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Agronomic consequences of growing field-transplanted hybrid potato seedlings

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Abstract

The introduction of hybrid breeding in potato (*Solanum tuberosum* L.) requires novel and efficient cropping systems for potato production based on true potato seed (TPS). Such systems address the limitations of conventional seed tuber–based systems, including low multiplication rates, high degeneration rates, and high costs of transport and storage. Of the possible cultivation pathways of TPS, we introduce and discuss the potential of field transplanting nursery-raised potato seedlings as an alternative system for seed and ware production. This review discusses the current knowledge available on field transplanting of potato seedlings, the key factors that influence the success or failure of the system, and some of the prospective factors that will influence the wide introduction and utilization of field transplanting of potato seedlings in diverse farming systems. A field transplanting system will require the successful production of seedlings in the nursery, a successful establishment of transplanted seedlings in the field, and successful crop management to attain a productive seed or ware crop. The contribution of various factors in the various phases of the system to the success of the transplanted crop is also discussed. The introduction and utilization of the field transplanting system will be accelerated when hybrid breeding focuses on the introgression of traits of interest into high yielding cultivars and when agronomic studies focus on defining factors influencing productivity in distinct phases of the system.

1 INTRODUCTION

The demand for seed potato (*Solanum tuberosum* L.) production systems with high multiplication rates, guarantee for clean and healthy seed tubers for ware potato production, and low requirements for transportation and storage

drive the need for novel seed and cropping systems for seed tuber and ware potato production (Box 1). Potato is traditionally clonally propagated in classical tuber multiplication systems where tubers are produced under protected environments (Lommen, [1995;](#page-16-0) Struik & Wiersema, [1999\)](#page-17-0) and later multiplied under field conditions in one or more generations (Lommen, [1995, 1999;](#page-16-0) Özkaynak & Samanci, [2006;](#page-17-0) Struik & Wiersema, [1999\)](#page-17-0). The system, called "clonal selection," uses pathogen-free and homogeneous plants as starting

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Abbreviations: CIP, International Potato Centre; G1−G9, Generations 1–9; Mg ha[−]1, Mega grams per hectare; OP TPS, open-pollinated true potato seeds; SSA, Sub-Saharan Africa; TPS, true potato seeds.

material to produce tubers that are subsequently multiplied through repeated multiplications under field conditions (Struik & Wiersema, [1999\)](#page-17-0).

Alternative rapid multiplication techniques, such as the use of apical cuttings, meristems, nodal cuttings, and mini- and micro-tubers, have also been developed, where in vitro systems are utilized, and certified seed tubers are produced in less time—3–5 years—as some phases are carried out in vitro and semi in vivo (Kawakami & Iwama, [2012;](#page-16-0) Struik & Wiersema, [1999;](#page-17-0) Vander Zaag et al., [2021\)](#page-17-0). The use of tissue culture and rapid multiplication through meristem culture, the production of mini-tubers, or nodal cuttings is currently a widely adopted system in both developed and developing countries (Harahagazwe, Andrade-Piedra, et al., [2018;](#page-16-0) Muthoni & Shimelis, [2023;](#page-17-0) Struik & Wiersema, [1999\)](#page-17-0). Several other systems are also available in which the multiplication of plant materials is conducted under seminatural conditions (i.e., semi-in vivo systems, such as glasshouse, screenhouse, and nethouse conditions) (Fornkwa et al., [2022;](#page-16-0) Muthoni & Shimelis, [2023;](#page-17-0) Muthoni et al., [2013;](#page-17-0) Struik & Wiersema, [1999\)](#page-17-0). These semi-in vivo systems commonly include the use of seed tubers as starting materials (Struik & Wiersema, [1999\)](#page-17-0) to produce cuttings—stem, sprout, leaf bud, and single-node cuttings—(Struik & Wiersema, [1999\)](#page-17-0) as well as mini-tubers (Lommen & Struik, [1992\)](#page-16-0). Other systems, such as aeroponics and hydroponics, have been introduced and applied in some countries for mini-tuber production (see Calori et al., [2018;](#page-15-0) Mateus-Rodriguez et al., [2013;](#page-17-0) Mbiyu et al., [2012;](#page-17-0) Muthoni & Shimelis, [2023;](#page-17-0) Muthoni et al., [2022\)](#page-17-0).

These aforementioned systems generate various propagule types, which vary in field performance and subsequent yield (Struik & Wiersema, [1999\)](#page-17-0). In general, the limitations of the rapid multiplication techniques are the cost of the production of large quantities of starting materials through the application of the in vitro and semi-in vivo technologies. Other overarching important limitations of both clonal selection and rapid multiplication techniques lie in the low multiplication rates of seed potatoes (Box 1)—currently factor 10—the high degeneration rates, and the high costs of storage and transport (Figure [1,](#page-3-0) Lindhout et al., [2011\)](#page-16-0). Collectively, all systems are laborious and time-consuming because they always require repeated multiplications under field conditions. Consequently, the accumulated costs of production of a single seed tuber over several years by first in vitro or semiin vivo production and later field multiplications are very high but become significantly lower with an increase in the number of field multiplications. However, more field multiplications also mean continued seed degeneration, especially when poor quality seed tubers are used in field multiplication and when high natural pest and disease pressure of either soilborne, waterborne, or airborne pests and diseases occur. This illustrates the trade-off between the price and quality of seed tubers.

- ∙ Hybrid true potato seeds from hybrid breeding provide cultivation pathways for seed and ware potato production.
- ∙ Field transplanting of potato seedlings is a novel, feasible, and resilient cropping system for potato production.
- ∙ Transplanting provides the fastest option to obtain the seed or ware of all true potato seed–based cropping systems.

An efficient production system for potato seed (and ware) is therefore required as suggested by Lindhout et al. [\(2011\)](#page-16-0). We envision a system that boasts high multiplication rates of clean starting material to generate even larger quantities of quality seed and ware potatoes in the shortest amount of time possible for both high and low mechanized farming systems and both large and small farm holdings. Furthermore, the system should be easily adaptable to various farming systems and prove profitable and sustainable for both large- and smallscale farmers and various players in the potato seed and ware production chains.

This review introduces the possibility of a field transplanting system of nursery-raised potato seedlings as a viable and efficient seed production and cultivation system for potato production. This review highlights the current status of the novel transplanting systems in potato production and the possible future of the system based on our knowledge and experiences. We, therefore, discuss how a field-transplanted seedling system in potato production would work. First, we propose and discuss distinct phases of the system by (1) outlining the activities that need to be conducted in each defined phase, (2) defining factors that would influence the success of the said phases, and (3) highlighting current knowledge and practice. Additionally, we highlight some requirements of the prospective system in contrast to the conventional potato production system, prospective drivers for the adoption of the system in selected cropping systems, and the research contributions required to address further various knowledge gaps of the phases of the systems to provide much needed knowledge and practice.

