Review Article

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Ekin International biannual peer-reviewed journal

Ekin
Journal of Crop Breeding and Genetics

12(2):74-85, 2026

Hybrid Potato Breeding, Seed Technology and Agronomy[(§)]

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Citation:
Struik PC., 2026. Hybrid Potato Breeding, Seed Technology and Agronomy. Ekin J. 12(2):74-85.

Received: 23.06.2026 ***Accepted: 28.07.2026*** ***Published Online: 31.07.2026*** ***Printed: 31.07.2026***

ABSTRACT

This article summarizes the advantages of hybrid diploid breeding of potato, with true potato seed as major propagule. Hybrid diploid breeding accelerates breeding of potato, allowing pyramiding resistance genes and introducing novel genes for maximum quality. The challenge is to compensate for the lack of positive effects of polyploidy by rapid progress in breeding and heterosis. Moreover, the use of true potato seed from such a breeding program makes it possible to produce large numbers of healthy seeds in a very short time that are very small, easy to store and easy to transport to remote areas. If successfully implemented, the use of such a new technology will revolutionize the breeding, seed systems, and seed and ware production systems of potato. Making maximum use of this technology requires identifying the best seed system model for different agro-ecological and socio-economic conditions and optimizing the production systems of seed tubers and ware potatoes based on the seed value chain selected and implemented.

Keywords: Diploid potato, hybrid breeding, seedling tuber, seed systems, transplant, true potato seed

Introduction

Potato (*Solanum tuberosum* L.) is commonly grown as an early crop, an intermediate short-cycle crop between two main crops, or as a main crop in many different cropping systems. It is also often grown as a temporary component crop in intercropping systems with perennial crops that have a long establishment phase, such as sugarcane or in intercropping systems in which the companion crop can provide some shelter (e.g., maize-potato intercropping in warm regions). In many parts of the world, it is a hunger-breaking crop because there are cultivars available with a very short crop cycle. Potato is very efficient in terms of resource use (land, water) and has a very high harvest index. Despite the international trade of ware and seed tubers, the potato crop is still very much a 'local for local' crop, because of the bulkiness of the seed tubers and the ware potatoes and because of the limited storability (Haverkort and Struik, 2015). As a crop for food security and income, the crop is developing rapidly, especially in Africa and Asia.

Despite its flexibility, potato also has some disadvantages. The most important ones are already mentioned: both the seed tubers and the ware potatoes are bulky and perishable. Moreover, the rate of multiplication is very low, making it necessary to use a large proportion of the area cropped with potato for seed production or save a large part of the harvest for seed. The crop is also affected by a plethora of pests and diseases, which are either air-borne (e.g., late blight), water-borne (e.g., bacterial wilt), vector-borne (e.g., viruses), or soil-borne (e.g., cyst nematodes), while many of these pests and diseases are (also) seed tuber-borne, i.e., can be transmitted from one generation to the next when the crop is multiplied vegetatively, a phenomenon often called "seed degeneration". This seed degeneration puts a lot of challenges on the production of high-quality seed and the institutionalization of a functional seed

(§) *This study was presented as an oral presentation at the V. International Plant Breeding Congress held in Antalya, Türkiye, on December 1-5, 2025.*

system. Several pests and diseases have quarantine status with zero tolerance, while others may result in declassification of the seed when tolerance levels are surpassed. The potato crop is also sensitive to abiotic stresses, including drought, excessive rainfall, heat, cold, salinity, contaminants, such as heavy metals and microplastics, and nutrient deficiencies. Finally, there are also physiological quality aspects for both seed tubers and ware potatoes that are very much influenced by environmental factors. The seed tubers may remain dormant for too long or may sprout too early, depending on conditions during production and storage conditions, while they might be ageing and losing vigour when the temperature sum during storage gets too high; these aspects are very important in potato production regions with more than one growing season per calendar year (Struik and Wiersema, 1999). The potato crop may also show a wide diversity of physiological disorders of ware potatoes, such as secondary growth, knobby tubers, growth cracks, translucent ends, and hollow hearts.

This paper first deals with recent developments in global potato cultivation, seed systems, and quality of seed tubers. It then describes in detail the various aspects of breeding and seed production of potato, using hybrid diploid breeding and true potato seed production as a set of alternative technologies to create robust varieties with strong resistance against abiotic and biotic stresses and the best possible quality for a wide diversity of consumers as well as healthy types of propagules that can be used in adapted seed and ware production systems. I also highlight the potential use of true potato seed in Sub-Saharan Africa.

The paper is based on the hope that the new developments of hybrid diploid breeding and use of hybrid TPS will benefit global potato cultivation, especially in countries in which traditional seed production and ware production are challenging.

