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Review

True potato seed quality

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Summary. Environmental influence on physiological factors that determine seed quality is discussed in relation to true potato seed (TPS). This review has been motivated by the need for high quality seed for the proper evaluation of TPS technology. The objectives of tuber production may not be in harmony with those required for the production of high quality TPS. The production of high quality TPS may be influenced by the stronger sink strength ability of fast developing tubers for assimilation of available nutrients. Earliness of tuber formation, which is needed in TPS progenitors, may tend to result in incomplete TPS development. Limiting conditions during seed development decrease the potential of the seed for field establishment. Seed vigor is the most important attribute of seed quality since it is essential for seedling performance under the adverse conditions commonly encountered during field development. The attractiveness of TPS technology for tropical areas, where potato production is limited by low-quality seed tuber availability, is decreased by the lack of seedling vigor and uniformity of seedlings derived from TPS. Current research indicates that considerable genetic improvement of TPS vigor and uniformity is possible. It is suggested that significant immediate improvement of TPS quality would result from agronomic techniques that reflect understanding of the physiological factors that influence the production and maintenance of high quality seed. Research areas needed to develop methodologies for TPS production with optimum expression of genotype are identified.

Key words: True potato seed, TPS – Seed quality – Seed vigor

Abbreviations: TPS = True potato seed, CIP = International Potato Center, Lima, Peru, SD = Short day, LD = Long day, INIA = Instituto Nacional de Investigaciones Agropecuarias, Chile, GA = Gibberellic acid

Introduction

True Potato Seed (TPS) technology is a radical departure from the traditional method of potato production, which is based on the use of seed tubers. One of the new areas of potato research connected with the development of this novel technology at the International Potato Center (CIP) in Peru is research on the production of high quality TPS.

For the production of high quality TPS it is important to recognize that increased transport of assimilates may have to be induced towards the developing reproductive structures when they are in competition with the developing tubers (Krantz 1939; Krauss 1978). When plant vegetative organs are rapidly storing food, they virtually cause the embryos to starve during seed development (Stout 1929). Long cultivation, with selection for tubers or fleshy roots or rhizomes, has generally resulted in plants with degenerated organs of sexual reproduction (Stout 1929). Evidence for the presence and the extent of such competition in potato was obtained by Ezeta (CIP 1977) who was able to increase tuber production up to 60% by pruning flowers.

The tuber is the ultimate evolutionary strategy for survival in the wild when the potato plant encounters conditions of limited resource availability. The true seed strategy, nevertheless, is of equal importance for the successful establishment of new ecological niches, which increase the chances for species survival. The difficult task of invading and colonizing new territory would be more likely accomplished if the dispersal structure (i.e. TPS) was formed under ideal nutrient and environmental conditions.

In potatoes the flowering period is generally associated with the onset of tuberization. The end of flowering usually coincides with the phase of significant tuber enlargement, which results from rapid translocation of photosynthates from aerial structures. As a plant ages its physiological activity decreases, and the translocation of important biochemical components (Abdul-Baki 1980) from leaves and roots to the seed (Thomas 1976) is thus reduced. Earliness in tuber production is desired in TPS progenies as a mechanism for adaptation to tropical conditions. Earliness suggests the presence of stronger sink strength of tubers in TPS progenitors, and is consequently potentially detrimental for optimum seed development. Incomplete seed development usually results in lack of uniform germination, loss of early seedling vigor and decreased seed performance under unfavorable conditions (Dickson 1980; Gray and Thomas 1982; Perry 1981).

This paper reviews the present knowledge about physiological factors that relate to the development and subsequent deterioration of seed, and the importance of these factors in sexually propagated crops. The review attempts to demonstrate that significant improvement of TPS quality is possible and indeed essential to assure the full expression of the potential of TPS technology.

Seed vigor: Essential component of seed quality

Quality seed has a high level of germination, and will produce uniform, vigorous seedlings without defects under various environmental conditions (Dickson 1980). A crucial attribute of seed quality for farmers is the ability of a seed lot to perform in the field. This factor of crop production is called "seed vigor" (McDonald 1980).

