Parental choice and selection in the early generations of a potato breeding programme

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1. Het voorstel van Brown & Caligari om tussen kaszaailingpopulaties te selecteren op knolopbrengst, zal niet leiden tot verbetering van het veredelingsmateriaal. Brown & Caligari, 1989, Theoretical and Applied Genetics 77: 246-252

2. Voorstellen voor nieuwe selectie-methoden dienen voorzien te zijn van de arbeidstechnische en bedrijfseconomische randvoorwaarden, om de erkenning te krijgen die ze verdienen. Dit proefschrift.

3. Strenge selectie in eerstejaars klonen verlaagt de kans op het vinden van raswaardig materiaal. Dit proefschrift.

4. Gebruik van primaire diploiden-populaties voor de bepaling van de geniteurswaarde van het moedergenotype is om arbeidstechnische, teeltkundige en genetische redenen af te raden. Dit proefschrift.

5. De beeldvorming die sommige amateur musici rond hun instrument opbouwen ten aanzien van de moeilijkheden van bespelen, geeft meer hun vaardigheden aan in het bespelen van het publiek dan van het instrument.

6. De kwestie "publish or perish" is zuiver academisch.

7. Afstoten van ontwikkelen van hoogwaardig kruisingsmateriaal bij het CPRO verkleint de kans dat de onderzoeksresultaten goed inpasbaar zijn in de veredelingspraktijk.

8. Mensen met een deeltijdbaan moeten ten aanzien van het aantal bij te wonen vergaderingen ontzien worden.

9. Met het oog op een Europa zonder grenzen moet in het middelbaar onderwijs onderricht in meerdere vreemde talen verplicht zijn.

10. De toekomstmogelijkheden van hybride-rassen bij raaigrassen zijn beperkt.

11. De stelling "Vater werden ist nicht schwer, Vater sein dagegen sehr" zou niet mogen gelden voor de aardappel. W. Busch (1876) Julchen.

Stellingen behorende bij het proefschrift:
A.E.F. Neele
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A.E.F. Neele

Parental choice and selection in the early generations of a potato breeding programme

Proefschrift
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van de Landbouwuniversiteit te Wageningen

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Voorwoord

Dit proefschrift is het resultaat van de onderzoeken, uitgevoerd door mijn vrouw Klazien Louwes en mijzelf bij de Stichting voor Plantenveredeling, het huidige Centrum voor Plantenveredelingsonderzoek. Klazien en ik zijn in december 1982 gezamelijk gestart met de selectie-methoden onderzoeken, maar in 1987 heeft Klazien zich uit de project teruggetrokken en is met onderzoek betreffende soortskruisingen begonnen. De afwerking van de proeven en de verwerking van de gegevens is daarmee met name op mijzelf neergekomen. Ik had dit echter niet zonder de hulp en ondersteuning van anderen kunnen doen, en ik wil vanaf deze plaats iedereen daarvoor oprecht bedanken. Een aantal mensen wil ik echter apart noemen.

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Bij de wetenschappelijke begeleiding noem ik in de eerste plaats Klazien. Zij had de twijfelachtige eer om als eerste mijn aanzetten tot publicatie te becommentariëren en dit tot iets leesbaars om te vormen. In dit kader dank ik ook Lidwine Dellaert en Coosje Hoogendoorn, die beiden veel energie en tijd hebben gestoken in de verbetering van mijn manuscripten, zowel qua Engels als ten aanzien van de inhoud. Ik heb veel gehad aan discussies met Bas Maris, Oene Dolstra, de helaas overleden Kees Spitters, Bert Vermeer en natuurlijk met mijn promotor Prof. J.E. Parlevliet. Speciale dank gaat naar Fred van Eeuwijk, die altijd voor ieder statistisch en rekentechnisch probleem het juiste boek kon aanwijzen.

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Contents

Chapter 1
Introduction

History of European potato breeding

The potato (*Solanum tuberosum* subsp. *tuberosum* L.) originates in South and Central America and with the colonization of this area by the Spanish, potatoes were brought to Europe. In Europe the potato was initially grown only in botanical gardens or as a medicinal plant, as food it was rarely used. The oldest reports about eating potatoes are from 1573 in Sevilla (Glendinning, 1983, Slicher van Bath, 1987). However, Burton (1966) suggested that these were in fact sweet potatoes (*Ipomea batata*). In Europe people originally used the potato as a vegetable, mixed with beans and peas. At the same time it was considered by others to be unsuitable for human consumption and in some areas potatoes were only grown for stockfeed (Slicher van Bath, 1987). In the middle of the 17th century, the potato became more generally accepted as a food crop and due to war, famine and high prices of wheat and rye, the potato became important in the European diet (Burton, 1966; Slicher van Bath, 1987).

By studying old herbaria, Salaman and Hawkes (1949) could classify the early introductions of potato as belonging to *S. tuberosum* subsp. *andigena*. These introductions probably came from North Colombia or Venezuela and the *tuberosum* characteristics were obtained by selection in populations derived from true seeds in Europe. One of the most important *tuberosum* characters was the adaptation to the long days of Northern Europe. The use of true seeds and selection resulted in differentiation between the *tuberosum* and the *andigena* subspecies, but not, however, in many distinct *tuberosum* varieties. Only from the middle of the 18th century onwards more effort was put in potato breeding and the number of varieties increased rapidly (Burton, 1966). The main reasons for the increased efforts in potato breeding were the acceptance of the potato as a major food crop and secondly the fact that, with the more intensive cultivation, diseases became a serious problem. The most important disease was described as 'Curl', while another factor affecting yield and quality was described as 'degeneration' or 'ageing' of potato varieties. Curl is likely to have been caused mainly by leaf roll viruses, and degeneration was thought to originate from prolonged asexual reproduction (Glendinning, 1983). Since most potato viruses are not transmitted by true seeds, virus free potatoes could be obtained by starting with true seeds. Starting with true seeds was generally considered also to be the best cure against degeneration. Most of the first potato breeders took naturally set berries, the use of crosses was exception rather than rule. Dorst (1924) claimed that the American Pringle was the first who used artificial cross pollination, however he did not indicate the year and the source of this information. Glendinning (1983) claimed this idea for Thomas Knight in 1807, as described in the Transactions of the Horticultural Society of London. Most breeders, however, started with seed from naturally set berries to initiate the selection cycle, and curing the crop from Curl and degeneration were their major breeding objectives. Hawkes (1966) described only one case, dating from 1768, with another breeding objective, namely early tuberization.

In the second half of the 19th century artificial crossing became more common, as is indicated by the ancestry of the varieties selected at that time. Examples of such pedigrees are given by Dijkhuis and Janssen (1981), Zingstra (1982), and Glendinning (1983). Hybridization requires careful consideration of which characters are to be combined in a new variety and consequently must be emphasized in the selection. Hence, selection of good parents or even the production through breeding of superior parents became important. The first who stressed the importance of a good breeding stock is Findlay (1905, in Glendinning, 1983). He considered establishing a stock of good parental clones to be one of the most important tasks for a plant breeder.

After hybridization, the best clones must be selected from the progenies. Breeding programmes were much smaller in the early part of this century than the large scale programmes of today and the selection intensity applied differed from that used nowadays. Goodrich selected some good varieties out of 8,400 seedlings in the period 1849-1856 and Veenhuizen selected many varieties using in total only 15,000 seedlings (Dorst, 1924). Dorst (1924) used for his own breeding programme in the period 1920 to 1922 each year only 400 to 800 seedlings. In contrast, in the breeding programmes of Fitschen (1984) 140,000 seedlings were used to obtain one variety and Howard (1978) at the Plant Breeding Institute, Cambridge, started with 25,000 seedlings intending to obtain only variety. Glendinning (1983) described a similar trend for the potato breeding programme at the Scottish Plant Breeding Station. From 1920 to 1930 only 253 progenies were evaluated, while in the period 1960 to 1970 this number had increased to 5379, i.e. a twenty-fold increase. The much higher number of seedlings needed to select one commercial variety indicates that the selection pressure has increased dramatically over the last fifty years. Partly this can be attributed to the increase in commercially important selection criteria, many of which, such as nematode resistance and processing quality, were not of any importance at the turn of the century. However, it cannot explain the entire increase in selection pressure.