Global potato cultivation

The potato crop is widely cultivated because of its wide adaptability, high resource use efficiency, and high nutritional quality, amongst other factors. It is grown in more than 100 countries, processed into many different products (e.g., in Dutch supermarkets well over 150 products based on potato are on display; Haverkort et al., 2023), regularly consumed by more than 1 billion people, while there are strong international markets for seed potatoes, ware potatoes, and processed potatoes. Mordor Intelligence (2026) estimated that the value of the international potato market equalled USD 210 billion in 2025. The same source estimated that this value would grow from USD 124.46 billion in 2026 to USD 149.38 billion in 2031. This continued growth is remarkable given the increasing frequencies of weather shocks (heat, drought), increasing regulatory pressure (e.g., restrictions on the use of biocides), and strong price volatility. The causes of continued growth include rising demand for frozen products (such as frozen French fries) and the strong expansion of quick-service restaurants. In addition, farmers across the globe manage to adopt climate-smart cultural practices to cope with adverse weather conditions.

One of the most remarkable changes in potato cultivation over the last 75 years is the shift in production from the so-called developed countries to the so-called developing countries (Haverkort and Struik, 2015). In the last 20 years, more potatoes are being produced in developing countries than in developed countries. This trend is caused by an increase in acreage, with China and India currently having the largest areas cropped with potato, and an increase in productivity (i.e., yield per hectare). In Africa, there is also a substantial increase in production, but that is mainly caused by an increase in acreage, whereas in some countries, the potato yield per hectare is declining (e.g., in Kenya; Atieno et al., 2023; 2026). Major reasons for the yield decline are expansion to marginal areas because of land shortage, increase in cultivation by resource-poor farmers, and increased seed degeneration, because of limited seed renewal by smallholder farmers.

Informal versus formal seed systems

Although the potato plant is very versatile in its propagation and multiplication (Struik and Wiersema, 1999), the common method of propagation is through seed tubers. The rate of multiplication is very low, compared with other important food crops, such as cereals. Therefore, a large proportion of the world's potato acreage is devoted to seed production. Properly functioning seed tuber production systems are crucial to supply ware growers with high-quality seed tubers in a reliable way and against affordable prices.

A seed system can be defined as "*all activities of various stakeholders related to breeding and selection of varieties and the development, maintenance, bulking, storage, management, exchange, distribution and dissemination, and use of seed*" (Struik, 2023). The main purpose of a seed system is to provide affordable, high-quality seeds of all varieties of all relevant crops at the right time. A seed system entails breeders, seed multipliers, and farmers, but also the informal and formal governance structures testing and controlling the quality of the seed.

In most countries, seed potato production is strictly regulated through certification schemes to prevent, or at least limit, transgenerational propagation of pests and diseases and guarantee true-to-type material of the right cultivar in this vegetatively propagated crop. Viroids, viruses, phytoplasmas, bacteria, fungi, nematodes, and insects can easily be transmitted from mother plants to progeny tubers or from the soil to the tubers. In formal seed systems, strict regulations for quarantine pests and diseases and strict tolerance levels for other pests and pathogens apply to guarantee that farmers can produce a good ware crop from healthy seed. Quality is maintained by testing fields, seed-tuber crops, and seed-tuber lots, and phasing out progeny after a number of field multiplications.

However, in many countries, for example, in Asia, South America, and Sub-Saharan Africa, at least 90% of the seed tubers come from informal seed systems (Thomas-Sharma et al., 2016). Informal seed systems of potato have significant advantages. They provide local seed of preferred varieties when required and at relatively low cost. However, the phytosanitary quality is often sub-standard, especially in regions with little seed renewal and large pressure of air-borne (e.g., *Phytophthora infestans*) or water-borne (e.g., *Ralstonia solanacearum*) pathogens, vectors such as aphids, or endemic soil-borne pathogens, such as *Streptomyces scabies*.

Quality of seed tubers

Seed quality includes genetic quality (no off-types), physical quality (no damage, right size), physiological quality (desired level of vigour and number of sprouts), and phytosanitary quality (absence of seed-borne pests and pathogens). The latter quality characteristic is especially important for potato as seed health is very difficult to control.

How farmers perceive the quality of the seed in the case of potato has been investigated for many different socio-ecological environments (e.g., for Kenya, see Atieno et al., 2023; Kwambai et al., 2024; for Ecuador, see Navarrete et al., 2022a, 2022b, 2023), and possible routes to alternative, sustainable seed systems bridging informal and formal systems have been described by Thomas-Sharma et al. (2016). Such seed systems aim to control seed degeneration. Seed degeneration is commonly defined as "the reduction in seed quality (and therefore the ultimate crop yield) due to pathogens and pests accumulating over successive cycles of propagation" (Struik, 2023). In some definitions, physiological ageing of the seed is also included in seed degeneration (Struik and Wiersema, 1999; Zou et al., 2024, 2025).