The definition of seed quality can be discussed more extensively than the need for high quality seed. The Vigour Test Committee of the International Seed Testing Association, for example, took 27 years to agree on the following definition of seed vigor: "Seed vigour is the sum total of those properties of the seed which determine the level of activity and performance of the seed or seed lot during germination and seedling emergence. Seeds which perform well are termed high vigour seeds and those which perform poorly are called low vigour seeds" (Perry 1981). The definition goes on to specify aspects of seed vigor that are associated with performance, such as biochemical processes, rate and uniformity of seed germination, seedling growth, field emergence and growth, and emergence under adverse conditions. Factors affecting the level of seed vigor were also identified: genetic constitution, growing conditions of the mother plant, stage of maturity at harvest, physical parameters related to size and density, integrity, aging, and pathogens (Perry 1981).

According to Perry (1981) in 1876 Nobbe recognized that different seed lots varied in their speed of germination and seedling growth and called this phenomenon "Triebkraft" (driving force). In English, it has been called germination energy, vitality, etc., but the term "seed vigor" has predominated (Perry 1981). Seed vigor, then, is a measure of the relative potential for seedling performance under the stress conditions commonly encountered in the field (e.g., unfavorable temperature, soil, water, and weeds) (Morris 1971). The effects of seed vigor may persist until harvest; however, fast achievement of field stand to increase efficiency of production and to obtain earlier yields are the main reasons for placing importance on seed vigor.

The use of TPS with optimum vigor is a necessity for acceptable seedling performance under suboptimal farming conditions. Vigorous seedling performance is needed to enhance the attractiveness of TPS technology as it is transferred from experimental stations to farmers' fields in developing countries.

Genetic aspects of TPS vigor

Hybrid TPS is generally superior in vigor to seeds resulting from open pollination (Macaso-Khawaja and Peloquin 1983; Peloquin 1983; White 1983b). Nevertheless, seed from openpollinated fruits of a late maturing variety showed superior vigor during seedling development in various field trials at CIP. Such superior performance may be an indication that longer growing periods of the mother plants are favorable for seed development. However, late maturing TPS progenies have a limited potential due to the short potato-growing seasons which characterize tropical environments.

It is important to separate the need for seed vigor from the need to identify high yielding progenies, since the effects of seed vigor may or may not affect yields. In recent work at CIP, parental lines with high heritability for vigor and uniformity have been identified (Golmirzaie 1985). This supports the view that there is considerable genetic variation for the trait TPS vigor and that significant improvement can be obtained by selection. Future TPS improvement will probably also be achieved through the use of unreduced gametes in $4\times-2\times$ crosses, since the highest levels of progeny heterozygosity have been obtained with 2n gametes (Iwanaga 1984; Peloquin 1983; Peloquin et al. 1984). In spite of an inbreeding depression observed in potatoes, the potential use of inbreeding for TPS production is being studied by Jackson et al. (1984). Recent work at CIP by Golmirzaie (CIP 1985) has demonstrated that when the appropriate parental materials are identified, tuber yields are increased in successive openpollinated generations. The production of TPS through selfpollination or through natural crosspollination would result in considerable reduction of seed cost.

The high level of sporophytic heterogeneity in the tetraploid potato is the reason for the lack of progeny uniformity observed during early seedling growth. The variability of a given TPS progeny may be considerably modified through pollen selection techniques. Preliminary evidence obtained at CIP (Pallais et al. 1986) indicates that modification of the sporophytic genotype frequencies is possible through the use of gametophytic screening techniques. This could lead to significant improvements of seedling uniformity and vigor in certain TPS progenies.

Since tropical areas are considered to have the best potential for the utilization of TPS, vigorous seed should result in seedlings with acceptable performance in warm environments. However, the germinability and vigor of TPS are impaired by high temperatures (White 1983; Sattelmacher 1983). In tomatoes (El-Hassan 1978) breeding and selection research has made it possible to extend production into the hot summer periods of the temperate zone. In potatoes, the availability of widely adaptable germplasm (Huamán 1982) suggests that the possibilities to identify TPS progenies with acceptable performance in warm environments are also high.

The physiology of seed quality

The understanding of the physiological process involved in early maturity of potatoes may make it possible to manipulate and delay the onset of senescence during TPS development. Information is needed about the conditions required for optimum TPS development, and their significance for TPS as a crop seed. Therefore, the physiology of potato sexual reproduction should be investigated with special concern for the factors which influence the sowing value of TPS.