The most drastic reduction of the genetic diversity occurs in the first and second field generation based on a visual evaluation of tuber and foliage characteristics, both in the past and in the present. In the scheme of Howard (1978), only 4% of the genotypes are retained after the first field generation; Fitschen (1984) retained 7% at that stage. Although selection for tuber and foliage traits was also important in the beginning of the century, the applied selection pressure was not so high. For instance Veenhuizen (1924) selected 25% to 33% in the first field generation. This suggests that the selection in the first clonal generations of present-day potato breeding is much more severe than at the beginning of this century. The most likely explanation for the increased selection pressure is found in capacity problems. It is much easier and cheaper to increase the number of seedlings to twice the original number than to double the number of third year clones. Therefore, the increase in the number of seedlings will not be matched by the increase of entries in the later stages of the selection programme resulting especially in an increased selection pressure in the first field generation.

Features of present-day potato breeding

A potato breeding programme can be divided in four main phases. The first is, of course, the phase of the parental choice and hybridization. Subsequently, in the second phase the botanical seeds are sown, often in the glasshouse, and one tuber per seedling is harvested. In general, only mild selection is carried out in this seedling stage. The seedling generation can therefore be seen as the transformation of botanical seeds to seed tubers. The third phase consists of the first and second clonal generation, when mainly visual selection is carried out. This phase is characterized by a high number of clones, each with a low number of field grown plants. Only in the fourth phase, the third and further clonal generations, more detailed studies are carried out with many plants per clone and traits are measured more precisely.

Parental choice. Selection of the proper parental combinations is the first step in a breeding programme. The selection of the combinations should be based on the combining abilities of the prospective parents. For the combining abilities we distinguish the General Combining Ability (GCA) as the average performance of a parent across hybrid combinations, and the Special Combining Ability (SCA) as the deviation of a specific hybrid combination from the expected performance based on the GCA-values of both parents (Sprague and Tatum, 1942). Reciprocal cross combinations sometimes differ in performance of characters, In potato, such reciprocal differences occur especially for characters influenced by the reaction to the photoperiod, like tuber yield and maturity type (Sanford & Hanneman, 1979 and 1982). Therefore, the performance of a hybrid progeny, Y_{ij}, can be characterized by the GCA of the parents *i* and *j*, the SCA of the cross combination and the reciprocal effect (RE): $Y_{ij} = GCA_i + GCA_j + SCA_{ij} + RE_{ij}$, with $SCA_{ij} = SCA_{ji}$ and $RE_{ij} = -RE_{ji}$ (Griffing, 1956). For the estimation of the combining ability designs like the diallel (Griffing, 1956) or North Carolina II (Comstock & Robinson, 1952) can be used. However, for the calculation of the combining abilities, these methods require complete cross designs, and in practice the production of all cross combinations is not possible or the required inputs for the complete diallel or NC II design are difficult to achieve. Therefore incomplete diallels or incomplete North Carolina II designs are often used, and combining abilities can be calculated by estimation methods developed by Garretsen and Keuls (Keuls & Garretsen, 1977; Garretsen & Keuls, 1978).

In practice, breeders generally do not allow themselfs time for estimation of the combining ability of potential parents. The parental combinations are selected by comparing the parental phenotypes and using the mid-parent value as predictor for the mean performance of the off-spring. Computers can help the breeder to evaluate a large number of potential parents (Dorozhkin & Kadychegova, 1989). In addition, an impression of the general combining ability of parents evaluated in previous cross combinations assist the breeder in designing the hybridization programme. This impression, however, is mostly based on experience, while a more precise estimate of GCA-effects would provide better information. A method specially developed to estimate the combining abilities within the framework of a normal breeding programme is described by Herdam (1984), but also the previously mentioned calculation method of Garretsen and Keuls can be used for this purpose.

A phenotype evaluation of genotypes is the most widely used selection method to identify potential parents, however, it is not always the best to identify the most successful parental combinations. Breeders are often disappointed by the actual performance of the hybrid population, found to be less interesting than was predicted. One explanation might be that the genetic effects are not predominantly additive, and that dominance and epistasis are playing a considerable role as well.

Another reason is that although traits such as tuber shape and eye depth are probably simply inherited, many other important characters are the result of interaction of many genes and are therefore characterized by strong SCA and weak GCA effects. Tuber yield, determined by the rate of assimilation and respiration and the distribution of the assimilates over roots, tubers, stems and leaves, is probably the most important example of such a complexly inherited character. Studying the inheritance of the separate underlying processes might identify larger GCA effects, and help to identify parental combinations with increased probability to obtain high performing offspring.

The seedling generation. The seedling generation, the second phase in a breeding programme, is often grown in the glasshouse. It has been suggested that by transplanting young seedlings to the field, plants can be obtained that can be subjected to normal visual selection (Lam & Grenard, 1976). By this procedure, one year would be gained in comparison to the conventional programmes. Many breeders, however, grow the seedlings only in the glasshouse, because the success of transplanting young seedlings is limited, particularly when the transplantation is followed by a period of drought or by night frosts. Furthermore, plants grown from botanical seeds have a development different fromcthe ones grown from seed tubers (Thijn, 1954), which makes selection less reliable.

The glasshouse raising of seedlingsis predominantly a procedure that converses the botanical seeds into seed tubers. In general the selection pressure is low (Fitschen, 1984), although good possibilities for selection have been described for many traits: maturity (Kranz, 1938; Engel & Möller, 1959; Maris, 1964; Tellhelm, 1975), tuber shape and eye depth (Thijn, 1954; Möller, 1956), resistance to leaf roll virus (Butkiewiez & Dziewonska, 1982), extreme resistance to virus X and Y (Wiersema, 1961), field resistance to *Phytophthora infestans* (Caligari et al. 1984, 1985), scab (Caligari & Wastie, 1985; Pfeffer & Effmert, 1986), *Rhizoctonia solani* (Elango, 1982) and tolerance for high temperatures (Sattelmacher, 1983). The tuber yield of glasshouse grown seedlings, however, was found to be only poorly related with the field performance (Livermore, 1939; Tellhelm, 1975). Using the mean of whole progenies, however, the correlation between the glasshouse performance of the seedlings and field performance in the following years was generally better (Brown & Caligari, 1989; Maris, 1988), but only Brown and Caligari found sufficient support for progeny selection for tuber yield in the seedling generation. In general not all of the above mentioned tests are carried out in the seedling generation, in a commercial breeding programme. Some of the tests demand special glasshouses, where seedlings are grown separated from other non-treated seedlings, such as the tests for leaf roll virus and *Phytophthora* resistance and high temperature tolerance. For tests for maturity the timing of the evaluation is very important while other traits, like tuber shape and eye depth, can be selected for easily in the subsequent field generations. Improved and novel seedling tests therefore have only practical value if the experimental conditions can be realized easily and if they offer an economic advantage over traditional selection in the field generations.

Visual selection. Selection in the first and second field generation, the third phase of a breeding programme, consists of visual selection for foliage, tuber and underground stem and stolon characteristics, and is based on a small number of plants per clone. The aim of this phase is to reject genotypes with clearly insufficient value for agriculture, industry and the market and to limit the number of genotypes to be tested in the much more costly fourth phase of selection. Because the evaluation is restricted to characters assessed by eye, genotypes with either poor growth vigour, long stolons, deep eyes, irregular tuber shape or growth cracks are eliminated. In the first clonal year each clone is represented by only one plant, in the second year by four to eight plants.