Seed degeneration of potato is common in areas where governance of seed quality is less strict. It is especially problematic in informal seed systems, although in such systems some level of tolerance to seed-borne pests and diseases in the commonly used varieties has been demonstrated. Simple techniques, performed by smallholder farmers, such as positive selection (Gildemacher et al., 2011; Schulte-Geldermann et al., 2012; Priegnitz et al., 2019, 2020), can slow down seed degeneration significantly. In extreme cases, these techniques might even reverse degeneration as some tubers of a secondarily infected plant do not contain a significant viral load (Bertschinger et al., 2017).

Physiological age of seed is especially problematic in regions with more than one growing season per calendar year. In such cases the seed can be either too young or too old for optimal performance. Lack of control of conditions during storage makes it difficult to manage physiological age and therefore seed vigour.

Breeding: from traditional breeding of tetrasomic cultivars to hybrid diploid breeding

Traditional breeding of potato is difficult. The tetrasomic inheritance and the associated complex genetics and huge linkage drag in traditional potato breeding systems make it very difficult to introduce desirable traits, such as resistance genes or quality traits. Introducing one gene through marker-assisted backcrossing takes 10 - 20 years, introducing two genes can easily take more than 25 years (Lindhout and Struik, 2023). The subsequent multiplication of seed tubers to commercialize the cultivar then takes another 5 - 10 years with traditional seed tuber multiplication.

In addition, there are many different traits to take into account (up to 50) as the crop is affected by many different abiotic and biotic stress factors, is very sensitive to genotype-by-environment interactions, and has many quality characteristics to be taken into account for the diverse outlets. Moreover, potato tubers need to be easy to store and process. Even when a new variety has been selected as promising, there is the problem of low multiplication rates: it takes many years to bulk up seed tuber lots to quantities that will allow wide testing in the field for performance under diverse practical conditions and subsequent commercialization.

Hybrid breeding is an advanced breeding system that might solve some of the problems with traditional potato breeding. Hybrid breeding involves generating inbred lines through repeated selfings over many generations followed by crossing inbred lines to generate hybrids. The inbred lines make it possible for breeders to better control genetics and better predict the outcomes of their crossings based on marker-assisted techniques; this results in a much more efficient breeding process. Hybrid breeding is common in many important food crops, also because it serves the business model of the breeding companies well (ter Steeg et al., 2022).

Hybrid breeding in tetraploid potato is difficult because of the tetraploid nature of commercial potato cultivars and because inbreeding depression hampers the development of pure inbred lines, despite the fact that often tetraploid cultivars are (partially) self-compatible. While tetraploid potato cultivars are traditionally vegetatively propagated via seed tubers, the preferred method of propagation in hybrid potato is through true potato seed. This makes it necessary to develop specific seed systems and cultivation pathways for seed and ware. The multiplication rate is strongly increased resulting in fewer years between making a cross and producing enough seed for commercial use of a new variety.

The limitations of the complicated tetraploid breeding system mentioned above have been overcome by hybrid diploid breeding. Several universities and commercial companies in different countries, including the Netherlands, China, and the United States of America have started hybrid diploid breeding programs (Lindhout et al., 2011, 2018; Jansky et al., 2016; Zhang et al., 2021). This was only possible after the problem of self-incompatibility during self-pollination, common in diploid potato, was solved by the introduction of the *Sli* gene. This *Sli* locus allows the pollen tube to reach the ovary without the pollen tube growth being arrested in the style before reaching the ovary (de Vries et al., 2023). For an overview of the recent advances in the insights into the molecular mechanisms and genetic basis of potato self-incompatibility and key technologies to overcome this self-incompatibility, see Sood et al. (2024), Zhang et al. (2019, 2025), and Wang et al. (2026). Sood et al. (2024) also provided an overview of the achievements in diploid potato breeding, including advancements in genomic purging and phenotyping strategies.

Producing diploid inbreds of potato is associated with strong inbreeding depression, creating relatively weak inbred lines. Heterosis effects when crossing inbred lines are not as strong as hoped for. Nevertheless, the flexibility of the hybrid breeding system (ter Steeg et al., 2022) and the opportunities for marker-assisted breeding are very promising, especially in breeding for resistance and novel quality traits. Introducing one gene through marker-assisted backcrossing takes 10 - 20 years in conventional breeding but only takes 2 - 3 years with hybrid diploid breeding. Introducing 2 genes through marker-assisted backcrossing can easily take more than 25 years in traditional potato breeding but merely 3 - 4 years in hybrid diploid breeding. Producing enough true potato seed for commercialization only takes one season. Moreover, the resulting seed lots are much less likely to be contaminated with seed-borne pathogens and are easier to store and transport than conventional seed tuber lots. How the comparison between a tetrasomic breeding system with polyploidy benefits versus ease of breeding and heterosis benefits of hybrid diploid breeding finally works out is still a matter of debate, certainly if one considers the disruption of the entire seed and cultivation system associated with the use of hybrid diploid true potato seed.