Assessment of seed vigor

Increased TPS size and weight is associated with high quality seed (Acuña 1985; CIP 1983; Dayal et al. 1984). The relationship between seed size and seed vigor appears obvious, but evidence indicates that seed contents and the genetic factor are often of overriding importance (Dickson 1980). The association of seed quality with physical parameters has to be considered with caution (Morris 1971) since important biochemical components of seed vigor (Abdul-Baki 1980; Ching 1982; Ching and Rynd 1978; McDonald 1980) are not easily measured. Ching (1982), for example, associated seed vigor with adenosine triphosphate (ATP) content and indicated that seed vigor reflects the efficiency of enzyme synthesis. In potatoes, the possible negative influence of tuberization on environment-conditioned gene expression (Evenari 1984) during TPS development may explain the widespread acceptance of associations of TPS quality with size and weight. Nevertheless, it is important to recognize that the problems of TPS technology have very little to do with the fact that TPS is a small seed.

Research at CIP is attempting to develop a practical and reliable method to assess the potential field establishment of TPS. Such a technique will help to ascertain associations between quality and TPS size and weight. Seed research has concentrated on optimal conditions for germination (Pollock 1971) but the significance of the concept that seed viability is different from seed vigor is gaining recognition (Abdul-Baki 1980; Ching 1982; McDonald 1975). Standard germination tests measure seed viability but are inappropriate for seed vigor evaluations. There are, however, a number of controlled seed tests which include germination under stress or measure autotropic potential and which have demonstrated potential for estimating the ability for field performance of a given seed lot (Abdul-Baki and Andersen 1973; Brocklehurst and Dearman 1980; Harrington 1971; Hegarty 1975; Lovato 1981; McDonald 1975; McDonald 1980; Perry 1981; Pinthus and Kimel 1979; Smith et al. 1973; Yaklich et al. 1979; Yaklich and Kulik 1979). In order to develop an appropriate method to evaluate TPS quality, it is essential to recognize that the difference between vigorous and non-vigorous seed is more clearly recognized under less than ideal growing conditions (Harrington 1971).

Influence of the environment on seed quality

"The future of the seed is partly predetermined by events (flower formation, flowering, nutrient flow from the mother plant, etc.) preceding fertilization and the formation of the gametophyte" (Evenari 1984). The formation and growth of the seed is often strongly affected by environmental and climatic conditions such as temperature, water, light, and the kind and quantity of available nutrients. The conditions present during seed maturation, at harvest, and during storage are principal factors that influence the uniformity of seedling emergence (Evenari 1984; Gray and Thomas 1982).

The production of vigorous seed is generally associated with ideal growing conditions and the availability of high levels of nitrogen (Abdus Siddique and Goodwin 1980; Delouche 1980; Garay 1975; George et al. 1980; Gray and Thomas 1982; Gutterman 1982; Harrington 1971; Pet and Garretsen 1983; Pollock 1971; Soffer and Smith 1974; Thomas and Raper 1979; Van Staden et al. 1982; Walter and Jensen 1970; Yaklich et al. 1979). "By controlling such conditions experimentally, many plants may be thrown into a relatively vegetative condition. Special studies . . . in the potato . . . suggest rather definitely that moderately cool weather, especially at night, favors the setting of seed and that a gradually falling temperature with a moderate amount of moisture is potentially favorable" (Stout 1929). Dry locations free of major diseases are generally suited for high quality seed production (Delouche 1980). The choice of location may also be influenced by economical considerations such as seed yields and labor costs. Physiological requirements such as temperature and photoperiod may limit the choices as is the case with cole crops (Delouche 1980). However, the necessity to produce high quality seed is most often the overriding factor when considering a location for seed production (Harrington 1971).

The role of the environment could be of particular importance for the production of vigorous TPS, since crops that have never been selected for seed vigor appear increasingly subject to the influence of the environment for the production of vigorous seed (Gray and Thomas 1982; Walter and Jensen 1970). The study of environmental effects on seed production may therefore be a rewarding topic for investigation within the framework of TPS technology. It should be realized, however, that the specific conditions needed to achieve optimum seed development may result in increased costs. The increase in seed quality will thus have to be sufficiently high to justify higher production costs. The significance of seed vigor as an attribute of TPS quality may, it must be emphasized, only become evident during growth under limiting field conditions (Harrington 1971; Pollock 1971).