Although many studies have indicated (e.g. Maris, 1962; Anderson & Howard, 1981; Brown *et al.*, 1984, 1987) that intensive selection in this phase is not very effective, the most drastic reduction of the breeding material is still carried out in this phase of potato breeding. Most of these studies, however, do not suggest a more reliable approach, or if alternatives are presented, the economic consequences are not clear. This might explain why up till now no clear change in the selection pressure in the third phase has occurred even though the oldest evidence of the poor reliability of severe visual selection date from the 1960's (Maris, 1962). It is important that in proposals for alternative selection schemes not only the genetic consequences and selection gains should be evaluated but also the impact on the economic resources.

Table 1. Parentage of the varieties Alcmaria, Désirée, Maritta, and Pimpernel, and of the breeding lines AM74-602 and MPI49-504/2 (up= mother, down =father). Unknown parents are indicated with a question mark.

clone	parents	grandparents	great-grandparents
Alcmaria	Sirtema	H-123	Tinwald's Perfection
			Berlicumer Geeltje
		Frühmolle	Sämling 118
			Jubel
	seedling nr?	Saskia	Rode Eersteling [a]
			Herald
		A-3	CPC 1673-20
			Furore
Désirée	Urgenta	Furore	Rode Star
			Alpha
		Katahdin	USDA 24622
			40568
	Depesche	Eersteling [a]	Early primrose
			King Kidney
		Imposant	?
			?
Maritta	seedling 66/102	?	
		?	
	Mittelfrühe	Hindenburg	Ismene
			Jubel
		Edeltraut	Indstrie
			seedling 158/06

clone	parents	grandparents	great-grandparents
Pimpernel	Populair	Robijn	Rode Star
			Preferent
		Monopool	Splendo
			Hassia
	seedling nr?	Bravo	Zeeuwse Blauwe
			Wilhelm Korn
		Alpha	Paul Kruger
			Preferent
AM74-602	AM65-130	VT^5 62-26-5 [c]	(S. vernei x Profijt)
			KA56-26
		VT^3 62-10-11 [c]	(VTT x Schwalbe)
			Schwalbe
	AM70-2166	VT^n 62-33-3 [c]	((V x Clb) x Profijt)
			(SVI-3 x Profijt)
		D-200	?
			?
MPI49-540/2	? [b]		
	Bona	seedling Ebsdorf S6	?
			?
		Flava	Erdgold
			Fransen

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[a] Eersteling is also called Duke of York, Rode Eersteling is a skin colour mutant of Eersteling.

[b] A leafroll-resistant clone with probably Aquila and *S. andigena* in its parentage.

[c] The index indicates the number of backcrosses of *S. vernei* with *S. tuberosum*.

Third and further years of clonal selection. The fourth phase of a breeding programme involves tests and selection for characters like yield at various locations, disease resistance, processing quality, table quality and tolerance for mechanical harvesting. While in the third phase the objective of selection was to obtain a population of genotypes with a good performance for visually evaluated characters, in this last phase individual genotypes are to be selected with such a good performance for various characters, often measured in special tests, that they can become new commercial varieties.

This thesis

In the above described potato breeding programme, four phases have been identified, the parental choice, the seedling generation, the phase of visual selection and lastly the selection from the third clonal generation on. Optimization of the first three phases are the subject of this thesis. Since potato breeding can be considered a commercial activity based on scientific principles and results, both genetic as well as economic considerations are important.

Most of the experiments of this thesis have been carried out with progenies of a partial 6x6 diallel. The parental clones of the diallel were chosen for a low coancestry, a high degree of male and female fertility, and a broad range in maturity and agronomical performance. The pedigrees of the six parental clones, as far as known, are shown in Table 1.

The incomplete diallel is used to investigate the inheritance of several characters (Chapter 2). The questions concerning parental choice are dealt with in Chapters 2 and 3. In Chapter 2, five methods for the evaluation of potential parental combinations are compared, namely performance of the glasshouse-grown seedlings, the mid-parent value, the average of diploid offspring, the average of selfed offspring and the average of 4x-2x test-cross offspring. These five methods are compared in their prediction of the actual field performance of twenty progenies, originating from the 6x6 diallel cross programme.

Chapter 3 focusses on tuber yield and a crop physiological approach is used to clarify its inheritance. Applications to improve parental choice are described.

Selection tests to be carried out in the seedling generation should be reliable and applicable to large numbers. This means that normally the characters selected for must be of economic importance and the required economic inputs must be compensated for later in the breeding programme. Simple tests for chip quality and dry matter content, that meet these requirements, are described in Chapter 4.

In Chapters 5, 6 and 7 the reliability and the efficacy of visual selection in the third phase of the breeding scheme is investigated. The advantages of enlargement of the number of plants per clone in the first clonal generation (Chapter 5), the manipulation of the selection pressure in relation to costs of field trials (Chapter 6) and alterations of the visual selection (Chapter 7) are evaluated.

Finally, in Chapter 8 the results are discussed both from a scientific and a practical point of view.

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Chapter 2

Identification of superior parents in a potato breeding programme

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Summary

An incomplete diallel cross was used to study components of genetic variation for a range of characters after early and late potato harvest. The progenies were also used to evaluate five predictors of progeny performance, namely the mean seedling performance, the mid-parent value, the mean of the selfed progenies, of the diploid progenies, and of the test-crosses progenies.

For almost all characters, the general combining ability effects were predominant. The specific combining ability effects present were greater at late than at early harvests.

The seedling performance for tuber yield, number of tubers and average tuber weight did not show any relevant relation to the field performance. The mid-parent value provided, in general, satisfactory predictions of the mean progeny performance obtained in the diallel, except for ware tuber yield. The mean value of the selfed and the diploids progenies did not predict of progeny means any better than the mid-parent value. The predictions based on the test-crosses surpassed those of the mid-parent value, particular for tuber yield at ware potato harvest. Methods to identify superior parents are discussed.

Introduction

Selection of superior parental combinations determines to a large extent the success of a potato breeding programme. Proper evaluation of clones as suitable parents is therefore crucial for breeders and several adequate methods, such as diallel crosses (Griffing, 1956) and the North Carolina Design II (Comstock & Robinson, 1952), have been described to be useful for this evaluation. In practical breeding, however, these are rarely used due to the considerable amount of time and labour required for these designs. Other less costly methods to predict the progeny performance therefore are required to improve the choice of parents and thus the efficiency of a breeding programme.

The most simple method to predict the value of cross combinations is to evaluate a progeny in the seedling stage. If a close relation between the seedling performance and the performance in the subsequent field generations exists, as found by Brown and Caligari (1989) for tuber yield and plant appearance and by Neele and Louwes (1989) for chip quality and dry-matter content, progeny selection could be carried out in the seedling stage, and identification of superior parental combinations would become less important.

An alternative approach for the North Carolina Design II might be test-crosses with desynaptic diploid 2n-FDR-pollen producing male parents. Since these genotypes produce genetically homogeneous pollen (Iwanaga, 1984), only small test-progenies would be needed to evaluate the breeding value of the female parents.

Diploids derived directly from a tetraploid clone by anther culture or by pollination with *S. phureja* (Hermsen & Verdenius, 1973) might also be used to evaluate the parental value of a clone (Hougas & Peloquin, 1958). Since by this method unfertilized pollen- or eggcells develop into plants, a view is offered in the genetic background of potential parents. Matsubayashi (1979) used this method to survey the segregation for morphological characters in the diploid progeny of cv Chippewa, and Maris (1973) used diploid offspring to study the inheritance of resistance to the wart disease (*Synchytrium endobioticum*). For each parental clone only one progeny needs to be assessed. This method, however, requires a lot of effort to obtain enough diploids. In earlier research we reported that by using pollination with *S. phureja* three months labour and 300 m^2 of glasshouse area were needed to obtain a total of 10000 diploid seeds from 22 varieties, while only about 50% of these seeds could be used for further evaluation. The other part did not germinate, died soon after germination or showed severe growth abnormalities (Neele & Louwes, 1986). Caligari et al. (1988) similarly reported a germination percentage of only 61%, and again only 61% of these were viable diploids.