1.1 Novel cultivation systems

Cultivation systems based on true potato seeds (TPS) were introduced as an alternative for seed and ware tuber production (Almekinders et al., [2009;](#page-15-0) Malagamba, [1988\)](#page-17-0) as they offered many advantages over the then existing conventional

Box 1: Definitions of different types of tubers

To facilitate the understanding of various terms in this review, we define the different types of tubers. We use the term *seedling tubers* to define tubers derived directly from TPS and these seedling tubers could be used as either seed or ware potatoes (Struik & Wiersema, [1999;](#page-17-0) Almekinders et al., [2009;](#page-15-0) Stockem et al., [2020;](#page-17-0) Kacheyo et al., [2021\)](#page-16-0). The term *seed potatoes*, on the other hand, refers to the end use of tubers derived from mother plants grown from either seedlings, seedling tubers, or any other tuber propagules (Struik & Wiersema, [1999;](#page-17-0) Almekinders et al., [2009;](#page-15-0) Stockem et al., [2020;](#page-17-0) Kacheyo et al., [2021\)](#page-16-0). *Ware potatoes* refer to any commercial end use of tubers derived from mother plants grown from all possible propagules of potato and are fit for consumption, processing, and all other possible end uses.

and rapid seed tuber multiplication systems. Past experiences with open-pollinated (OP) TPS already set precedence for the choice of cropping system as detailed research was conducted to explore different aspects of the TPS technology, including breeding, seed management, sowing, and agronomy (Almekinders et al., [1996, 2009\)](#page-15-0). Regarding the agronomy aspects of the technology, various cultivation systems for OP TPS were proposed: direct field sowing of OP TPS and the use of nurseries to produce either transplants, seedling tubers, or ware tubers (Figure [2,](#page-3-0) Almekinders et al., [1996,](#page-15-0) [2009\)](#page-15-0). The main disadvantage of OP TPS was the high heterogeneity of the material, especially with the increased need for highly uniform cultivars in the processing markets (van Dijk et al., [2021\)](#page-17-0). However, these challenges are now addressed through the introduction of hybrid diploid breeding (Lindhout et al., [2011\)](#page-16-0), through which the resulting F1 hybrid TPSs are highly uniform and still maintain the many advantages of OP TPS (see Lindhout et al., [2018\)](#page-16-0).

Results of the studies on the feasibility of the TPS-based systems highlighted multiple advantages of the individual cultivation pathways and the challenges that should be addressed to ensure the success of the systems (Almekinders et al., [1996;](#page-15-0) Struik & Wiersema, [1999;](#page-17-0) Almekinders et al., [2009\)](#page-15-0). OP TPSs were proven too vulnerable for direct field sowing and multiple bottlenecks, mainly agronomic, plant physiological and genetic, which influence successful crop establishment, vigor and growth were previously defined (Almekinders et al., [2009;](#page-15-0) Martin, [1983\)](#page-17-0). On the other hand, the use of seedling tubers is still a viable option, nonetheless, it still revolves around the success of a direct-

sown or field-transplanted crop to generate seedling tubers for use in the second generation (Figure [2\)](#page-3-0). Alternatively, seedling tubers could be produced under nursery conditions as described by Struik & Wiersema [\(1999\)](#page-17-0). The clear downsides to this system are, however, the costs of the production of seedling tubers under these protected environments and the additional time required for further multiplications in the field to produce large quantities of larger seed or ware tubers that are—especially for ware tubers—much more desirable for the processing markets (Struik & Wiersema, [1999\)](#page-17-0). Additionally, the nursery-based seedling tuber production requirements could still be considered demanding in smallholder farming systems, because, although the planting of TPS and TPS-derived propagules has been practiced by farmers in different regions—Bangladesh, China, Vietnam, Peru, Nicaragua, India, and so on (Almekinders et al., [2009\)](#page-15-0)—for years, the levels of knowledge for intensive nursery management and the production of quality starting materials are still limited, and more so for regions where the TPS technology is relatively novel or not introduced yet. The transplanting system is, therefore, currently the most feasible of the three TPS-based cultivation systems and the first step of seed or ware tuber production directly from TPS.

2 FIELD TRANSPLANTING OF NURSERY-RAISED HYBRID POTATO SEEDLINGS

A transplanting system involves the production of seedlings from TPS sown in nurseries and later field transplanting to produce seedling or ware tubers. Compared to the direct sowing system, field transplanting overcomes the problems during the early growth phase by closely growing and managing seedlings under more protected conditions, in the nursery, instead of under field conditions (Almekinders et al., [2009;](#page-15-0) Struik & Wiersema, [1999;](#page-17-0) van Dijk et al., [2021;](#page-17-0) van Dijk, Kacheyo, et al., [2022\)](#page-17-0). Depending on the nursery, seedling growing conditions can be largely controlled and optimized to enhance germination, emergence as well as seedling vigor, and quality. Additionally, the control of pests and diseases and other potentially harmful biotic and abiotic stresses can be easily managed in the nursery as smaller unit areas of production and even smaller volumes of substrate and water are utilized as opposed to field conditions, making the disinfection of materials manageable. The transplanting system, therefore, guarantees clean and healthy seedlings at field transplanting, after which field conditions will determine crop health and phytosanitary quality.

In this paper, we define seedling quality as the capacity of a seedling to establish, grow, and develop well after field transplanting; seedling quality could be categorized into low, medium, and high depending on the performance of

FIGURE 1 Graphic illustration of seed multiplication in both conventional (a) and true potato seed (TPS)-based (b) seed tuber multiplication systems. In the conventional system (a), Generations 1–9 (G1–G9) represent the generations taken to achieve a particular number of tuber copies over time—multiplication ratio of 10 seed tubers per plant (see Struik & Wiersema, [1999;](#page-17-0) van Dijk et al., [2021\)](#page-17-0). In these systems, tuber multiplications face high risks of tuber degeneration over time especially when quality and health of seed tubers is not maintained. In hybrid TPS-based systems (b), a single seed of an inbred line is the starting point of the production chain, and the plant generated is self-pollinated to further produce seeds that are utilized as female parental plants—multiplication ratio of 5000 seeds plant⁻¹ (Almekinders & Wiersema, [1991\)](#page-15-0). These female plants are further cross-pollinated to produce hybrid seeds—using similar multiplication rate—thereby achieving higher copy numbers in both the TPS and subsequent tubers generated within a crop cycle, early on in the production chain. The male pollen-donor plants are not included in the illustration. The dashed line represents the shift from TPS to tuber starting materials and the subsequent change in multiplication rate between the two systems. Due to the clean hybrid TPS utilized, the quality and health of successive generations can be guaranteed for larger quantities of tubers in the TPS systems in contrast to similar quantities in the tuber system.

FIGURE 2 Schematic representation of true potato seed (TPS)-based cultivation pathways for seed and ware production adapted from Almekinders et al. [\(2009\)](#page-15-0) and van Dijk et al. [\(2021\)](#page-17-0). Propagules are depicted in blue boxes and green ovals depict the activity required to generate the propagule. Light gray boxes depict first-generation harvested tubers and their possible uses, similar to dark gray boxes, which depict the second-generation harvests and their possible uses.

the seedling. On the other hand, we define seedling vigor in hybrid seedlings, as comprising properties that define the potential for rapid field establishment, growth, and development of seedlings under a wide range of field conditions (see Ros et al., [2003\)](#page-17-0). For hybrid true seedlings, seedling quality and vigor attributes have not been further explored beyond the application of the number of leaves and stem length as selection criteria as utilized by van Dijk et al. [\(2021\)](#page-17-0), van Dijk, Kacheyo et al. [\(2022\)](#page-17-0). In comparison, for in vitro potato plantlets, leaf initiation rate—increase in the number of leaves—individual leaf area, and accumulated leaf dry matter are used as quality indicators (Tadesse et al., [2000\)](#page-17-0). These attributes reflect vigor, thereby proposing additional attributes for the description of seedling vigor in potato.