Light and climate. Photoperiod and temperature effects on potato flowering and berry set are well known (e.g., long days and cool temperatures are favorable), still there is also genetic variability for these traits. Light intensity and photoperiod during seed development have significant effects on subsequent seed performance of many crop species (Gutterman 1982). A general observation is that seed produced in long days (LD) is heavier and more dormant than short day (SD) seed (Taylorson 1982). These observations have been supported by results obtained from an on-going collaborative research project on TPS production methodology between CIP and INIA (Instituto Nacional de Investigaciones Agropecuarias) in Chile. Gutterman (1982) attributed the phenomenon of intensified dormancy in seeds produced under LD to increased dry matter accumulation which causes a thickening of the testa and imposes a physical restraint on germination. He also suggests that LD induce changes in endogenous hormone levels, such as an increase in concentration of the germination inhibitor ABA (abscisic acid). In tomatoes, for example, SD seed was found to contain lower levels of germination inhibiting substances than seed produced in LD (Gutterman 1982). Leaves of potato plants grown under SD were shown to contain significantly lower levels of endogenous gibberellins (germination promoters) than those grown under LD (Railton and Wareing 1973). Higher concentrations of growth substances found in seeds may indicate the presence of a mechanism that recognizes an evolutionary advantage for plant survival in increasing resource allocation to the seed.

Decreased TPS germinability as a result of dormancy enhancement due to LD is not evidence of a detrimental effect on seed quality. In India, Dayal (pers. commun.) observed that TPS produced under longer photoperiods had far better germination than TPS produced under SD conditions. Large quantities of superior quality hybrid TPS (i.e., seeds with increased size and weight) were produced in southern Chile under 16 hours of daylength (CIP/INIA, on-going collaborative project). Indications of a photoperiodic effect on seed quality were also obtained in The People's Republic of China where TPS is used extensively (Song 1984). TPS from Northern Inner Mongolia is preferred by farmers to seed from the lower South West mountainous region where photoperiods are shorter than in the north. Farmer preference for TPS grown in northern China is due to the better quality of the seed and the higher potato yields obtained. If the influence of photoperiod is limited to germinability or dormancy effects, its importance for TPS production may be minimal. However, if TPS field performance is influenced by light during seed development, then research is needed to identify the environmental conditions required in the areas where seed is produced.

Soil nutrition. The competition for nutrients between tubers and TPS suggests that nitrogen, through its influence on vegetative growth and tuberization, may be of special significance for TPS production. For example, when nitrogen is supplied continuously to the potato plant it causes a steady growth of shoots and roots and prevents tuberization; when nitrogen application is discontinued, tuberization begins within two days (Krauss 1978). These findings indicate that cultural practices required for tuber production may not coincide with those required for the production of high quality TPS. Nitrogen applications higher than those required for crop production have long been recognized by seed physiologists to improve seed vigor (Delouche 1980; Garay 1975; Gray and Thomas 1982; Pillay et al. 1964; Soffer and Smith 1974; Thomas and Raper 1979; Van Staden et al. 1982). The application of nitrogen during seed development generally results in earlier seedling establishment under suboptimal conditions. Some examples include tobacco, where increased nitrogen applications to the mother plant increased seed germination rate and enhanced its uniformity (Thomas and Raper 1979). In lettuce a linear correlation exists between seed vigor, nitrogen supply, and soil fertility

(Soffer and Smith 1974). Higher yields were obtained from bean (*Phaseolus vulgaris* L.) seed of low weight but high in nitrogen content than from heavy seed with a low nitrogen content (Ries 1971). Ching concluded that seeds with high nitrogen result in a faster rate of seedling growth, due to faster transport of hydrolitic products from the endosperm to the embryo and to a higher supply of energy (Ching and Rynd 1978). Improved seed vigor due to nitrogen is not, however, necessarily associated with improved germinability (Gray and Thomas 1982). Results of ongoing research at CIP on the effects of nitrogen applications during and after pollination include a dormancy enhancement effect, delayed plant senescence, and increased TPS vigor, size and weight.