Another method to predict the breeding value might be the use of selfed progenies. This method has also the additional advantage that it requires only one offspring population per evaluated parent, but it can only be applied to male fertile parental clones. Feistritzer (1952) used the selfed progenies to predict the breeding value of parental clones, but the data did not provide acceptable predictions for hybridization programmes and only described the rate of homozygosity of the parents. Brown and Caligari (1989) found moderate correlation coefficients between the 'mid-self value' (in analogy to the mid-parent value) and the actual mean value of a progeny for plant appearance, mean tuber weight and number of tubers. For total tuber weight the correlation was even better.

The most widely used predictive method is the mid-parent value. Maris (1989) obtained moderate to good correlation coefficients ($r=0.51$ to $r=0.85$) between the mid-parent value and the actual progeny performance for various agronomically important characters. For yield and number of tubers, however, the correlations were relatively poor ($r=0.51$ and $r=0.59$ resp.). Brown and Caligari (1989) could not accurately predict the progeny performance by the mid-parent value, suggesting that a prediction based on the mean of the parental values might have limited value only.

In this paper the genetic and economic advantages and drawbacks of five methods to predict the performance of cross combinations are compared, the seedlings, the mid-parent value, diploid progenies, selfed progenies and test-cross progenies obtained with diploid 2n-FDR pollen producing males.

Materials and methods

Genotypes. Six tetraploid clones, the varieties Alcmaria, Désirée, Maritta and Pimpernel, and the breeding lines AM74-602 and MPI49-540/2, were used in a hybridization programme. These clones cover a wide range in agronomic performance and maturity. Furthermore, the clones are unrelated, the coefficient of parentage (I) (Kempthorne, 1957) for the progeny of Alcmaria x Désirée was $I=0.016$ and of Désirée x Pimpernel $I=0.008$, for the other progenies $I=0$. Since the parental clones used reflect a wide range in performance, maturity and genetic background, which is the common situation in potato breeding, the results obtained in this study may be indicative for breeding programmes in general.

The clones were crossed in 1983 and 1984 in a incomplete diallel resulting in 20 progenies. Each parent was represented in six or seven progenies, equally as male and as female parent.

Diploid progenies were produced after pollination with *Solanum phureja* IVP35 and IVP48 (Hermsen & Verdenius, 1973). Six diploid males producing 2n-FDR pollen M6, SY7, BE-62, CE-10, FB-107 and Phu75-1136-1936-680 (P680), were used for the test-crosses. The first four are desynaptic and the last two synaptic.

Experiments. The seedling generations were grown in 11x11 cm pots during the spring and summer of 1984 (diallel) and 1985 (diploids, selfed progenies, and test-crosses) under glasshouse conditions in Wageningen. All further trials were performed on a clay soil in the Dutch New Polders on an experimental farm near Lelystad. The plant distance was 35 cm within and 75 cm between the ridges.

For practical reasons, the experiments were spread in time. The mid-parent value predictor was evaluated in 1986 and 1987, the diploid progenies were grown in 1986 (early harvest only), 1988 and 1989, the selfed progenies in 1987 to 1989 and the test-crosses in 1986 (early harvest only), 1987 and 1988. The diallel was evaluated during the years 1986, 1987, 1988 and 1989.

In all trials, progenies were the main experimental unit and per progeny 30 clones, taken at random, were randomized within these plots with two plants per clone. The experiments were performed in two replications. In 1988 and 1989, the clones within each progeny of the diallel were not distinguished individually and the progenies were evaluated as a single experimental unit. The latter experiments were performed in four replications. In 1986 and 1987, the parental clones of the diallel were randomized among their offspring, to calculate the mid-parent value. Each growth season two harvests were carried out, in mid-July, to harvest virus-free seed potatoes, and mid-September, for the mature crop evaluation.

Characters measured. Of every seedling of the diallel, the tuber weight and number of tubers were assessed. Subsequently the mean tuber weight was calculated. During the growing season, the field experiments plots were evaluated for early season growth (1=slow growth, 9=rapid growth) and in mid-June for number of stems. At harvest, plant appearance (1=poor, 9=excellent) was assessed, and at the seed potato harvest stolon length

(1=long, 9=short) and fresh weight of the foliage (g). Afterwards tuber yield (g) and the number of tubers over and under 30 mm were determined. In addition, visual assessments were made of skin colour (1=yellow, 4=purple), tuber shape (1=round, 5=long), regularity of tuber shape (1=irregular, 9=regular) and eye depth (1=deep eyes, 9=shallow). At ware potato harvests also the underwater weight (in g per 5 kg tubers) was determined. Subsequently, the following characters were calculated: the average tuber weight, the proportion of the total tuber weight accounted for by tubers under 30 mm, total biomass (=tuber yield + foliage yield) in July (g), and harvest index (=tuber yield/total biomass) in July.

Table 1. Model for the Analysis Of Variance of the general and specific combining ability effects (GCA and SCA) and the reciprocal effects (RE) for the incomplete diallel.

Source	df	Expected mean squares
GCA	5	$5.3\sigma^2_{gca} + 1.43\sigma^2_{sca} + 3.10\sigma^2_{re} + \sigma^2_e$
SCA	9	$1.26\sigma^2_{sca} + 0.86\sigma^2_{re} + \sigma^2_e$
RE	5	$0.79\sigma^2_{sca} + 3.55\sigma^2_{re} + \sigma^2_e$
Error [a]	38	σ^2_e

[a] The error variance is calculated in the analysis of variance of the trials of 1986 and 1987 based on the progeny means.

Analysis. The 20 progenies were used to estimate the general and specific combining ability (GCA and SCA) effects. For all characters the GCA, SCA and Reciprocal Effects (RE) were analyzed following Keuls & Garretsen (1977) for the random model (Table 1). Since the expected mean squares of the RE-effects contain variances of the Reciprocal Effects as well as of the Specific Combining Ability effects, significant RE-mean squares can be found although the variance of the Reciprocal Effects is zero.

The analyses were carried out using the progeny means as well as the within-progeny variance. The latter calculations were performed to examine whether differences between within-progeny variances could be attributed to certain parents or to specific parental combinations. If differences in the within-

Table 2. Estimated variances of the analysis of variance of the General and Specific Combining Ability (GCA and SCA) and Reciprocal Effects (RE) of the diallel for characters determined during the growth season, and during and after harvest as seed potatoes and as ware potatoes of 1986 and 1987. ('-' means not measured, variances estimated negative were set at 0).

	Seed potato harvest				Ware potato harvest			
	σ^2_{gca}	σ^2_{sca}	σ^2_{re}	σ^2_{e}	σ^2_{gca}	σ^2_{sca}	σ^2_{re}	σ^2_{e}
Early season growth	0.172	0.020	0.018	0.008	-	-	-	-
Number of stems	0.519	0	0.154	0.126	-	-	-	-
Stolon length	1.218	0.146	0	0.030	-	-	-	-
Plant appearance	0.881	0.105	0	0.025	0.271	0.091	0	0.024
Skin colour	0.200	0.047	0	0.001	0.237	0.052	0	0.001
Tuber shape	0.194	0.050	0	0.004	0.127	0.053	0	0.003
Regularity tuber shape	0.230	0.098	0	0.038	0.342	0.086	0	0.012
Eye depth	0.910	0.152	0	0.036	1.178	0.223	0	0.025
Tuber yield	68185	4337	0	513	34752	29981	5909	2707
Number of tubers	16.34	3.15	1.30	0.79	13.49	5.46	0	0.96
Prop. weight by tubers < 30 mm	0	21.5	8.0	0.84	0.686	0.553	0.161	0.086
Number of tubers per stem	0.164	0.073	0.004	0.038	-	-	-	-
Av. tuber weight	55.0	7.8	0	1.2	75.6	29.5	4.7	2.6
Foliage weight	3015	932	890	1497	-	-	-	-
Harvest index	56.2	6.1	0	0.6	-	-	-	-
Total biomass	49353	8037	0	2584	-	-	-	-
Underwater weight	-	-	-	-	808.0	109.9	0	9.9

progeny variances depend strongly on specific parental combinations, breeders can focus on the prediction of the progeny mean. On the other hand, if certain parents contribute to the within-progeny variation more than others, this should also be evaluated in order to obtain a proper prediction of the success of a progeny. In such case, estimates of the mean and the within-progeny standard deviation should be calculated for the prediction of the chance that superior clones can be obtained in a hybrid population.