2.1 High multiplication factors

The demand for fewer generations of multiplications from seed (TPS or seed tuber) to commercial seed tubers makes the field transplanting system a more desirable system as, under field conditions, a single generation is required to generate large quantities of uniform "true to type" seedling tubers from hybrid seedlings (Figures [1](#page-3-0) and [2,](#page-3-0) de Vries et al., [2016;](#page-15-0) Muthoni et al., [2014;](#page-17-0) Stockem et al., [2020\)](#page-17-0). TPS systems, therefore, boast high multiplication rates, with multiplication ratios of *>*1000 true seeds per plant (Almekinders, [1995;](#page-15-0) Almekinders & Wiersema, [1991\)](#page-15-0), which is in contrast to the conventional and rapid clonal multiplication techniques that typically achieve multiplication ratios of 10 seed tubers per plant (Figure [1,](#page-3-0) see de Vries et al., [2016;](#page-15-0) Struik & Wiersema, [1999;](#page-17-0) van Dijk et al., [2021\)](#page-17-0). With hybrid TPS, large quantities of seeds can be sown and developed into seedlings that are field-transplanted in shorter periods of time. Furthermore, by manipulating crop management factors, such as plant density, tillage systems, and fertilization, tuber size distributions can be influenced, and production can be easily steered to develop material for either seed or ware already in the first field season (Struik & Wiersema, [1999;](#page-17-0) van Dijk, de Vries, et al., [2022\)](#page-17-0). Currently, the cost of hybrid seedlings is not known and will also depend on region and farming system. Therefore, differences in economies of cost between seedlings and tubers as well as the complete economic advantage of the seed tuber as opposed to the TPS-based systems cannot be discussed. However, van Dijk et al. [\(2021\)](#page-17-0) assessed the potential impact of transplanted hybrid seedlings on the total acreage of the Dutch potato value chain using standard planting densities of 66,667 and 44,444 plants ha⁻¹ for seed tuber and ware production, respectively, and a seed to ware crop acreage ratio of 1:10 (Struik & Wiersema, [1999\)](#page-17-0). It was calculated that 7.8 ha of greenhouse nursery is needed to serve the Dutch ware production (77,557 ha) with first-generation seedling tubers derived from transplants. For exported seed

tubers, 3.6 ha of greenhouse nursery for seedling production is required to produce third-generation seed tubers, in three seasons, on 30,422 ha to cover the export demand. Additionally, by using hybrid transplants—raised in 11.4 ha of greenhouse nursery—producing these first- and third-generation seed tubers instead of the current conventional clonal propagation, which takes 5–8 years to reach a sufficient amount of seed tubers, a country like the Netherlands can save almost 900 ha of acreage (using above 1:10 ratio) needed for clonal propagation.

2.2 Success in field transplanting systems

The adoption of the field transplanting of seedlings of vegetables and other arable crops also provides a large basis for a possible transplanting system in potato production. Currently, in both large- and smallholder farming systems, various vegetable crops, such as lettuce (*Lactuca sativa*, Kerbiriou et al., [2013\)](#page-16-0), cabbage types (*Brassica* spp.), onion (*Allium cepa*, Elhami et al., [2021\)](#page-15-0), tomato (*Solanum lycopersicum*, Garner & Björkman, [1999\)](#page-16-0), and other arable crops, such as rice (*Oryza sativa*, Liu et al., [2017\)](#page-16-0) and tobacco (*Nicotiana tabacum*, Bennett et al., [1999\)](#page-15-0), are field-transplanted. Transplanting provides seedlings a higher competitive ability toward weeds as opposed to direct field sowing (Kerbiriou et al., [2013\)](#page-16-0) and provides a crop with high uniformity and robust crop stands (Lewthwaite & Triggs, [1999\)](#page-16-0) by providing the possibility to select uniform and highly vigorous seedlings for transplanting. Additionally, transplanting provides multiple possibilities for crop scheduling (Kerbiriou et al., [2013\)](#page-16-0), especially in rotations with other primary and/or catch crops (van Dijk, Kacheyo, et al., [2022\)](#page-17-0). Seedlings can be raised in nursery structures with varying levels of technology while still maintaining seedling quality aspects required for field transplanting.

In potato, field transplanting of seedlings generated from other propagules such as in vitro plantlets (Lommen, [1999,](#page-16-0) [2015\)](#page-16-0) and apical and axillary cuttings (Parker, [2017, 2019;](#page-17-0) Struik & Wiersema, [1999,](#page-17-0) Vander Zaag et al., [2021\)](#page-17-0) has been reported. In contrast to these systems, seedlings generated from TPS are true seedlings, as they are generated directly from botanical seed and therefore physiologically differ in comparison to the in vitro plantlets and cuttings. In vitro plantlets and cuttings do not originate from botanical seeds and therefore require clean starting material for production and similar to other rapid multiplication techniques, the generation of large quantities of materials will prove costly when large quantities of materials are required, especially for in vitro plantlets.

Additionally, to obtain the required quantities and the size of seed tubers for ware production, multiple seasons of multiplication are still required under field conditions, because

Source	Year	Genotype	Tillage system	Density (plants ha^{-1})	Average yields $(Mg ha^{-1})$	Seed tuber yields $(Mg ha^{-1})$
van Dijk et al. (2021)	2017		Ridge	66,667	28.20	
	2018		Ridge	66,667	28.50	
	2017	H ₀₃	Ridge	66,667	30.30	
		H ₀₄	Ridge	66,667	26.20	
	2018	H03	Ridge	66,667	32.40	
		H04	Ridge	66,667	24.70	
van Dijk, de Vries et al. (2022)			Flat bed	$\overline{}$	107.00	
			Ridge	$\qquad \qquad -$	45.00	
			Ridge	31,300	12.48	8.65
				46,900	14.18	10.72
				62,500	17.69	13.40
				125,000	23.82	17.24
				250,000	29.79	21.16
				500,000	28.52	19.91
			Flat bed	62,500	35.80	24.07
				125,000	45.63	31.19
				250,000	53.68	39.50
				500,000	68.35	51.83
				1,000,000	68.33	45.33
				2,000,000	70.25	40.76
Adams et al. (2022)	2019	806 Experi- mental	Ridge	53,333	22.40	

TABLE 1 Yields of transplanted hybrid seedling crops as reported in literature (van Dijk et al., [2021;](#page-17-0) van Dijk, de Vries, et al., [2022\)](#page-17-0).

hybrids

Note: Yields were attained in trials where crop management factors were assessed on their contributions to field transplanted potato crop yields and yield components.

the first rounds of multiplication are never intended for ware (Parker, [2017;](#page-17-0) Struik & Wiersema, [1999;](#page-17-0) Tadesse et al., [2000\)](#page-17-0). Ultimately, the use of TPS-based systems boasts more advantages in comparison to these systems as seedlings produced are uniform, vigorous, and robust and also produce a large number and wide size range of tuber size, which can be immediately used for seed or ware (Figures [1](#page-3-0) and [2;](#page-3-0) Table 1; van Dijk et al., [2021;](#page-17-0) van Dijk, de Vries, et al., [2022;](#page-17-0) van Dijk, Kacheyo, et al., [2022\)](#page-17-0). This reinforces the notion that the uses of transplanted seedlings outperform most of the rapid multiplication technologies currently utilized in production in terms of multiplication factors as well as the purpose of first-generation tubers. Additionally, the conventional technique of tuber multiplication is still considered resilient thereby making it the most prevalent method for seed and ware tuber production, especially in Africa (Muthoni & Shimelis, [2023\)](#page-17-0); therefore, the comparison of field transplanting to the conventional systems still remains vital.

2.3 Yield prospects for potato transplant systems

Yield differences in field-transplanted seedling crops have so far—to the best of our knowledge—been attributed to transplanting density (Çalişkan et al., [2009;](#page-15-0) van Dijk, de Vries, et al., [2022\)](#page-17-0), crop cycle length (van Dijk, Kacheyo, et al., [2022\)](#page-17-0), and growing season (Engels et al., [1994\)](#page-16-0). Kacheyo et al. [\(2021\)](#page-16-0) also suggested that morphological differences between crops from seedling and tuber propagules may contribute to differences in yield and yield components in these crops. Moreover, within the transplanting cultivation pathway, three physiologically distinct hybrid TPS-based propagules are generated: (1) seedlings from TPS, (2) seedling tubers from field-transplanted seedlings, and (3) tubers from seedling tubers (Box 1, Figure [2,](#page-3-0) Kacheyo et al., [2021\)](#page-16-0). Struik and Wiersema [\(1999\)](#page-17-0) compared and discussed differences among directly sown TPS, seedling transplants, and seedling tubers based on OP TPS. Seedling performance was in between the two propagule types. Studies on the improved hybrid TPS are required to ascertain the differences in performance between propagules.