A possible diploid hybrid potato breeding strategy is illustrated in Figure 1, based on Eggers (2025). Details on producing advanced inbred lines of diploid potato while coping with inbreeding depression and eliminating deleterious alleles, the use of genetic markers, genomic selection, and genomic prediction, implications of genotype × environment × management interactions, trait introgression, and the optimization of hybrid vigour are provided in the following sections.

Diploid hybrid breeding: from gene pool to advanced inbred lines

As in any breeding program, diploid potato breeding starts with the creation of a pool of crossable genetic resources that contains a wide set of useful genes, including genes that contribute to high yielding ability and quality, pest and disease resistance, resistance against abiotic stresses, and a wide diversity of other traits that are desirable in potato. With this germplasm, inbred lines are created making use of the *Sli* gene. An alternative could be to create knockout mutations in the incompatibility locus (Bradshaw, 2022). These inbred lines need to be fertile to enable their use in crossings, either as male or female plants, must have adequate vigour to produce adequate amounts of gametes, and must be homozygous (de Vries et al., 2023). Although the self-incompatibility issue has been solved, fertility might still be an issue, as it is associated with the vigour of the inbred lines. Moreover, homozygosity does not come easy due to the large heterozygosity: it requires a long, multi-annual process to achieve complete homozygosity (Bradshaw, 2022; de Vries et al., 2023), required to obtain a maximum level of uniformity in hybrids.

Strategies for reducing inbreeding depression, genomic selection, genomic design, and genomic prediction

Hybrid breeding also suffers from the presence of many deleterious alleles that are often hidden in tetraploid genotypes but become very harmful in homozygous diploids. Inbreeding depression is a major bottleneck in diploid potato breeding. Zhang et al. (2019) mapped the genome-wide incidence of constrained, deleterious mutations, obtained 344,831 predicted deleterious substitutions, and examined their phenotypic effects. They found that some deleterious recessive mutations indeed cause very large effects on vigour. They also demonstrated that lines that seemed to have high initial mutation burdens appeared to yield better elite inbred lines, a finding that is paradoxical. They also observed that most deleterious mutations were line specific. This suggests that a high degree of heterosis is possible when crossing inbred lines of different lineages. Zhang et al. (2021) used genome design to develop pure, fertile inbred lines by systematically purging the harmful mutations, selecting for genome complementarity, thus leveraging heterosis. They showed that using genetic design made purging of deleterious alleles through recombination not that difficult. They finally developed vigorous F_1 hybrid seeds. In yet another study, Zhang et al. (2025) unravelled the regulatory mechanism underlying the male gamete-specific expression of the *Sli* gene, which could support diploid hybrid breeding.

It is clear from the above that in order to cope with very negative inbreeding effects, pedigree-based selection for fertility and vigour has to be conducted before selection for other performance traits, like yielding ability, can start. The common strategy in diploid breeding is therefore to start with selection processes to reduce inbreeding depression, thus creating a pool of fertile and vigorous inbred lines. This step is followed by recurrent selection to recombine favourable alleles to contribute to positive complex traits. For the identification and deletion of deleterious alleles (so-called marker-assisted purging; see Bradshaw, 2022) and finding QTLs for desired complex traits that contribute to the yielding ability, molecular marker techniques and genetic design approaches come in very useful. Marker technology can also be very useful for trait introgression, for example for pyramiding late-blight resistance genes.

Once inbred lines have been produced, creating genetic maps of useful traits and developing molecular markers can be conducted using common techniques that allow marker-assisted selection. However, as indicated by various research teams, the development of diploid breeding varieties involves recent, shallow pedigrees with only a few founders. Detection of QTLs of complex traits in diploid potato therefore requires alternative methods as, for example, proposed by Korontzis et al. (2020). These authors identified QTLs through a Genome Wide Association Study model, a tailored linkage approach, and by modelling multiallelic QTLs in complex pedigrees using identity-by-descent probabilities. They showed that all three approaches allowed them to detect QTLs, but they preferred the last approach as it gave a more direct and detailed interpretation.

Genotype × Environment × Management interactions

The genotype × environment × management interactions in potato are very strong, because growth and development of the potato crop are very sensitive to environmental conditions throughout its crop cycle with strong feedback and feed-forward effects. These strong interactions reduce selection progress and make achieving consistent and rapid genetic improvement more difficult. Stockem et al. (2020) compared widely grown tetraploid cultivars with hybrid diploid genotypes under contrasting environmental conditions and crop management regimes. They found that the genotype × environment × management interactions were similar for both types of material. Moreover, they made a yield component analysis to assess what yield components contributed most to variation in yield across environments and crop management. Yield gain was strongest related to an increase in the number of tubers per stem in both types of material.