Since the variance estimates of normally distributed characters are themselves not normally distributed but chi-square distributed, a logarithmic transformation (ln) was performed on the within-progeny variances to carry out an analysis of variance.

The predictive value of the seedling performance and the four alternative predictors was evaluated using correlation coefficients. For each of the predictive methods the mean performance of the parents was calculated. For the selfed and the diploid progenies the progeny mean was calculated and for the test-crosses the mean performance of a maternal clone averaged across the male testers. Subsequently, these values were combined following the scheme of the diallel and this predictor was correlated to the actual values obtained in the diallel. In equations:

Predictor for cross P_i x P_j	Equation
Mean of Diploid Progeny (D)	$0.5(D_i + D_j)$
Mean of Selfed Progeny (S)	$0.5(S_i + S_j)$
Mean of Test-Cross Progenies (P x (male testers)) (TC)	$0.5(TC_i + TC_j)$
Mid Parent Value (P)	$0.5(P_i + P_j)$

Subsequently the predictor was averaged over all experimental years and correlated with the progeny mean results from the diallel over the years 1986 to 1989.

Results and discussion

Analysis of the incomplete diallel

The GCA variance was the most important source of variation at the early and late harvest for almost all characters (Table 2), except for the proportion of weight contributed by tubers under 30 mm at early harvest. At late harvest the

Table 3. Estimated variances of the analysis of variance of the General and Specific Combining Ability (GCA and SCA) and Reciprocal Effects (RE) of the (logarithmically transformed) within-progeny variance of the diallel progenies for characters determined during the growth season, and during and after seed potato harvest and ware potato harvest.('-' means not measured, variances estimated negative were set at 0).

	Seed potato harvest				Ware potato harvest			
	σ^2_{gca}	σ^2_{sca}	σ^2_{re}	σ^2_{e}	σ^2_{gca}	σ^2_{sca}	σ^2_{re}	σ^2_{e}
Early season growth	0.0408	0.0424	0	0.0232	-	-	-	-
Number of stems	0.0059	0.0088	0	0.0324	-	-	-	-
Stolon length	0.0874	0.0451	0	0.0310	-	-	-	-
Plant appearance	0.0195	0.0147	0.0055	0.0114	0.0220	0.0234	0.0135	0.0094
Tuber shape	0.0300	0.0500	0.0170	0.0175	0	0.0120	0	0.0104
Regularity tuber shape	0.0073	0.0419	0.0059	0.0147	0.0546	0.0589	0	0.0133
Eye depth	0.0195	0.0293	0	0.0151	0.0515	0.1051	0	0.0174
Tuber yield	0.0024	0.0402	0	0.0088	0.0322	0.0283	0.0020	0.0087
Number of tubers	0.0817	0.0204	0	0.0146	0.0771	0.0378	0.0006	0.0146
Prop. weight by tubers < 30 mm	0.4103	0.0906	0.0681	0.0189	0.1167	0.3862	0	0.0997
Number of tubers per stem	0.0568	0.0746	0	0.0617	-	-	-	-
Av. tuber weight	0.1649	0.0638	0	0.0193	0.0853	0.0375	0.0070	0.0203
Foliage weight	0	0.0108	0.0013	0.0119	-	-	-	-
Biomass	0	0.0330	0	0.0115	-	-	-	-
Harvest index	0.0314	0.0079	0.0173	0.0104	-	-	-	-
Underwater weight	-	-	-	-	0.0001	0.0375	0.0009	0.0092

differences between the GCA and SCA variance of tuber yield and the proportion of weight contributed by tubers under 30 mm were not large. If the prediction of the performance of hybrid populations is mainly based on the correlation with the parental GCAs, the possibilities of predictions seems to be promising, except for ware tuber yield and the contribution of tubers under 30 mm. Maris (1989) also found predominating GCA variances for most characters, with the exception of yield, where the RE-variance was largest. Brown and Caligari (1989) described a predominant GCA-effect for total tuber yield, number of tubers and plant appearance, and the mean tuber weight to be dependent on GCA and SCA effects. Killick (1977) found SCA to be of most significance for many characters of agricultural importance. Killick, however, probably used more related parents, since all originated from the Scottish Crop Research Institute, in contrast to the genotypes used in our study and that of Maris (1989) and of Brown and Caligari (1989). In related material the number of different alleles is likely to be more limited. Consequently variation in additive gene action is limited as well, whereas non-additive gene action, like epistasis, can result in a relatively large between progeny variation. In such experiments the SCA-effects are likely to be more prominent.

The GCA effects for within progeny variance clearly exceeded the SCA and RE effects only for the characters stolon length, number of tubers, weight proportion of tubers under 30 mm, average tuber weight, and harvest index (Table 3). Parents with short stolons like Alcmaria and MPI49-540/2 contributed less to the within progeny variance than parents with long stolons, like Pimpernel. The progenies of Alcmaria also showed less variation for proportion of tubers under 30 mm, and for harvest index. The progenies of Désirée and Alcmaria showed lower variation for average tuber weight at early as well as at late harvest. Clones with early tuber formation like Alcmaria and Désirée have been found to dominate toward early tuberizing clones in their offspring (Neele, 1990). In early tuberizing progenies, a small proportion of the clones had small tubers, expressed in the proportion of tubers under 30 mm, or a low harvest index, resulting in a significant GCA-within progeny variance. This shows that for most characters the within-progeny variance mainly depends on the parental combination and therefore is not predictable while for some characters it could be attributed to the time of tuberization. This suggests that parental effects on within-progeny variances are likely to be combination dependent and are not expected to be predictable by any of the five methods tested.

Table 4. Correlation coefficients of the progeny means of the incomplete diallel with the mid-parent value for characters determined during the growth season, and during and after harvest of seed potatoes and of ware potatoes of 1986, and 1987, and with the average performance over the years 1986 to 1987 for the upper nine characters and over the years 1986 to 1989 for the eight characters at the bottom (df=18).