Van Dijk et al. [\(2021\)](#page-17-0) reported the first yields of fieldtransplanted hybrid potato seedlings under Dutch conditions using experimental hybrid genotypes at a planting density of 66,667 plants ha⁻¹ (Table [1\)](#page-5-0). These yields were slightly lower than the average Dutch seed tuber yields of 36 Mg ha⁻¹ (2010–2019) and much lower than the average ware potato yields of 49 Mg ha⁻¹ (2010–2019) (van Dijk et al., [2021\)](#page-17-0). Furthermore, Adams et al. [\(2022\)](#page-15-0) presented the yields of a large panel of 806 field-transplanted experimental hybrids, with an average of 22.4 Mg ha⁻¹, with more than 50 of these hybrids yielding more than 40 Mg ha⁻¹. These yields (Table [1\)](#page-5-0) give the yields of the field transplanting system some competitive abilities against the yields of the typical Dutch conventional system, especially since experimental hybrids were used in these trials. Moreover, comparing seed tuber yields from seedlings to the Dutch average, the yield gap can be closed under specific conditions. When breeding focuses on improving hybrid cultivar yields and introgressing desirable traits into hybrid cultivars, a larger competitive advantage will be attained for hybrid TPS-based systems, especially for the field transplanting system (de Vries et al., [2023\)](#page-15-0).

2.4 Bottlenecks

The primary limitation of a possible field transplanting system is the high susceptibility of potato seedlings to transplanting shock, which in extreme situations leads to crop losses (Almekinders et al., [2009;](#page-15-0) van Dijk, Kacheyo, et al., [2022\)](#page-17-0). Transplanting shock and poor establishment of transplanted seedlings can be caused by a wide range of factors, the impact of which may vary depending on cropping and farming system as well as resource availability. Currently, little is known about transplanting shock in seedlings grown from hybrid TPS, but recent successful transplanting of potato seedlings in contrasting field seasons under Dutch (Adams et al., [2022;](#page-15-0) van Dijk et al., [2021;](#page-17-0) van Dijk, de Vries, et al., [2022;](#page-17-0) van Dijk, Kacheyo, et al., [2022\)](#page-17-0) and East-African conditions (de Vries et al., [2016\)](#page-15-0) have been reported. Studies on transplant establishment, in varying environmental and farm management conditions, are therefore still required, to guide farm decisions on managing a transplanted crop. Other bottlenecks in the systems include the possibility of early tuberization even in the nursery due to the overdevelopment of seedlings or possible seedling stress, which translates into premature tuberization even in the field (Almekinders et al., [2009\)](#page-15-0). Yield losses due to premature tuberization have not been quantified in literature; however, it has been linked to poor field establishment and low tuber yields in the field (Engels et al., [1994;](#page-16-0) [1995\)](#page-16-0). During

transplanting, seedlings, especially root tissue, are exposed to mechanical damage risking susceptibility to soilborne pests and diseases as wounding facilitates their entry into plant tissue (Kerbiriou et al., [2013;](#page-16-0) van Dijk et al., [2021;](#page-17-0) van Dijk, Kacheyo, et al., [2022\)](#page-17-0).

3 ASPECTS OF SEEDLING TRANSPLANT AND FIELD CROP MANAGEMENT

The success of a field-transplanted seedling crop hinges on (1) the successful production of quality seedlings in seedling nurseries, (2) successful establishment of seedlings under field conditions, and, ultimately, (3) successful crop management to generate a productive seed and ware crop (Table [2\)](#page-7-0). In this section, we discuss in detail selected critical factors that should be considered (as described in Table [2\)](#page-7-0) to assure success in the aforementioned phases of the transplanting system.

3.1 Seedling nursery management

In seedling production systems, seeds are sown and raised under more protected environments compared to field conditions with the goal of producing high-quality seedlings suitable for transplanting (Struik & Wiersema, [1999\)](#page-17-0). Nursery systems range from controlled, semi-controlled to traditional structures, where factors, such as temperature, light, humidity, and water, can be fully or partially regulated (Villalobos et al., [2016\)](#page-18-0). In the nursery, substrates can be prepared depending on crop requirements, and adverse conditions for seedling production such as pests and diseases, weeds, predators and adverse environmental conditions—drought, salinity, wind, hail, heat—can also be circumvented. Various factors still influence the success of nursery seedling production, including both environmental and nursery management factors. Studies to assess the growth and development of seedlings under nursery conditions with a focus on these factors would provide boundaries and optimal conditions for successful seedling production. Previous studies on germination capacity and dormancy breaking in TPS have been reported (Pallais, [1987;](#page-17-0) Tuku, [1994;](#page-17-0) Pallais et al., [1996;](#page-17-0) Cha et al., [2011\)](#page-15-0). Alpers and Jansky [\(2019\)](#page-15-0) also described characteristics such as germination percentage and leaf area and their influence on seedling vigor in TPS based on seed germination and seedling vigor studies. Van Dijk et al. [\(2021\)](#page-17-0), on the other hand, described a protocol for hybrid potato seedling production under greenhouse conditions for the development of seedlings for field transplanting experiments. A seedling was deemed transplantable when possessing five to eight fully developed true leaves and a stem length between 7 and

TABLE 2 Summary of description of key success and key failure factors in the transplanting system for both the nursery and field phases.

Nursery phase High seedling quality Poor seedling quality Nursery management Environmental stress factors Climate management Poor nursery management Seed dormancy Premature tuberization Field phase Optimal field preparation Seedbed preparation Poor field preparation Poor seedbed quality
Tillage
Seedling establishment Transplanting shock Transplanting date Poor seedling vigor
Fertilization Adverse environmental conditions
Irrigation
Density
Optimal crop management Biotic stress Poor crop management Crop management
Pest and disease Abiotic stress management
Weed control Premature tuberization
Harvesting date
High crop productivity Low crop productivity High yields Low yields
Shifts in tuber size Desired tuber size distributions distributions
Poor quality tubers High quality tubers

12 cm (Kacheyo et al., [2021;](#page-16-0) van Dijk et al., [2021;](#page-17-0) van Dijk, Kacheyo, et al., [2022\)](#page-17-0). In the protocol, a hardening-off exercise was also carried out by placing trays in a screenhouse for 1 week, but the effects of hardening-off in hybrid TPS were not quantified (van Dijk et al., [2021\)](#page-17-0). Therefore, little is known about the contribution of a seedling's condition at the time of transplanting to successful field establishment for hybrid potato seedlings, and of the many factors, seedling age and growth stage are the only factors, the effects of which have since been reported (van Dijk, Kacheyo, et al., [2022\)](#page-17-0). Further studies on the contribution of environmental factors and their accumulated effects over time to seedling vigor and possible premature tuberization in the seedling nursery are required. Additionally, the effects of seedling conditions at field transplanting on seedling establishment and potential mitigation of transplanting shock should be conducted to provide more critical information on potato seedling production.

