fact a new crop – has to be generated. This requires



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a considerable investment, even higher than the present investment in the development of HTPS, as the (diploid) hybrid breeding germplasm is well adapted to grow in the regions where potato is already cultivated. Given the very large genetic variation in wild related *Solanum* species that are crossable with cultivated potato (*Solanum tuberosum*), such a tropical lowland HTPS breeding programme is feasible and realistic. This requires strong public private partnership where inputs and results are shared (Beumer and Stemerding, 2021; Beumer *et al.*, 2020).

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