	Seed potato harvest			Ware potato harvest		
	1986	1987	Average	1986	1987	Average
Early season growth	0.61	0.81	0.83	0.55	0.68	0.68
Number of stems	0.40	0.59	0.58	-	-	-
Number of tubers per stem	0.79	0.79	0.86	-	-	-
Stolon length	0.86	0.90	0.90	-	-	-
Plant appearance	0.88	0.84	0.89	0.73	0.55	0.64
Skin colour	0.90	0.89	0.90	0.89	0.87	0.89
Tuber shape	0.58	0.68	0.63	0.39	0.59	0.50
Regularity of tuber shape	0.86	0.77	0.87	0.85	0.79	0.85
Eye depth	0.83	0.84	0.85	0.84	0.72	0.78
Tuber yield	0.92	0.90	0.90	0.16	0.24	0.14
Number of tubers	0.32	0.77	0.55	0.38	0.59	0.57
Prop. weight by tubers < 30 mm	0.81	0.87	0.87	0.63	0.72	0.73
Average tuber weight	0.89	0.92	0.86	0.72	0.76	0.81
Foliage weight (July)	0.32	0.48	0.54	-	-	-
Total biomass (July)	0.70	0.59	0.67	-	-	-
Harvest index (July)	0.86	0.92	0.89	-	-	-
Underwater weight	-	-	-	0.67	0.75	0.74

$P(r \geq 0.44) < 0.05$
$P(r \geq 0.56) < 0.01$

Evaluation of the predictive methods

Mean seedling performance. After harvest, the tubers of the seedlings of the diallel were weighed and counted. The correlation coefficients between the seedling progenies and the ware potato harvest performances in the subsequent years varied between r=-0.36 and r=0.07 for total tuber yield, between r=-0.08 and r=0.14 for number of tubers and between r=-0.26 and r=-0.19 for mean tuber weight. The almost insignificant correlation coefficients show that the seedling progeny performance is not likely to be a good measure for the field performance. Maris (1988) also observed poor relationships between glasshouse seedlings and field performance for number of tubers and average tuber weight, while the correlation for tuber yield was moderate (r=0.44 to 0.52). In contrast Brown and Caligari (1989), using the progeny mean added to the within progeny standard deviation, found a high correlation coefficient for tuber yield (r=0.90), moderate for mean tuber weight (r=0.46) and poor for number of tubers (r=0.11). A similar approach, however, did not improve the low correlation coefficients found in our study. Because the correlation between the seedling performance and these three important characters was extremely poor, no further analyses using seedling performance were carried out.

Mid-parent value. The seed potato harvest prediction by the mid-parent value was found to be very good for most characters, with many correlation coefficients exceeding r=0.8 (Table 4). Only foliage weight had a poor correlation coefficient and those of the number of stems, tuber shape and number of tubers were moderate. At ware potato harvest, the correlation coefficients were lower, particularly tuber yield was poorly predicted by the mid-parent value. In general the correlation coefficients of the results averaged over years, were better than the mean of the coefficients of 1986 and 1987 and in many cases even better than each of the separate correlation coefficients. Hence, using the mean performances over years for calculation of the correlation coefficients, a slight overestimation in respect to correlation in one year is likely to occur. These results are similar to those obtained by Maris (1989) and Brown and Caligari (1989).

Diploids. The predictive value of the diploid progeny of a tetraploid clone for the breeding value of a clone was found to be limited (Table 5). Many correlation coefficients were equal to or lower than those obtained with the

Table 5. Correlation coefficients of the progeny means of the incomplete diallel averaged over the years 1986 to 1989, with either the average of the means of the diploid progeny of the parents or those of the selfed progeny, or those of the 4x-2x test cross progenies, for characters determined during the growth season, and during and after harvest of seed potatoes and of ware potatoes (df=18).

	Seed potato harvest			Ware potato harvest		
	Diploid progeny	Selfed progeny	Test crosses	Diploid progeny	Selfed progeny	Test crosses
Early season growth	0.22	0.91	0.57	0.20	0.74	0.74
Number of stems	0.54	0.74	0.75	-	-	-
Stolon length	0.55	0.89	0.94	-	-	-
Plant appearance	0.87	0.95	0.96	0.52	0.43	0.84
Skin colour	0.91	0.90	0.91	0.92	0.91	0.93
Tuber shape	0.75	0.81	0.91	0.63	0.46	0.80
Regularity of tuber shape	0.93	0.64	0.94	0.83	0.32	0.92
Eye depth	0.88	0.77	0.94	0.85	0.66	0.93
Tuber yield	0.82	0.96	0.93	-0.32	0.50	0.83
Number of tubers	0.53	0.36	0.69	0.58	0.85	0.74
Prop. weight by tubers < 30 mm	0.88	0.51	0.87	0.50	0.75	0.47
Number of tubers per stem	-0.46	-0.42	0.37	-	-	-
Average tuber weight	0.88	0.86	0.87	0.51	0.82	0.70
Foliage weight (July)	0.29	0.58	0.70	-	-	-
Total biomass (July)	0.41	0.87	0.32	-	-	-
Harvest index (July)	0.79	0.91	0.93	-	-	-
Underwater weight	-	-	-	0.83	0.94	0.94

$P(r \geq 0.44) < 0.05$
$P(r \geq 0.56) < 0.01$

mid-parent value. At ware potato harvest the correlations were very poor, except for underwater weight and skin colour, regularity of tuber shape and eye depth averaged over years. A possible reason for the poor value of this predictor is that in the diploid progenies many poorly growing plants occurred which seemed to be unrelated to the breeding value of the tetraploid parent. In the diploid progeny of Désirée, for instance, a large proportion of small, slowly developing plants were found, which was not so in its tetraploid progenies. It is thought that in diploids, obtained after pollination with *S. phureja*, recessive deleterious alleles are present in a homozygous state. In a tetraploid most of such recessive alleles will go unnoticed.

Selfed progenies. The seed potato harvest prediction by means of the selfed progenies (Table 5) was similar to that obtained with the mid-parent values (Table 4).

At ware potato harvest, the correlations proved to be inadequate for the prediction of most characters. Only for underwater weight the correlation coefficients were higher than those obtained using the mid-parent value; a few were equal, like for skin colour, tuber yield and number of tubers, others were worse. Therefore, there is likely to be little or no advantage in using the mean of two selfed progenies as predictor for the ware potato harvest instead of using the mid-parent value.

4x-2x Test-crosses. Of the six testers used in these experiments two, CE-10 and FB-107, were tuberizing very late. A significant number of clones from the progenies of these clones crossed onto the late varieties Pimpernel and Maritta were unable to produce enough seed tubers in mid-July, and therefore all progenies with these males were eliminated. When using 4x-2x test-crosses in breeding only early tuberizing males should be used.

Both at seed and at ware potato harvest, the test-crosses provided good estimates for the actual values of the progenies (Table 5). For many characters the correlation coefficients exceeded $r=0.8$ at seed potato harvest as well as at ware potato harvest.

For the prediction at seed potato harvest the test crosses were of at least equal quality as the mid-parent value. Only the early season growth and the number of stems were better predicted by the mid-parent value, the prediction by the test crosses of the other characters was equivalent or better. At ware potato harvest, the results of the test-cross predictions seemed to be superior to those of the mid-parent value, especially for tuber yield and underwater weight. These characters are of main importance in a commercial breeding programme, and test-crosses with diploid 2n-FDR pollen producing males should be considered in preference to the mid-parent value.

Economic and agronomic considerations

Mid-parent value. The mid-parent value is the predictor that is generally used in potato breeding programmes, since the method is quick, cheap and easy. No time is lost with the production of hybrid seed and seedlings, and the data are available from the experiments already performed with the clones of interest. If additional information is needed, the costs of trials is not likely to interfere with a large number of entries to be tested. For tuber yield at ware potato harvest, however, the relationship between the predicted progeny performance and the actual one was not good. This relation might be improved by carrying out harvests at intervals during the growth season, as reported earlier (Neele, 1990). Although this procedure would increase the costs of land and above all labour, it provided an accurate estimate of the progeny yielding ability.

Diploids. The efforts and costs required to obtain a sufficiently large diploid progeny are considerable. Furthermore, the occurrence of poor growing plants in diploid progenies makes this approach a poor predictor and disqualifies it. Many of these small plants hardly produced tubers, which were needed as seeds for the next year generation. The small plants were also affected by strongly growing neighbour plants, which made it difficult to estimate the genetic potential of these clones as well as that of their neighbours (strong interplant interference).

Selfed progenies. The production and maintenance of the selfed progenies did not raise major difficulties for the varieties and breeding lines used in this study. These clones, however, were selected for good male fertility, while many varieties which could be potential parents produce little pollen or are male sterile. Therefore, a major drawback in using selfed progenies in comparison to the other predictors is that the possibilities of selfing are restricted to male fertile clones. In addition, selfed progenies, apart from demanding the effort, provided no more information than the mid-parent value.