3.2 Transplanting and field crop management

Currently, both mechanical and manual transplanting of seedlings is possible. The use of vegetable transplanting machines for potato transplanting has been successfully

attempted for large-scale seed production from transplanted seedlings. The possibility of adopting preexisting mechanized vegetable transplanting methods for potato seedlings is paramount as it would allow for minimal to zero changes in systems for vegetable growers who wish to include transplanted potato in their systems (van Dijk et al., [2021;](#page-17-0) van Dijk, Kacheyo, et al., [2022\)](#page-17-0). Detailed agronomic studies on transplanting machinery and their applicability for transplanted potato systems are required. Another critical factor to take into account is the field history relevant for soilborne pests and diseases and other factors that could reduce transplant productivity, because seedling quality is guaranteed from the nursery up until transplanting and exposure to adverse field conditions will greatly influence product quality and quantity. After field establishment, seedling crop management practices need to be conducted to promote fast canopy development and closure as well as tuberization processes in the seedling crop, especially due to the known influence of several crop management factors on tuber yield and quality (Struik & Wiersema, [1999\)](#page-17-0).

3.2.1 Timing of field transplanting exercises

Transplanting timing involves scheduling the moment of transplanting to avoid coincidence with adverse weather conditions and to mitigate the effects of transplanting shock

(Almekinders et al., [1996;](#page-15-0) Muthoni et al., [2014;](#page-17-0) van Dijk et al., [2021;](#page-17-0) van Dijk, Kacheyo, et al., [2022\)](#page-17-0). Depending on region and cultivation systems, windows for transplanting differ in length (Vavrina, [1998\)](#page-18-0). Under Dutch conditions, the effects of transplanting date were assessed, and van Dijk, Kacheyo et al. [\(2022\)](#page-17-0) reported the possibility of transplanting greenhouse-raised hybrid potato seedlings at any moment in the Dutch spring, provided conditions remain suitable since extreme weather conditions such as frost cause irreparable damage to potato plants and remain a high risk to potato production (Hijmans et al., [2003\)](#page-16-0). In the study, van Dijk, Kacheyo et al. [\(2022\)](#page-17-0) reported that shorter and less severe frost events were bearable for the hybrid transplanted seedlings. In other regions, transplanting could coincide with limited rainfall, which needs to be supplemented with irrigation, especially during field establishment, and applied close to the seedlings to ensure uptake and avoid water loss. Irrigation could reduce transplant shock. Therefore, a transplanting exercise for field-transplanted potato seedlings should be carried out to assess which field conditions will favor seedling establishment. Hardening-off could be a possible method to improve seedling resilience under field conditions; however, the role of hardening-off in mitigating transplanting shock in hybrid seedlings is still unknown.

3.2.2 Tillage systems

The choice of tillage system is crucial, especially in a field transplanting system, as the effects of tillage techniques on tuber quality have been previously reported (Struik & Wiersema, [1999\)](#page-17-0), and good seedling bed preparation is required to provide moisture and aeration, easing seedling establishment and root growth, and also allowing effective growth of the seedlings (Stark & Thornton, [2020\)](#page-17-0). Seed tuber grown potato is cultivated largely on ridges (Bohl et al., [2014;](#page-15-0) Kouwenhoven, [1970;](#page-16-0) Kouwenhoven et al., [2003;](#page-16-0) Pavek, [2014\)](#page-17-0) with variations in inter- and intra-row spacings depending on cropping systems and purpose of the crop in various regions (see Deb et al., [2013;](#page-15-0) Oliveira et al., [2016;](#page-17-0) Stockem et al., [2020\)](#page-17-0). For tuber-grown potato crops, the relationships among ridge quality, potato growth, yield, and tuber quality have been previously studied (Bohl et al., [2014;](#page-15-0) Djaman et al., [2022;](#page-15-0) Kouwenhoven et al., [2003;](#page-16-0) Love et al., [2020\)](#page-16-0). Increase in ridge height reduced tuber greening and ridge shape and height influenced average tuber sizes and yield (see Bohl et al., [2014;](#page-15-0) Djaman et al., [2022;](#page-15-0) Kouwenhoven et al., [2003\)](#page-16-0).

Bed systems, on the other hand, are also commonly used where multiple rows of potato plants are planted in elevated flat areas (Mundy et al., [1999;](#page-17-0) Taberna, [2009\)](#page-17-0). Bed systems improve soil water retention (Harms & Konschuh, [2010;](#page-16-0) Mundy et al., [1999\)](#page-17-0), albeit with little effect on yield (Mundy

et al., [1999\)](#page-17-0). In contrast, Fisher et al. [\(1995\)](#page-16-0) showed a yield gain in flat beds compared to ridge systems. For transplant systems, studies on the influence of various bed and ridge systems on crop management and yield should therefore be conducted, especially considering the possibilities for adopting existing potato tillage systems as well as other systems used in transplanted vegetable crops for the field transplanting system as suggested by van Dijk et al. [\(2021;](#page-17-0) van Dijk, Kacheyo, et al., [2022\)](#page-17-0). We hypothesize that the differences in morphology of seedling-grown versus tuber-grown crops influence the subsequent position of tubers in a seedling bed (see Kacheyo et al., [2021\)](#page-16-0). Therefore, the choice of a tillage system and the transplanting depth of seedlings used in the said system will influence tuber placement in the root zone and tuber greening. A hilling exercise could therefore be used to add additional soil layers to cover tubers and also allow for the creation of more tuber formation positions on the stems (Struik, [2007\)](#page-17-0) in transplanted systems. Studies show that additional hilling did not increase yield but led to an increase in the number of small tubers produced (van Dijk et al., [2021\)](#page-17-0). Other possibilities include using V-shaped ridges as illustrated by van Dijk et al. [\(2021\)](#page-17-0) and/or including mechanical weeding that will concurrently "earthen-up" the seedlings, similar to a hilling system.

3.2.3 Transplanting density

Planting density is one of the tools in potato production used to steer tuber size distribution to desired tuber sizes required for particular markets (Struik et al., [1990;](#page-17-0) van Dijk, de Vries, et al., [2022\)](#page-17-0). Yield enhancement and changes in the trends of tuber size distribution emanated from the manipulation of densities of transplanted seedlings (Çalişkan et al., [2009;](#page-15-0) van Dijk, de Vries, et al., [2022\)](#page-17-0). van Dijk, de Vries et al. [\(2022\)](#page-17-0) reported that the optimum density for larger tubers (*>*50 mm) was 12.5 plants m^{-2} on sandy soils and that of small tubers (20 *<* size class ≤ 35 mm) was 200 plants m−² showing that increasing densities resulted in reduced numbers of larger tubers and observed increases of smaller tubers (Table [1\)](#page-5-0). Recently, van Dijk, de Vries et al. [\(2022\)](#page-17-0) reported yields of transplanted potato seedlings on both ridge and bed systems where higher densities of up to 200 plants m^{-2} were realized in bed systems compared to the 50 plants m^{-2} realized on ridge systems. Higher densities on beds did not significantly influence yield but increased costs of planting materials and the optimum densities were not very different between the two systems (Table [1;](#page-5-0) van Dijk, de Vries, et al., [2022\)](#page-17-0). Additionally, Çalişkan et al. [\(2009\)](#page-15-0) reported higher interplant competition in higher seedling densities in addition to the higher tuber numbers per unit area compared to seed tubers (2002: 58.4, 68.0, 76.4, and 82.2 tubers in TPS hybrids at 15, 20, 25, and 30 plants m[−]2, respectively, and 25.1 tubers for a tuber grown cultivar; 2003: 56.5, 66.9, 75.1, and 79.6 for TPS hybrids at 15, 20, 25, and 30 plants m^{-2} , respectively, and 31.2 tubers for the tuber grown cultivar) even with similar stem numbers per unit area. These results provide possibilities to enhance the production of seed or ware from field transplanted seedlings. Therefore, depending on the purpose of production and to target specific tuber sizes for production, transplanting density should be considered before transplanting (see Beukema & van der Zaag, [1990;](#page-15-0) Çalişkan et al., [2009;](#page-15-0) Struik & Wiersema, [1999;](#page-17-0) van Dijk, de Vries, et al., [2022\)](#page-17-0).