Seed technology: towards novel diploid hybrid propagules

Figure 1 already showed that it is not just the creation of new cultivars but also the optimization of cultivation pathways for the production of true seed or seed tubers and the production of ware potatoes that require a lot of research and attention and new skills of practitioners.

Seed production systems are complex agronomic, social, and regulatory systems. This is certainly true for the complex seed potato systems (Struik and Wiersema, 1999). Potato is very versatile in methods of multiplication. Despite the intrinsic conservatism of the potato sector, tremendous changes have occurred over the past 50 years in terms of different multiplication technologies that have been developed, both in developing and developed countries. An overview of these developments is presented in

Figure 2. These techniques differ in the duration of each separate cycle of multiplication and in number of daughter propagules produced per mother propagule.

The last development is hybrid diploid potato breeding with potentially different end products. These might entail true potato seed (TPS), seedlings for transplanting (transplants), seedling tubers (i.e., progeny tubers of TPS-grown plants), and seed tubers (i.e., progeny tubers of crops grown from seedling tubers or their progeny).

Every seed system aims to multiply as fast as possible (either in terms of number of propagules, or in terms of weight, or a combination of the two), multiply as cheaply as possible, keep the material free of diseases during multiplication, and produce material that is suitable for the next multiplication cycle or use in commercial ware production in terms of size, vigour, and physiological, genetic and phytosanitary quality. However, the traditional system of seed tuber production is notoriously slow in bulking up seed. About 10 - 15% of the total acreage of potato worldwide is used for seed (Struik and Wiersema, 1999). This is a much higher proportion than for most other crops, especially cereals, such as maize and barley.

Using hybrid true potato seed (HTPS) varieties has the following five advantages:

1- The multiplication system is very fast: one plant can easily produce 10,000 uniform seeds instead of 10 seed tubers.
2- The seeds of HTPS varieties are very light: one hectare requires 25 g of true seed instead of 2,000 kg of seed tubers.
3- The seed is free of almost all seed-borne pathogens (potato spindle tuber viroid being one of the very few exceptions).
4- The seed can be easily stored for many years in simple, dry containers, whereas seed tubers require special facilities (diffuse light store, cold store) and can even then only be stored for 6 - 8 months at most.
5- Breeding is much faster, making it possible to incorporate resistance genes, pyramid different resistance genes in one variety and breed for yield and quality traits in years rather than in decades (see also the earlier section on breeding).

These advantages are especially important in remote areas with poor infrastructure and failing governance of seed systems, such as Eastern Africa. I therefore refer for further reading to den Braber et al. (2023) and the website of the Sepia Foundation (https://sepiapotato.nl/), but will also elaborate on using hybrid true potato seed in Sub-Saharan Africa in a separate section further below.

Physiology of the potato crop when grown from true seed or transplants

Kacheyo et al. (2021) published augmented descriptions of growth and development stages of potato (*Solanum tuberosum*) grown from different types of planting material. They showed that crops grown from true potato seed or seed tubers differ in the number of stems per plant, the presence of below-ground branches, the position of stolons on the main stem, the branching of the main stem, both at lower nodes and higher nodes, the sympodial branching intensity, and the number and uniformity of tubers. Despite these strong differences in below-ground and aboveground architectures, Gu et al. (2025) demonstrated that one fundamental aspect is very much the same for both types of crops: there is a very close relationship between the rate of photosynthesis or stomatal conductance on the one hand and the leaf nitrogen content (in amount of nitrogen per unit area of leaf) on the other hand. This relationship holds across leaves from different origins (either from main stem or branch or from different orders of branches) and across leaf ages.

However, the different architectures will have consequences for tuber yield, number of tubers per stem, and tuber size distribution and therefore the cropping system for crops grown from propagules from hybrid diploid varieties needs to be newly designed.

Novel cultivation systems required

There are several different cultivation pathways possible for using true potato seed for the production of transplants, seed potatoes, and ware potatoes. The different options are illustrated in Figure 3.

van Dijk et al. (2025) showed that direct sowing is an option, but requires very special care, due to the small size of true potato seed, the low vigour of the seedlings, and the physiology of crops grown from TPS. They showed that plants can meet numerous challenges, from environmental factors (both abiotic and biotic, including weeds) and associated with crop management such as hilling. Best results are obtained when the true potato seeds are pelleted, have received some additions in the pelleting material to stimulate growth, and are covered by plastic mulch during early growth. Nevertheless, the success rate of seed germination and seedling establishment can be relatively low and therefore sowing density must be high. There is a strong positive relation between sowing density and yield, especially when sowing takes place when conditions for emergence and plant establishment are not very conducive.