Hormonal contents. Environmental factors that affect seed development and consequently influence seed performance are associated with the hormonal system of the mother plant (Gutterman 1982). Gibberellins (Khan and Samimy 1982) and cytolinins (Van Staden et al. 1982) are present at high concentrations in developing seeds and create the sink strength necessary for successful nutrient competition. The presence of cytokinins during seed development supports the theory that these compounds help to induce the preferential transport of sugars and amino acids (Van Staden et al. 1982). When nitrogen availability was limited, cytokinin transport from roots to shoots in the potato plant was reduced (Krauss 1978). Reduced levels of cytokinins were suggested to be the sole factor responsible for inducing senescence in potato plants; however, it is now known that other hormones are also involved (Krauss 1978). The increased germinability of cytokinin-treated seed under limiting high tempertures, which is often reported (Harrington 1971; Taylorson 1982; Thomas 1976), further underscores the need for research on the potential importance of endogenous growth regulators during TPS development.

Seed maturity. "The environmental conditions under which the seed matures affect its final physiological constitution. This fact has mostly been neglected by seed physiologists" (Evenari 1984). The importance of proper seed maturity at harvest for subsequent seed performance has been demonstrated in many crops (Gray and Thomas 1982). In carrots, mature seed contained more protein and nucleic acid than immature seed (Brocklehurst and Dearman 1980). These biochemical differences in the composition of mature carrot seeds were suggested to account for their faster germination rate. In common beans, high temperatures decrease time of fruit ripening and result in less vigorous seed which is more susceptible to deterioration than seed produced in cooler and drier environments (Abdus Siddique and Goodwin 1980). In tomatoes, ripening of the fruit on the vine contributes to increased seedling uniformity and resistance to seedling diseases (Malagamba 1983). Thus, the extension of the potato berry maturation period on the vine may also be associated with the production of high quality seed. TPS is reported to require at least six weeks of on-plant berry maturation in order to germinate (Simmonds 1962 b). Observations at CIP indicate, however, that berry ripening is highly dependent on the environment, and varies from four (Almekinders, pers. commun.) to eleven weeks. Ripening periods were longer in cooler temperatures. The identification of the optimum period of potato berry development on the vine may, therefore, be of obvious importance for the production of high quality TPS. This information is needed to facilitate the description of climatic conditions that would permit the production of TPS with optimum quality.

Physiological and genetic factors affecting the preservation of TPS vigor during storage

The quality of seed prior to harvest is determined by genetic constitution, stage of development, and content of biochemical components. The quality of seed before storage can be greatly modified by the conditions present during harvest and the mode of seed extraction. All these factors influence the storability of seed (Roberts 1979; Thompson 1971; Welch 1973).

Seed deterioration begins in the field, probably soon after seed development has ended on the mother plant (Roberts 1979). Stored TPS is usually evaluated on the basis of germination under favorable conditions. Decrease of seed germinability during storage, however, is preceded by decreases in seed vigor, expressed by a slower rate of germination and a slower rate of seedling growth (Harrington 1971; Van Staden et al. 1982; White 1983). Stored TPS, however, is remarkable in its ability to germinate even after 25 years at mild temperatures; forty years or more of viability could be expected if the seeds are thoroughly dried (Howard 1980). Unfortunately, the long viability of TPS has caused many workers to disregard the need to preserve the fragile sowing value of TPS.

TPS dormancy. TPS is dormant at harvest, a condition which generally disappears after 6 months with traces remaining for 18 months (Simmonds 1963 a). Therefore, although crop seeds normally lose germinability during storage (Thompson 1971), dormant TPS increases germinability during storage. The physiology of TPS dormancy is not well understood but the inhibition factors for germination are considered to reside both in the testa and in the embryo (Simmonds 1963 a, b). Dry storage intensifies dormancy of dormant TPS but does not reimpose it on nondormant seed; cool storage (0–5 °C) holds dormancy constant, while air storage causes a steady decline (Simmonds 1963 a, b). The presence of germination inhibitors in the embryo or endosperm of TPS has not been demonstrated. The presence of inhibiting substances for germination in the testa of TPS has been suggested (Simmonds 1963 a) and is supported from the evidence in many species (Van Staden et al. 1982) and from our results with certain TPS progenies released from dormancy following leaching of freshly extracted TPS. However, TPS progenitors often vary at the species level (Mendoza 1983), and Simmonds (1964) found wide differences in the intensity of dormancy between different *Solanum* species. Therefore, it is possible that a similar physiological control of dormancy is not present in all TPS progenies.