Transplanting density (Engels et al., [1993;](#page-15-0) Fleisher et al., [2011;](#page-16-0) van Dijk, de Vries, et al., [2022\)](#page-17-0) and choice of tillage systems (Djaman et al., [2022;](#page-15-0) van Dijk, de Vries, et al., [2022\)](#page-17-0) will influence canopy development and canopy closure in transplanted crops. The influence of these factors and many more on canopy development and in turn its influence on crop management, yield, and yield components in transplanted crops, have, however, not been reported. Moreover, expected differences in canopy structure, growth rates, and senescence rates based on starting material are already a probable cause for differences in canopy development but have not been explored, nor have their effects quantified. Further studies on canopy development should be quantified to ascertain their contributions to yield and yield components in transplanted seedling crops.

3.2.4 Fertilization

Similar to tuber-grown crops, recommendations for fertilizer application for seed or ware crops for determinate and indeterminate transplanted seedling crops should be developed. Studies should focus on the effects of (1) the timing of fertilization in the cropping season, (2) split applications of nitrogen, and (3) fertilizer application systems, such as foliar applications, granular fertilizer applications, as well as fertigation on tuber number and tuber size distribution. Considerations should also be focused on crop demand– based application of nutrient as opposed to general, blanket applications.

3.2.5 Other cultural practices

Cultivation practices in conventional tuber-based production systems could currently be adapted to field-transplanted systems; however, some critical points should not be overlooked when managing crops of field-transplanted seedlings. Application of crop management in transplanted crops should particularly consider the slow initial growth and resulting longer crop cycle in transplanted crops to avoid high disease pressure, which results in reduced tuber quality and unfa-

vorable tuber size distribution. Additionally, the variation in starting material should be considered to accommodate the differences between transplanted and tuber-grown crops.

4 REQUIREMENTS OF THE NOVEL TRANSPLANTING SYSTEM

Table [3](#page-10-0) summarizes the important contrasts between a TPSbased transplanting system and the conventional tuber-based system, specifically for multiple phases of the growth cycle. The most important contrasts lie within the earlier phases of the systems from seedling production under nursery conditions up until field establishment after transplanting.

4.1 Starting materials

The differences in starting material, between TPS and seed tubers, contribute differently to the requirements of each respective system (Table [3\)](#page-10-0). Other starting materials, such as in vitro plantlets and mini-tubers can come closer to seedlings in terms of demand for various factors as described in Table [3.](#page-10-0) In vitro plantlets are costly and not a feasible alternative for the mass production of seed tubers in the field. On the other hand, the use of mini-tubers might be accompanied by various limitations, including the mostly delayed emergence, slow initial growth vigor, and long growth cycles in some genotypes (Struik & Wiersema, [1999\)](#page-17-0) because, generally, smaller tubers are utilized under field conditions. Moreover, multiple crop cycles are required to produce enough seed, in preferred tuber sizes, for ware production (Figure [1\)](#page-3-0).

4.2 Nursery phase

The nursery phase is unique to the transplanting system and introduces distinct factors that are only relevant when a transplanting system will be carried out. Nursery facilities and the factors that contribute to successful seedling production raise the requirements for the transplanting system. Depending on the nursery system of choice—from high-tech systems to traditional systems—the costs of facilities will also range from high to low, respectively. However, the cost of greenhouse nursery space may also be high, especially when large quantities of seedlings need to be produced for mechanized transplantation or to achieve higher densities in the field (see van Dijk et al., [2021\)](#page-17-0). Even more so, the requirements for seed germination, seedling nursery management, and the control of environmental conditions to steer seedling growth are high for transplant systems and nonexistent for the conventional system.

Conventional seed tuber–based

TABLE 3 Comparison between true potato seed (TPS)-based and conventional tuber-based seed systems.

Seed quality and health High-quality and healthy seed Requires rigorous selection to health Very high multiplication factors Very low multiplication factors es in tuber cially when not and longer time frames (*>*3 years) seedling growth and development **Pre-(trans)planting conditioning** (Preparation of starting material for planting) Sprouting \qquad sprout Seedling/Tuber size High impact of seedling size on seedling field establishment and transplant shock mitigation Clear and defined outcomes for use of particular seed tuber size. Preference for tuber size is based on intended outcomes Hardening-off High requirements to enhance resilience of seedlings to field conditions – Selection Moderate requirements to select for uniformity and seedling vigor High requirements to maintain health and quality **Field establishment** (from transplanting up to 4 weeks after transplanting) Timing of planting Scheduling required to avoid coincidence with adverse field conditions Minimal scheduling required Seed bed preparation Highly important for seedling establishment Not extremely critical for seedling emergence Water supply at transplanting – High requirements to maintained moist seed bed Weed control Very critical due to slow growth in transplants Low requirements compared to transplant systems **Crop growth and development (**from field establishment to harvest) Water supply Similar requirements Weed control High requirements until full crop canopy cover Low requirements Pest and disease management — Similar requirements Fertilization Similar requirements

4.3 Conditions of starting materials

Before transplanting, the requirements for the conditions of starting materials also differ. Seedling vigor is one of the main aspects required in the soon-to-be transplanted seedlings. To achieve high seedling vigor and ensure successful field establishment, selections for high uniformity and vigor should be carried out before transplanting, especially because the condition of the seedlings at transplanting also contributes to mitigating transplant shock. For seed tuber-based systems, selections are critical especially to maintain seed tuber quality and health in the subsequent seed multiplications. When high-quality and uniform cultivars are used, the requirements for selection can subsequently be reduced. A hardening-off exercise can also be carried out to ensure the seedlings are hardy and more resilient to field conditions.

4.4 Field establishment

The possibility of the occurrence of transplanting shock in the field increases the demand for high-quality seedlings for field transplanting as well as the need to carry out crop management activities that can help mitigate the transplanting shock. For tuber-grown crops, seed tubers are planted and left to produce emerging stems and establish minimal requirements for environmental conditions and crop management. The fragility of a seedling, as opposed to tuber starting materials, proves at the very least that the requirements for a successful crop in the early phase of production might be higher for a seedling crop.

4.5 Canopy development and tuberization

Currently, recommendations for crop management practices have not been developed for the transplanting system as such the demand for both systems remains similar for most aspects of crop management. However, for factors such as weed control, extra care should be taken in transplant systems as slow canopy development may require more effort in weed control for the transplant crop. Additionally, the high viability of hybrid TPS increases the potential for the high incidence of volu.nteer plant infestations from fieldtransplanted seedling crops (Askew & Struik, [2007\)](#page-15-0). This is due to the high likelihood of berry setting in hybrid plants as such critical control strategies should be considered during field management to reduce the volunteer potential of the field-transplanting system (Askew & Struik, [2007\)](#page-15-0).

Although the requirements of the transplant system prove higher, more complex, and more demanding in some phases, the benefits of the system over the conventional system as earlier discussed may outweigh the overall costs of the requirements.

5 ACCELERATING UTILIZATION OF TRANSPLANTING SYSTEMS IN POTATO PRODUCTION

Various factors will influence the introduction and adoption of transplanting systems into existing potato cultivation systems and into new systems such as vegetable production systems among others. The introduction and utilization of the transplanting system in various regions may equally be influenced by the success of current cropping systems in said regions, levels of mechanization in these farming systems, and the ease of integration of transplanted potato systems into their current practice. Discussing the factors that will influence the

adoption of the novel cultivation system is beyond the scope of this review; however, we non-exhaustively identify some of the factors that we believe will contribute to the accelerated introduction and utilization of the transplanting system for seed and ware production.