4x-2x Test crosses Test crosses were found to offer good possibilities to

Table 6. Ranges of correlation coefficients of the progeny means of the incomplete diallel with the sum of the GCA values of the mother and the father as estimated with testcrosses with each of the testers seperatly or in six combinations of two diploid testers for characters determined during the growth season, and during and after the harvests of 1987 (df=18).

	Seed potato harvest		Ware potato harvest	
	One tester	Two testers	One tester	Two testers
Early season growth	-0.68 - 0.75	-0.52 - 0.78	-0.15 - 0.89	0.11 - 0.89
Number of stems	-0.55 - 0.41	-0.50 - 0.44		
Stolon length	0.92 - 0.95	0.93 - 0.95		
Plant appearance	0.55 - 0.94	0.81 - 0.96	0.72 - 0.83	0.75 - 0.82
Skin colour	0.89 - 0.91	0.89 - 0.91	0.85 - 0.90	0.89 - 0.90
Tuber shape	0.47 - 0.91	0.84 - 0.93	0.45 - 0.81	0.66 - 0.82
Regularity tuber shape	0.67 - 0.87	0.75 - 0.87	0.78 - 0.85	0.81 - 0.85
Eye depth	0.82 - 0.90	0.85 - 0.93	0.74 - 0.93	0.83 - 0.91
Tuber yield	0.85 - 0.97	0.89 - 0.96	0.40 - 0.82	0.68 - 0.84
Number of tubers	-0.23 - 0.78	-0.13 - 0.50	0.04 - 0.68	0.38 - 0.71
Prop. weight by tubers < 30 mm	0.75 - 0.87	0.80 - 0.87	0.33 - 0.63	0.42 - 0.59
Number of tubers per stem	-0.35 - 0.78	-0.16 - 0.85		
Average tuber weight	0.83 - 0.89	0.85 - 0.91	0.61 - 0.81	0.69 - 0.81
Underwater weight			0.66 - 0.93	0.88 - 0.96

$P(r \geq 0.44) < 0.05$

$P(r \geq 0.56) < 0.01$

evaluate the value as a breeding parent of potato clones. However, time is needed to carry out the test crosses and to grow the seedlings. Moreover, many clones have to be tested per test cross, even though we used a sample size of only 30 clones per test cross. Since four male testers were used for the evaluation of one parent clone, 120 clones had to be examined. This high number of clones would be a major restriction to the number of advanced breeding clones and varieties that can be studied. However, this number might be reduced, since we observed that the correlation coefficients hardly decreased by using two instead of four tester clones (Table 6). In Table 6 the year 1987 is taken as an example, the other years showed similar results. Only in the cases of poor or moderate prediction the correlation coefficients found using two testers might be lower. In addition, none of the six combinations of two testers were superior to the others. This means, that only 60 clones per parent have to be tested and this number will allow evaluation of a considerable number of entries. Furthermore, while three of the testers were desynaptic, SY7, M6 and BE-62, and the fourth, P680, synaptic no differences were observed between prediction with synaptic or desynaptic testers. Therefore, desynapsis in the tester clones might not be required.

Using only one tester clone, however, is not recommended since in that case lower correlation coefficients for the predictors were found for most characters, indicating the risk of incorrect parental choices (Table 6). Identification of a superior male tester was not possible.

Conclusions

The parents used in this study presented a large variation in agronomical performance, maturity and genetic background. Therefore, the results obtained in this study are likely to be representative for breeding programmes in general.

For most of the characters studied, the general combining ability, GCA, was the major source of genetic variation between the hybrid populations. Although for the ware potato harvest the specific combining ability, SCA, was significant, for almost all characters the GCA was still the more important. For most characters, differences in the within-progeny variance could not be assigned to certain parents, but were the results of specific parental combinations. For the characters with a predominant GCA for the within-progeny variance, it seems that this could be contributed to the time of tuberization and the distribution of the assimilates afterwards.

The seedling performance for tuber yield, average tuber weight and number of tubers was not correlated to the field performance in the years afterwards. These results suggest that the seedling performance should not be taken in consideration for progeny selection for the characters mentioned.

The mid-parent value, generally used in breeding programmes, provided proper predictions for almost all characters. A major exception was tuber yield at ware potato harvest. This means that if the seed potato harvest performance is important, the performance of the progeny is predicted satisfactory by the mid-parent value. At ware potato harvest, this estimate is likely to be of less value, particularly for tuber yield. A better predictor based on traits of the parents themselves was found by using crop physiological components of the parental tuber yield, which has been reported elsewhere (Neele, 1990).

Progeny means of diploid and selfed offspring did not produce better predictors of the progeny performance than the mid-parent value. In addition, the diploid progeny was difficult to produce and to maintain over the subsequent clonal generations. Therefore the results indicate that both methods should not be recommended.

The predictive ability of test crosses with diploid 2n-FDR pollen producing males seems to be at least as good as that of the mid-parent value, and for yield and underwater weight at ware harvest the test crosses in this study were superior. A drawback of this method is the investment in the production of true seeds and seedlings, although this can be done together with crossing and seedling raising already routinely carried out in any potato breeding programme. Moreover, commercially interesting clones might arise as a spin-off of this prediction method.

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Chapter 3

Study on the inheritance of potato tuber yield by means of harvest index components and its consequences for choice of parental material

A.E.F. Neele

Summary

The inheritance of potato tuber yield was studied considering the seasonal course of harvest index. Harvests of several progenies and their parents were performed at intervals and fresh weight of foliage, underground stems, tubers and stolons was assessed.

Tuber yield depends on the time of tuber initiation and the proportion of the assimilates allocated to the tubers, as reflected in the increase rate of harvest index. The time of tuber initiation of the progenies was associated with the time of tuber initiation of the earliest tuberizing parent. The mean increase rate of the harvest index of the progenies was in most cases equal to the mean values of parents, however in crosses combining early with late maturing parents the rate equaled the value of the maternal parent. Using these relations, differences in harvest index between progenies can be predicted with a high degree of precision by using the harvest index parameters of the parents. This estimated harvest index showed a fairly good correlation to tuber yield at mid-September and can be used in the prediction of the yield of the progeny. The use of the mid-parent value for this purpose is not suitable.

Introduction

Tuber yield is one of the major selection criteria for new breeding material in potato breeding. Selection of proper parental combinations would be most efficient to obtain high yielding progenies. Accurate prediction of the yielding ability of the progeny is, however, not possible since non-additive gene action plays an important role in the inheritance of tuber yield as indicated by the significant specific combining ability effects for tuber yield found by many authors (Plaisted et al., 1962; Plaisted, 1973; Tai, 1976; Killick, 1977; Veilleux & Lauer, 1981; Maris, 1989).

The complex inheritance of tuber yield might be clarified by a crop physiological approach, where tuber yield is described as a function of total light interception, light utilization efficiency and harvest index. Differences in tuber yield of potato cultivars can be described accurately by this procedure (van der Zaag & Doornbos, 1987; Spitters, 1987; Spitters et al.,1989). By studying the inheritance of these characters, relations to the tuber yield of progenies might be found.

Of the three parameters mentioned above, total light interception and harvest index have a high heritability (Spitters et al., 1989) in contrast to light utilization efficiency. Since the first two characters offer more prospect in breeding, I confined to these characters.

Total light interception mainly depends on the ability of a genotype to prolong the maintenance of green foliage at the end of the growth period (Spitters et al., 1989). This character can easily be assessed in the field at the end of the growth period, and genotypes showing little or no foliage senescence can be selected. However, selection for prolonged maintenance of green foliage alone, results in late maturing genotypes, and this might not be the objective of the plant breeder.