A seed is considered dormant when it is unable to achieve germination under favorable conditions. This condition of physiological quiescence is not limited to germination sensu stricto and may include decreased growth rate if this phase is disturbed (Côme and Thevenot 1982). Seedlings of many species are dwarfed if gibberellic acid (GA) is used to "break dormancy" (Chao and Walker 1966; Fogle and McCrory 1960; Pillay et al. 1964; Wareing 1982). Slow seedling growth is exhibited by dormant seeds of peach induced to germinate due to GA application (Fogle and McCrory 1960). Before sowing, TPS is generally soaked for 24 hours in a 1,500 ppm concentration of GA (Spicer 1961); nondormant seed is often treated as well. The significance of seed dormancy for TPS technology has not received deserved importance due to the effectiveness of GA to induce germination. The slow rate of seedling growth exibited by TPS may be a partial indication of the inadequacy of GA to break dormancy.

The potential confounding effect of dormancy on seed vigor levels must be considered when evaluating TPS vigor. A long list of important questions could be asked regarding various aspects of TPS dormancy and its influence on seed vigor. The answers to these questions may benefit the production and utilization of vigorous TPS. The evidence available suggests that most dormant seeds do not begin to lose vigor until dormancy has been broken (Osborne 1982). However, it is not known whether TPS vigor decreases or remains constant during the dormancy period. Should dormant TPS be sown while dormant following GA treatment and, if so, is it important to consider the intensity of dormancy? Is dormancy being influenced by conditions during seed dehydration and hydration? Is optimum vigor obtained after dormancy has naturally broken? Should TPS be stored to intensify dormancy, hold it constant, or to induce its steady decline? It is evident that the acceptance of GA as an appropriate answer to TPS dormancy must receive research attention.

Control of dormancy. Seed dormancy is generally under phytochrome control in wild plants, except for a few recalcitrant and large-seeded species (Taylorson 1982). Phytochrome control of seed germination is effective for a short period during the initial phases of seed imbibition (Taylorson 1982). Therefore, when the proper photoregulation signal is not present during seed hydration, germination will not ensue. The advantage of phytochrome control on germination of hydrated seed in nature usually lies in the prevention of germination under canopy shade conditions. Environmental conditions may cause embryo dormancy where it previously did not exist. This phenomenon is described under the term "secondary dormancy" (Côme and Thévenot 1982; Taylorson 1982). The interactions between temperature, light intensity, and photoperiod have been shown to induce secondary dormancy in TPS (Lam 1968; Lam and Erickson 1966). In our laboratory at CIP, excised embryos were inhibited to germinate in vitro when intact seeds were first imbibed under different photoinhibiting conditions. Studies are continuing at CIP to obtain increased understanding about the environmental regulation on TPS dormancy.

Potato tubers which are dormant at harvest are a desired objective of most breeding programmes. Tuber dormancy has been associated with TPS dormancy (Simmonds 1964). Therefore, to select TPS progenies with little or no seed dormancy which produce tubers with moderate levels of dormancy appears difficult. However, close examination of the evidence provided by Simmonds (1964) indicates that some variability of the tuber and TPS dormancy correlation may occur. Physiological studies on the significance of TPS dormancy are needed before genetic studies may be considered appropriate. If the objective of selecting seed dormancy out of TPS proves to be essential to increase seed vigor, potatoes produced from TPS may have to be consumed soon after harvest as is the case with cassava roots.

In the future, breeders may face the unique challenge of selecting for the untraditional character of seed dormancy, just as primitive humans did during domestication of sexually propagated crops. Evidence on a few natural populations of weeds suggest that seed dormancy may be selected out of a population in as few as three generations (Thompson 1981; Witcombe and Whittington 1972). It seems logical that sexually propagated plants improved their prospects as agricultural crops by acquiring the ability to germinate when required and with vigor.