5.1 Introgression of traits of interest

Adoption could be accelerated when advancements in diploid hybrid potato breeding focus on traits of interest that will allow the easy integration of the field-transplanted potato crop into current cultivation systems. Traits of interest include yield, disease resistance, and tuber quality traits, such as tuber color, size, and shape (Werij, [2011\)](#page-18-0). Furthermore, internal quality aspects, including nutritional properties, culinary properties as well as processing quality that is defined by traits, such as starch quality, protein and carbohydrate content, flavor, and dry matter content, are also favorable especially for the processing industry (Carputo et al., [2005\)](#page-15-0). The availability of traits of interest in hybrid cultivars would increase the demand for such genotypes as currently, especially in the case of late blight, there is high demand for commercially successful but highly susceptible cultivars, which limits the cultivation of late blight-resistant cultivars (Kessel et al., [2018\)](#page-16-0). Breeding for resilience to both biotic and abiotic stresses and quality- and consumer-driven traits will target distinct markets and create demand for hybrid cultivars (see Bethke et al., [2019\)](#page-15-0). Additionally, the hybrid breeding system in combination with the high seed multiplication rates lends itself useful for the targeted development of cultivars for specific conditions, while taking into account user and consumer demands, to be made available globally for growers (de Vries et al., [2023;](#page-15-0) ter Steeg et al., [2022\)](#page-17-0).

5.2 Availability of information on transplanted potato production

Another driving factor for interest in the prospective transplanting system is the availability of information on potato production using transplanting systems. When strides are taken to reintroduce TPS-based systems and the transplanting system as the cultivation system of choice to various stakeholders in potato seed systems, chances of adoption will be higher. The availability of protocols and demonstrations of practice can help close the knowledge gaps and increase the interest in transplanted seedling crops because information will be readily available for dissemination to both researchers and farmers as well as other actors in the value chain (see Table [4\)](#page-12-0). TPS-based seed and cropping systems challenge

TABLE 4 Non-exhaustive list of possible stakeholders in the cultivation pathway of field-transplanted nursery raised hybrid potato seedlings.

Farming				Utilization phase	
system	Production of TPS	Nursery phase	Field phase	Seed potato	Ware potato
High-input	Breeders	Seedling producers	Current potato growers	Trading companies	Consumers
farming systems	Seed multipliers (TPS)*	Farmers	New growers e.g., vegetable growers*	Farmers	Processing companies
		Cooperatives			Trading companies
Low-input farming systems	Breeding companies	Seedling producers	Current potato growers	Farmers	Consumers
	Agricultural universities (plant breeders)	Farmers	New growers, e.g., vegetable growers*	Development NGOs	Traders and vendors
	Government Agricultural Research departments	Cooperatives		Cooperatives	Processing companies
	Development NGOs				
	Cooperatives				
	Seed multipliers (TPS)*				

Note: Stakeholders are divided into various phases of the crop cycle and are distinguished for high-input and low-input farming systems. New actors, who were not present in the conventional system value chain are marked with an asterisk (*).

Source: Partially adapted from Beumer and Edelenbosch [\(2019\)](#page-15-0).

the conventional system and provide multiple benefits for various limitations currently faced in potato production. However, these benefits need to be known to create experiences for the various stakeholders and narrow the current knowledge gaps. The currently available information, as reported in this review, is a clear stepping stone to address the knowledge gaps in the production of seed and ware through field-transplanted systems for all stakeholders in the prospective transplanting value chain (see Table 4).

5.3 Availability of TPS and the profitability of the transplanting system

One of the most important factors is, perhaps, the current and future availability of hybrid TPS and the profitability for all stakeholders within the TPS value chain. In the past, the OP TPS technology was only economically beneficial when the use of seed tubers proved costly or when tubers were unavailable (Almekinders et al., [2009\)](#page-15-0). Although hybrid TPS is a great improvement over the past OP TPS, economic benefits are still a large driver not only for the use of the hybrid breeding technology to produce new potato cultivars but also for seed and ware tuber producers using TPS-based systems, more especially the transplanting system. When the utilization of the system is proven to be profitable as opposed to the methods currently utilized in various regions, there is a high likelihood for increased interest in field transplanting for potato production. Major factor that may inhibit the availability of hybrid TPS are registration and certification procedures. Regulations concerning these have been set up for clonal seed tuber–based varieties; TPS-based variety registration can be a bottleneck to make certified quality starting material available to growers (de Vries et al., [2023;](#page-15-0) Struik et al., [2023\)](#page-17-0).

6 OPPORTUNITIES IN THE NOVEL FIELD TRANSPLANTING VALUE CHAIN

The transplanting system introduces new opportunities and players in its prospective value chain. Table 4 summarizes some of the prospective actors in the transplanting system value chain and new opportunities that arise in the different phases for new players. Depending on the level of input required in the farming system, more opportunities may arise for even already existing players. In the nursery phase, for example, due to the need to develop uniform and vigorous potato seedlings, under short time spans, seedling raisers have the opportunity to produce potato seedlings to feed into the value chain. The need to produce large quantities of seedlings for mechanized systems allows for seedling producers, who mostly raise vegetable seedlings, among other crops, to include potato into their business. Van Dijk et al. [\(2021\)](#page-17-0) indicated that about 7.8 ha of greenhouse space is required to produce enough seedling tubers to serve the Dutch ware crop production demand in only two seasons with, first, field transplanting then seed tuber multiplication from seedling tubers as illustrated in Figure [2.](#page-3-0) Similarly, for low-input farming systems, where potato is mostly grown in vegetable growing regions, and most farmers already have existing knowledge in raising seedlings of other vegetable crops, producing potato seedlings from TPS can be done with ease.

Transplanting systems have been successful in vegetable and field crops, even under both low- and high-input

farming systems. We hypothesize that the adoption of transplanted potato into these existing vegetable systems would require minimal effort. This will therefore help introduce new growers and open up additional area for seed and ware potato production. As previously discussed by van Dijk et al. [\(2021\)](#page-17-0), van Dijk, Kacheyo et al. [\(2022\)](#page-17-0), minimal changes in the mechanized vegetable cropping systems can be anticipated should vegetable farmers produce potato seed or ware. To further discuss the opportunities specifically for high-input and lowinput farming systems, we introduce prospective scenarios for the introduction and utilization of the field-transplanting cultivation system in contrasting regions and farming systems.

6.1 Scenario 1: Low-input farming systems

In the past, prospects for the adoption of TPS-based systems were only high for developing countries where the use of TPS proved a possible solution to the poor seed tuber supply systems (Struik & Wiersema, [1999\)](#page-17-0), and TPS was therefore considered a pro-poor technology (Almekinders et al., [2009\)](#page-15-0). With the recent advancements in hybrid potato, the benefits of the use of TPS-based systems for smallholder farmers still remain with added advantages in the introduction of more uniform crop stands and complex traits of interest into low-input farming systems. Low-input farming systems are mostly characterized by small unit farm size, lower amounts of required starting materials, low use of inputs, such as fertilizer, pesticides, and herbicides, as well as the use of more traditional and low-tech equipment and facilities on their farms. This is the common characteristic of most smallholder farming systems in Sub-Saharan Africa (SSA). A transplanting system, in these locations, could be used to produce clean seedlings for field transplanting, as illustrated by de Vries et al. [\(2016\)](#page-15-0), and address most of the limitations of the current traditional potato systems (see Harahagazwe, Condori, et al., [2018;](#page-16-0) Haverkort & Struik, [2015\)](#page-16-0). Additionally, for farmer cooperatives, which aim to produce clean seed tubers to feed into the value chains, a new starting material—with high multiplication rates—can be introduced, thereby reducing the number of multiplications required to produce desired quantities of seed tubers and overcoming the requirements for storage and transportation faced in the tuber-based system. Additionally, a higher guarantee for low use of pesticides and herbicides, especially when resistant hybrid cultivars are utilized in the system, can be assured. Furthermore, the first-season seedling tubers, when clean and disease free, can be used for both seed and ware and can provide feasible alternatives for farm-saved seed systems (Lindhout et al., [2011\)](#page-16-0). This could subsequently lower the degeneration rates in seed potatoes because new seeds can be purchased to start the cycle when quality becomes low.