Success is more likely when sowing takes place in a nursery and vigorous transplants are produced that can then be transplanted into the field after some hardening. Kacheyo et al. (2024a) showed that temperature and light intensity during raising of the seedlings are crucial to create enough leaf area per seedling and to produce compact seedlings (i.e., seedlings with a large amount of dry matter per unit of length of their stem) to make them vigorous. Stockem et al. (2023) indicated that not only light intensity, but also the proportion of far-red light is important for increasing the number of tubers per seedling, and not only temperature, but also the difference between day and night temperature is important in determining the size of the individual tubers formed. Age of the transplant at transplanting is important but less critical than originally assumed, as long as progress to tuberization is not advanced.

By using different trays differing in plug size and volume, Kacheyo et al. (2025) showed that it is important to grow transplants at the right density and with a proper plug volume to give the transplants enough vigour and to make seedling production easier in terms of water management. There is a very strong trade-off between number of seedlings produced per unit area and individual seedling vigour, reflected by the seedlings' leaf area, leaf dry mass, stem dry mass, total dry mass, root: shoot ratio, height, and compactness.

Crops of the same genotype but grown from transplants or seedling tubers perform differently when used in the field to produce daughter tubers. Gu et al. (2024) showed that the branching pattern and the leaf area distribution over the different types of branches are different between TPS-grown crops and seedling-tuber grown crops with similar stem densities per unit area. Differences between the two types of crops depended on the year, most likely because of differences in soil tillage and environmental conditions during early growth; effects of year and propagule type interacted with the stem density effects created in the experiments. Most striking were the larger number of high-order branches in TPS grown plants. These architectural differences were also visible below-ground: crops grown from TPS produced many more tubers per stem, especially in the smaller size classes than crops grown from seedling tubers at the same stem density. Differences were most pronounced at low stem density but significant at all densities, with the higher densities producing fewer tubers per stem. Differences in number of tubers per stem had strong consequences for the tuber size distribution with more tubers obviously resulting in a shift to smaller tubers.

Kacheyo et al. (2024b) demonstrated that the shape and size of ridge or bed was extremely important for the number of tubers per unit area and the tuber yield per unit area of field crops produced from transplants. Especially planting in raised or flat beds gave more tubers and higher tuber yields than various ridge systems. Soil tillage is crucial to obtain the right number of tubers and the right yield but is also important for tuber quality as greening and other physiological disorders might also differ among various soil tillage systems.

Stockem et al. (2024) conducted a detailed yield component analysis on crops of different hybrids and grown from seedling tubers of the same size or weight but showing different numbers of eyes per seedling tuber. They found that within a hybrid, seedling tubers with fewer eyes produced more stems per eye resulting in almost the same number of stems per seedling tubers. Seedling tubers with fewer eyes also produced slightly more tubers per stem so that the number of tubers per plant was very similar for seedling tubers with more eyes and those with fewer eyes. The outcome was that crops from both types of seedling tubers provided the same yield, the same number of tubers, and similar tuber size distribution.

The results of our agronomic studies show that there is work to do to optimize a cropping system involving direct sowing of true potato seed. However, there are opportunities to grow potato crops from transplants and seedling tubers. Use of such propagules also requires adaptation of some of the general cultural practices, partly because of the differences in above- and below-ground architectures. A system producing normal seed tubers from a crop grown from seedling tubers is also an option in areas where seed degeneration is relatively slow.

Table 1 summarizes the characteristics required for high-quality propagules of the different types that might be produced in a diploid hybrid potato seed system.

Use of true potato seed in Sub-Saharan Africa

Lindhout et al. (2011) were the first to publish on the development of hybrid true potato seed. de Vries et al. (2016) reported that the first field trials with potato hybrids were conducted in 2015; These trials were repeated in Africa, in the Democratic Republic of the Congo, in 2016 (see also Lindhout and Struik, 2023), a country where informal seed systems are dominant and seed tuber degeneration is fast. These experiments demonstrated the benefit of hybrid true potato seed in terms of seed health and resistance against late blight, but there were two problems. First, the material was still too heterozygous; second, the regulatory legal framework did not permit hybrid true potato seed varieties to be grown (Lindhout and Struik, 2023).

den Braber et al. (2023) analyzed the potato sector in East Africa and concluded that for the introduction of hybrid true potato seed it was essential to develop a solid understanding of three important elements: a) how farmers evaluate innovations, b) what the local farm realities are, and c) the local seed systems in which the farmers operate. Using hybrid true potato seed requires a drastic change in the configurations of the local seed systems, and how the potato crop is grown, taking into account the agroecological and socio-economic context. They argued that in order to achieve that change, an iterative research cycle linking researchers, breeders, farmers, and other stakeholders should be designed and institutional embedding should be facilitated based on shared views on this innovation.