Influence of TPS extraction methods on TPS vigor maintenance during storage

Most TPS is handled, transported, and stored extensively. Seed handling requirements for different types of TPS utilization differ considerably. While seed viability may be sufficient for breeding and selection, seed vigor is indispensable for increasing the success of crop production. The effects of various TPS extraction methods on the maintenance of seed vigor during storage have not been previously reported. Studies have concentrated on the effect of extraction methods on seed germinability soon after extraction. For example, a blender has been recommended to macerate potato berries if run for less than 20 sec (Lauer et al. 1965). The increase in germinability reported as a result of blender extraction has been attributed to damage of the testas (Simmonds 1963a). A hand-operated meat grinder is considered more efficient and safer because it apparently does not affect germination soon after extraction (Pallais et al. 1984) indicating that the testa does not suffer damage in the extraction process. Increased rates of TPS germination as a result of fermentation of macerated berries have been reported from Brazil (Fedalto, pers. commun.), Colombia (Zapata, pers. commun.) and Peru (Pallais et al. 1984). The increase of germination rates was, however, only observed if the TPS was germinated soon after fermentation. If the TPS was sowed after eight months of storage, a significant germinability deterioration was observed (CIP 1985). Such deterioration occurred in seed that had been fermented for more than 48 h (e.g. 72 and 96 h). The positive effects of some extraction methods on seed germinability might be due to the removal of inhibition factors from the testa of freshly extracted seed. Such removal, however, might negatively affect TPS storability.

TPS conditioning and storage

High temperature and humidity are the most critical factors influencing seed deterioration in the tropics (Gregg 1984; Thompson 1971). It is generally accepted that in seed containing 5–14% moisture, each 1% decrease of seed moisture doubles the storage life of the seed (Gregg 1984; Harrington 1971). Rapid drying after extraction to safe moisture levels decreases seed quality reductions before and during storage. However, long drying periods are often necessary in environments with high relative humidity (Gregg 1984). Large amounts of forced air may therefore be required for drying TPS in high humidity environments, as temperatures in excess of 25 °C have to be avoided (White 1983 a, b).

When considering the general lack of seedling vigor of TPS, and the need to avoid further decreases of seed planting value, proper conditioning of the seeds immediately after harvest appears to be of great importance. It may be recommended that TPS should be immediately dried after extraction to moisture levels of 2–5% and sealed and stored at 2–5 °C (Hegarty 1975) but it must be emphasized that these conditions preserve TPS dormancy (Simmonds 1963 a, b). A detailed evaluation of the potential significance of storage conditions is essential. It is evident that it is necessary to consider TPS handling and storage methods as integral parts of the high quality production process.

Conclusions

The evidence presented indicates that there are many possibilities for improving the sowing value of TPS. It is suggested that improvements in seed quality will result from the physiological understanding of the strategies (sexual and vegetative) for survival with which evolution has equipped the potato. It can be concluded that physiological and genetic approaches to TPS quality will increase the acceptance of TPS technology as a viable alternative to traditional potato production.

There are considerable differences between the requirements for optimum TPS production and the optimum production of tubers. The process of transforming a vegetatively propagated crop into a sexually propagated crop requires thorough evaluation of the current techniques of potato production as they relate to TPS vigor.

The present emphasis on identifying ideal conditions for the production of vigorous TPS will probably decrease as advances are made in research on breeding and selection. Research at CIP aims to develop a practical seed test that will reflect the potential for field performance of TPS.

The potential significance of TPS dormancy is also discussed. During the domestication of sexually propagated crops humans selected for the characteristic of seed dormancy present in most wild species (Witcombe and Whittington 1972). In nature, dormancy confers on the seed the ability to germinate under more favorable conditions for growth. This characteristic, however, is a nuisance in crop production. It is proposed that selection for TPS dormancy appears as a logical breeding strategy in order to facilitate the utilization of TPS for crop production. Physiological studies are under way at CIP to provide the evidence needed to motivate genetic studies on TPS dormancy.

When TPS is viewed with an ecological focus it seems clear that the TPS-bearing potato plant can be considered an undomesticated species. Before sexually propagated crops were domesticated, primitive humans must have acquired, conscious or unconsciously, knowledge of seed germination requirements: 1.) for survival in the wild, as opposed to 2.) for sowing a crop (Heiser 1981). It is logical to ask, therefore, to what extent research on seeds from a few agricultural crops subjected to human selection – during the origin of agriculture – can be extrapolated to other non-domesticated plants (Evenari 1984). Answers to this question appear vital for constructing a proper framework from which the viability of TPS technology can receive a fair evaluation. The transcendental attempt to convert a vegetatively propagated crop into a sexually propagated crop has never been a challenge for modern man. To undertake such an outlandish proposition is overly justified in light of the evidence from TPS technology obtained at CIP (Accatino and Malagamba 1983; Mendoza 1983). However the approach, in order to achieve optimum success, must be thoroughly scientific; in short, it must be inspired in nature.

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