The current yields of experimental hybrid genotypes in transplanted systems, as earlier discussed (Table [1;](#page-5-0) Adams

et al., [2022;](#page-15-0) de Vries et al., [2016;](#page-15-0) van Dijk et al., [2021;](#page-17-0) van Dijk, de Vries, et al., [2022\)](#page-17-0), are comparable to or even higher than the yields attained in most potato systems in SSA. Continental yields in Africa range from 0.7 to 36 Mg ha⁻¹; in SSA, this yield range is 6–10 Mg ha−¹ (see Harahagazwe, Condori, et al., [2018;](#page-16-0) Muthoni & Shimelis, [2023\)](#page-17-0). If the current requirements for SSA potato production systems remain clean starting material and to a lesser part yield and other traits of interest, we foresee an interest in TPS and transplanting systems for tuber production in these low-input farming systems. Furthermore, when developments in potato processing markets arise, more demand for quality and uniform tubers will increase thus increasing the need for alternative cropping systems, such as transplanting systems, to help meet the increased demand for ware.

6.2 Scenario 2: Dutch potato sector

Huge possibilities arise from the introduction of the hybrid breeding technology and transplanting systems for highly mechanized potato value chains with high standards for basic consumption as well as processing. Van Dijk et al. [\(2021\)](#page-17-0) and van Dijk, Kacheyo et al. [\(2022\)](#page-17-0) provided a clear overview of the implications of the field transplanting system on the Dutch seed tuber system as well as the opportunities for vegetable growers in Dutch vegetable growing systems. In the prospective novel value chain for transplanted hybrid potato, new players (Table [4\)](#page-12-0) are introduced in the various phases of the system thereby widely increasing the benefits of the technology to the whole sector. To produce TPS, seed multipliers have the opportunity to produce TPS for breeding companies as they currently do for most vegetable companies. Similarly, seedling producers, who specialize in seedling production of various crops, including vegetable crops, also have the opportunity to benefit from the novel value chain. Due to the high acreages allocated to transplanted vegetable systems, the integration of transplanted potato into these existing systems could be easier due to the minimal changes required by these vegetable farmers to accommodate the novel crop (van Dijk et al., [2021\)](#page-17-0). As the Netherlands is also one of the largest producers of seed potato, the introduction of TPS will promote shipment and the subsequent use of seedlings for seed or ware production in other regions. Additionally, this will allow traders to ship to various countries without facing phytosanitary restrictions as would vegetative starting materials.

Regardless of these many advantages and opportunities, the hybrid breeding technology is still considered a potentially disruptive technology (Beumer & Stemerding, [2021\)](#page-15-0). The introduction of TPS-based tuber production systems will cause huge disruptions to the current potato production systems and the actors involved (Beumer & Edelenbosch, [2019\)](#page-15-0). The reduction of years of tuber multiplication and the subsequent reduction of need for costly transportation are among some of the disruptions that may occur. Additionally, the complete blanket adoption of TPS systems would highly impact actors involved in the first phases of rapid multiplication techniques such as mini-tuber producers and users of in vitro systems to produce clean starting materials for the generation of seed. Such implications definitely have huge consequences on the potato sector, the general livelihoods of those involved in the potato sector as well as the society in general. On the downside, high-input farming systems also have specialized machinery, fit for their cropping systems, and it is possible that more investments would be required to accommodate hybrid potato seedlings in current potato growers' farming systems.

We anticipate, therefore, the gradual adoption of TPS-based systems for high-input farming systems. Actually, we foresee that the adoption of TPS-based systems will be similar to that of rapid multiplication techniques where the utilization of a system is based on the ease of application and profitability for each individual actor, as such different actors utilize various systems in the same regions. Similarly, actors interested in hybrid breeding technology will easily pick up the system for implementation, especially when hybrid cultivars are more competitive to current commercial cultivars in terms of traits of interest.

Based on the two contrasting scenarios, we can safely conclude that the introduction and utilization of TPS-based systems, especially the use of seedling field transplanting as a cropping system of choice for seed and ware cultivation, will greatly differ in various regions. Depending on the current limitations in a potato system, and if hybrid cultivars, address those needs, there will be a high likelihood of utilization.

7 FURTHER RESEARCH

This review highlights a field-transplanting system for hybrid potato seedlings as an efficient system to produce seed and ware. Throughout, we have highlighted general knowledge gaps in various agronomic aspects of the prospective transplanting system, with emphasis on aspects of the seedling production and field cultivation of transplanted seedlings. Currently, various current and potential stakeholders lack the knowledge and experience with transplanted hybrid seedling crops for seed and ware production. To address this, efforts need to be put into place to reintroduce TPS as a novel system for seed and ware production. This reintroduction will help create new opportunities and experiences that will help shape the future for TPS-based systems in various regions in the world. When protocols for seedling production and cultivation are developed, communicated, and disseminated, more effort can be put into place to adapt the protocols into local systems. Therefore, efforts in developing these protocols should focus on general factors that influence the productivity of field-transplanted hybrid seedlings and should be tailored to facilitate the adoption of the systems by various stakeholders (Table [4\)](#page-12-0).

Further studies should focus on understanding current cropping systems for potato production and aligning the novel transplanting system to suit such conditions. Such studies could include understanding factors influencing hybrid seedling growth and development under nursery conditions, understanding transplant shock and factors that influence the mitigation of transplant shock in potato seedlings as well as exploring the contributions of crop management factors on canopy development, yield, and other yield components of field-transplanted seedlings. Conducting these studies under various agroecological zones and in contrasting cropping systems will be of great importance for bridging the knowledge gap in the productive cultivation of transplanted potato seedlings.

8 CONCLUSIONS

This review promotes the possibility of utilization of a field transplanting of hybrid potato seedlings for seed and ware potato production. With the recent demands for more resilient cropping systems, we believe a resilient cropping system can be developed and adopted more readily for a transplanting system than the conventional tuber-based system. We anticipate shifts of current cropping systems to the novel transplanting system especially when hybrid TPS are introduced into different regions and even more when hybrid cultivars are more competitive to commercial cultivars. We propose that further studies and the demonstration of practice be conducted, made available, and disseminated to the important actors in the potato value chain. Introduction and utilization of transplant systems will occur differently in various regions, and the drivers for demand and utilization would be therefore different and very cropping system dependent. Field transplanting of hybrid potato seedlings for seed and ware production is therefore a novel cultivation pathway that promises fast, efficient, and sustainable seed and ware production.

AUTHOR CONTRIBUTIONS

Olivia C. Kacheyo: Conceptualization; Investigation; Project administration; Visualization; Writing-original draft; Writing-review & editing. **Michiel E. de Vries**: Conceptualization; Funding acquisition; Resources; Supervision; Writing-review & editing. **Luuk C. M. van Dijk**: Conceptualization; Writing-review & editing. **Hannah M. Schneider**: Supervision; Writing-review & editing. **Paul C. Struik**: Conceptualization; Funding acquisition; Project administration; Resources; Supervision; Writing-review & editing.

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CONFLICT OF INTEREST STATEMENT

Olivia C. Kacheyo and Michiel E. de Vries work at a hybrid potato breeding company.

DISCLAIMER

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