Gildemacher and ter Steeg (2023) argued that the use of hybrid true potato seed rather than seed tubers can greatly simplify the production system of early generation seed as it no longer requires a system of *in vitro* plantlets and minitubers that requires advanced technology, reliable infrastructure, and skilled labour. Additional advantages include, but are not limited to, absence of most seed-tuber borne pests and diseases, lack of seed dormancy, absence of physiological ageing, and long storability. But most of all: ease of logistics in storage, transport, and use. However, for smallholder farmers in Sub-Saharan Africa there are also major disadvantages, preventing instant success. These include factors related to their needs, economics, risk avoidance, and stressful environments, with large disease pressure and strong abiotic stresses. Under such conditions, plants from seed tubers are more robust than seedlings. Adoption of hybrid true potato seed will require a seed system based on decentralized seed tuber producers who can handle hybrid true potato seed of suitable varieties and produce seed tubers from it, that match the demands of the smallholder ware growers in Sub-Saharan Africa, including short dormancy, earliness, marketability, resistance to late blight, and tolerance to bacterial wilt.

Conclusions

We conclude that hybrid diploid true potato seed has great potential. The story of hybrid true potato seed is a story of hope that might revolutionize the potato sector, but in ways that are still largely unknown. Hybrid breeding might open new avenues for pyramiding resistance genes, introgressing novel traits such as heat tolerance and health promoting characteristics. The use of true potato seed opens new opportunities for tailor-made seed systems in Sub-Saharan Africa where the production of healthy seed is difficult and governance of seed systems complicated. However, this potential still requires validation in practice in different cropping systems and agro-ecologies. There are different models possible for producing propagules from hybrid diploid varieties. It is not yet fully crystalized what would be the best model for the use of hybrid varieties in developed and developing countries. Moreover, different propagules create crops that differ in crop physiology although some basics are very much shared. But because of the differences, crops from different propagules require different cultural practices and there is still a lot of research required to optimize seed systems and cropping systems of potato from hybrid varieties in different parts of the world. Capitalizing on the potential is therefore still a huge challenge. But in regions where the advantages are large and weigh heavily it is definitely worth trying.

Nevertheless, the technology of hybrid true potato seed could become a driver of change in the potato sector development, especially in Sub-Saharan Africa.

The technology addresses some fundamental challenges of the conventional vegetative multiplication system, including land requirement for seed production, availability of healthy early generation seed tubers, seed degeneration, and logistics of seed storage and transport.

Acknowledgements

This paper is an extended version of the abstract published in the Proceedings of the 5th International Plant Breeding Congress (December 01-05, 2025, Antalya, Türkiye).

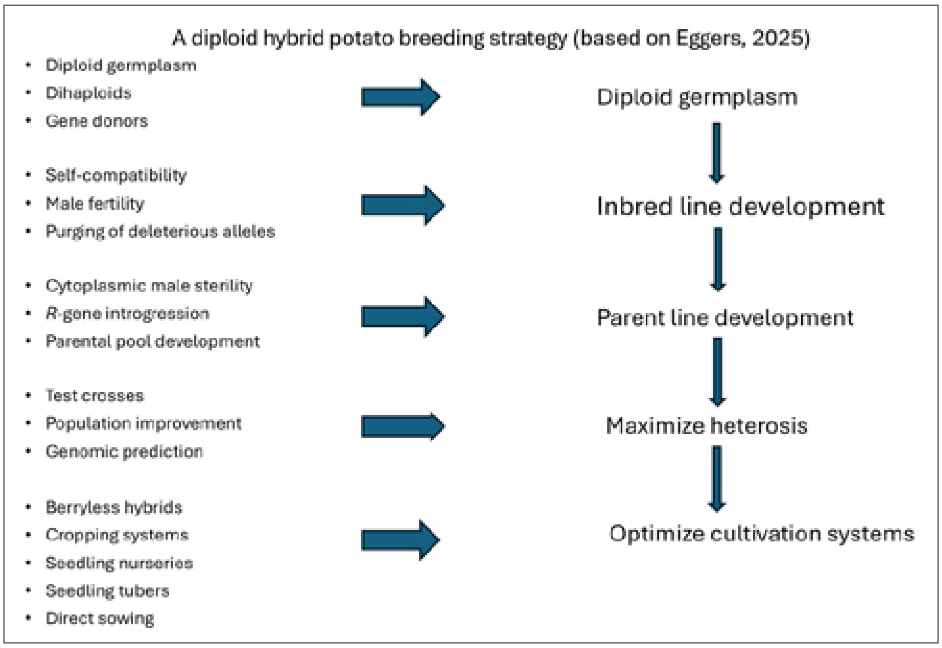

Figure 1. A strategy to create diploid hybrid cultivars, from collecting diploid germplasm through inbred line and parent line development to diploid cultivars with maximum heterosis and finally optimizing cultivation systems making use of novel propagules.

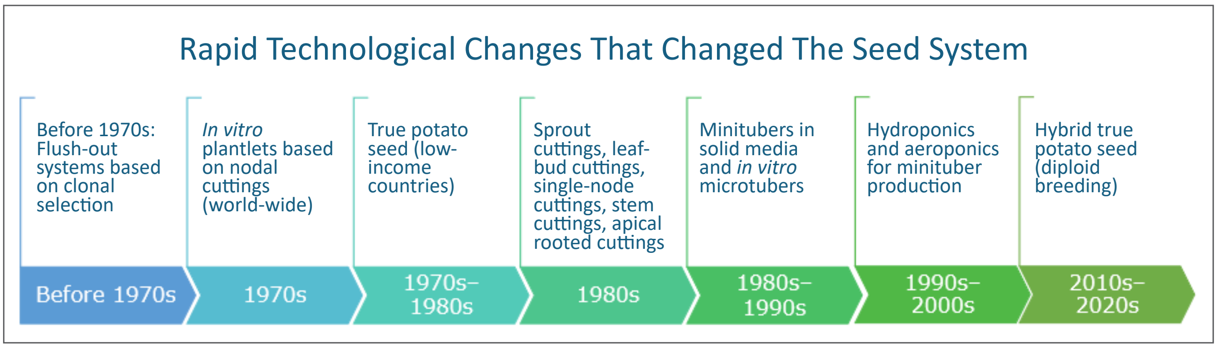

Figure 2. The rapid changes in multiplication of potato over the last 50 years. Based on Struik (2023).

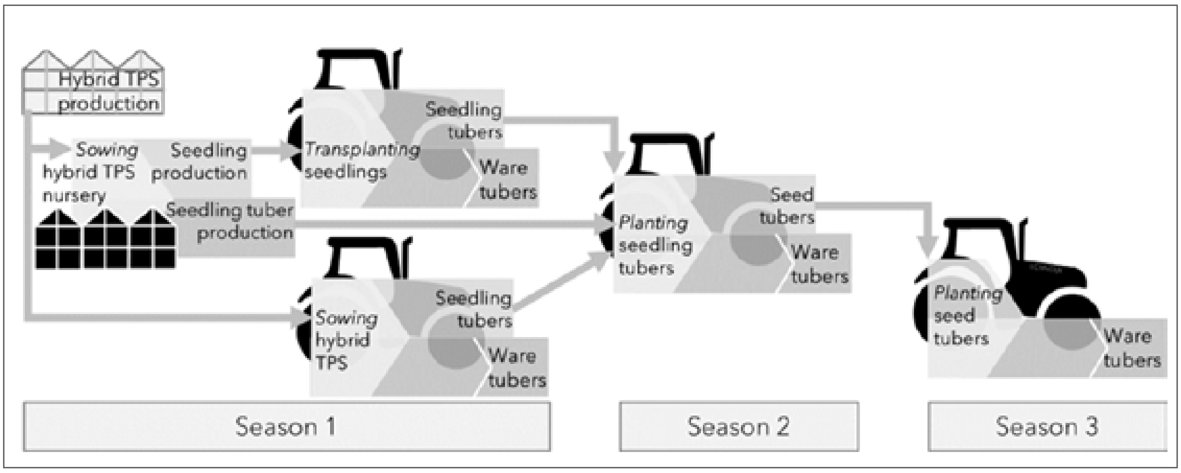

Figure 3. Different cultivation pathways starting from hybrid true potato seed (from van Dijk et al., 2021).

Table 1. Desired characteristics of the different types of propagules that can be produced in a diploid hybrid potato seed system.

Propagule Type	Size	Health	Physiology	Pre-Treatment	Other Characteristics
True Seed	Large and uniform	Disease-free (no viroids)	No dormancy; Maximum germination rate and seedling vigour	Seed priming	Properly enriched coating; Pellet size and shape should match sowing machine
Transplant	Right size; Proper leaf area; Compact; Sturdy; Vigorous	Disease-free	Proper age and status; No progress to tuberization	Properly hardened; Transplant-shock proof	Uniform
Seedling Tuber	Right size; Right number of eyes	Disease-free	Proper physiological age	Pre-sprouted	Proper number of sturdy sprouts after pre-sprouting
Normal Seed Tubers	Right size	Disease-free	Proper physiological age	Pre-sprouted	Proper number of sturdy sprouts after pre-sprouting

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