A likely better concept is to select, within the maturity classes that are generally used in potato breeding, for an long period of tuber bulking, being the time between tuber initiation and foliage maturity. Hereto, genotypes with an early tuber initiation and a relative low tuber bulking rate should be identified. A lower tuber bulking rate means that a smaller proportion of the assimilates is allocated to the tubers and thus a substantial proportion remains for maintenance and growth of the foliage, resulting in a relative long period of green foliage. The harvest index, the proportion of tuber weight in total biomass, can be used for identification of genotypes with an early tuber initiation and a relative low tuber bulking rate.

The development of the harvest index during the growing season is characterized by three parameters: tuber initiation, the increase rate during tuber bulking and the maximum level of harvest index as reached in the mature crop. Tuber initiation can be determined easy by harvesting several times during the first part of the growing period, the increase rate by performing harvests during the whole growing period. The increase rate of the harvest index is a measure for the relative distribution of the assimilates over tubers and foliage. Genotypes with a prolonged maintenance of green foliage allocate a substantial proportion of the assimilates to the foliage for support of the existing foliage and formation of new leaves. As mentioned above, this results in a relatively low increase rate of harvest index.

This low rate can be combined with an early tuber initiation, resulting in a long tuber bulking period. The cultivar Désirée is an example of such a genotype (Spitters et al., 1989).

The last parameter of interest is the maximum level of harvest index, as found at the end of the growing period. The maximum level of harvest index, however, is difficult to determine; the total biomass at the end of the growing period, used for calculation of the index, concerns all biomass produced during this period, including the lost biomass in terms of rotten stems, leaves, stolons etc.. Accurate corrections for the lost biomass can only be calculated by performing harvests with certain time intervals during the growing period. Fortunately, Spitters et al. (1989) found that differences between genotypes in harvest index at the end of the growing period were closely related to differences found in mid-July. The harvest index in mid-July is easy to determine, since no loss of leaves has occurred at that time, and the inheritance of harvest index can be examined at the harvest of mid-July.

In the present paper the genetic relations between parents and progenies are studied for characters connected to harvest index, like the tuber initiation and the increase rate of the harvest index. Subsequently, the relation to tuber yield is discussed.

Materials and Methods

The experiments consisted of two series of trials. The material was taken from a partial 6x6 diallel of 20 progenies; each progeny consisted of 30 genotypes. The parents of the partial diallel were chosen on the basis of four criteria: contrasts in foliage maturity classes, no identical ancestors till the fourth generation, a good male fertility and a good female fertility. Four of the parents are or were commercial varieties and two are breeding lines (Table 3).

All trials were performed on a clay soil near Lelystad in the Dutch New Polders with plant distance of 35 cm within and 75 cm between the ridges.

In the first series emphasis was put on growth analysis of parental clones and their progenies. Of the parents as well as of all genotypes of several progenies, the time of tuber initiation and the increase rate of harvest index were determined.

In the second series all 20 progenies of the partial 6x6 diallel were involved, but only two harvests took place. The second series were used to calculate GCA- and SCA-effects of harvest index and of tuber yield and also to determinate whether the mean progeny value can be predicted out of parental evaluations.

Series 1 In 1986 the dynamics of harvest index was studied in nine progenies and in their parents. Three of them were evaluated in 1987 as well, together with six other progenies.

Pre-sprouted tubers were planted on April 28, 1986 and April 24, 1987.
The experimental design was a split-plot in two replications, with harvests on May 20, June 2 and 18 and July 7, 1986 and at June 3, 17 and 24, July 1, 8, and 15, August 5 and 26, and September 16, 1987, as main plot and the progenies as sub-plots. The clones were randomized within the progenies and were represented by one plant per experimental unit.

The parents of the progenies were grown in an experiment adjacent to the progenies. Harvests took place at the same days as for the progenies. Experimental design was a split-plot with two replications in both years, using the harvests as main plots and the parents as sub-plots. The plot size was 8 plants.

Series 2 The partial diallel was planted on April 26, 1986, on April 21, 1987 and on April 22, 1988 and harvested on July 7 and September 15, 1986, on July 15 and September 13, 1987 and September 8, 1988. The design of the experiments was a split-plot in two replications with the harvests as main plot and the progenies as sub-plots. The clones were randomized within the progenies and were represented by two plants per clone. In contrast to the experiments of 1986 and 1987, 1988 the clones were not harvested separately, but all clones of one progeny were harvested together. Each clone was represented by one plant in a progeny and the experiment was performed in four replicates.

For both series of experiments fresh weights of foliage, underground stems, stolons and tubers were determined at harvest for each clone. Then the harvest index was calculated as fraction of the tuber weight of the total biomass weight, or in formula:

$$\text{Harvest index} = \left(\frac{\text{weight of tubers}}{\text{weight of tubers + foliage + underground stems}}\right)\text{x}100\%.$$

In cases the foliage weight had decreased due to senescence, the maximum foliage weight was used in the calculation of the total biomass.

Analysis of variance was performed to assess the genetic variance, the error variance and the genotype-year interaction. The partial diallels of 1986 and 1987 were analyzed for estimation of general and specific combining ability effects (GCA and SCA) and reciprocal effects (RE) in the inheritance of harvest index of mid-July and the tuber yield of mid-September using the method of Keuls and Garretsen (1977). In this analysis reciprocal effects are divided in general and specific reciprocal effects; the subspace of the specific reciprocal effects was, however, absent in this partial diallel. The 1988 experiment was used for evaluation of the prediction of progeny means from parental GCAs.

In the course of the harvest index in the growth season, three parameters are important, namely the time of tuber initiation (T_0), the increase rate after tuber initiation (R) and the maximum level of harvest index (HI_m) (Figure 1). For the calculation of the time of tuber initiation a negative exponential curve fit was used on the harvest indices till mid-July. For the increase rate a negative exponential curve fit was used as well, taking all data into

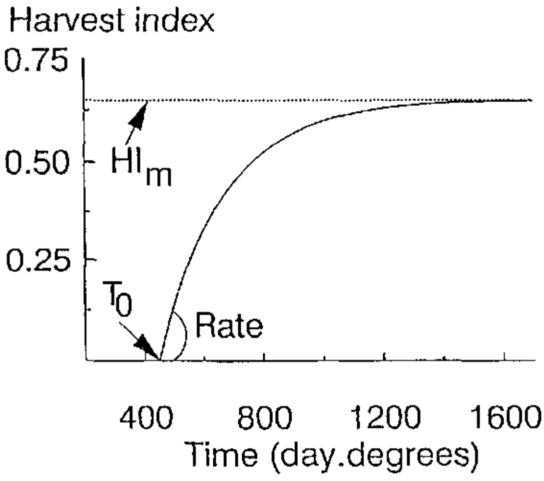

Figure 1. Course of harvest index in time

Table 1. Analysis of variance for the character harvest index (%) at mid-July of 1986 and 1987.

Source of Variation	df	Sum of Squares	Mean Squares	Expected Mean Squares
Year	1	15483.93	15483.93^{**}	$1200\sigma^2_y + 600\sigma^2_{b(y)} + 60\sigma^2_{yp} + 2\sigma^2_{yc(p)} + \sigma^2_e$
Progenies	19	171404.23	9021.28^{**}	$120\sigma^2_p + 60\sigma^2_{yp} + 4\sigma^2_{c(p)} + 2\sigma^2_{yc(p)} + \sigma^2_e$
Blocks within years	2	1091.08	545.54^{**}	$600\sigma^2_{b(y)} + \sigma^2_e$
Years x progenies	19	3294.21	173.38^{**}	$60\sigma^2_{yp} + 2\sigma^2_{yc(p)} + \sigma^2_e$
Clones within progenies	580	196428.31	338.67^{**}	$4\sigma^2_{c(p)} + 2\sigma^2_{yc(p)} + \sigma^2_e$
Years x clones within progenies	580	27078.81	46.69^{**}	$2\sigma^2_{yc(p)} + \sigma^2_e$
Error	1166	27992.51	24.01	σ^2_e
Overall mean			42.15	
Heritability			0.74	

**) significant at $P<0.01$

estimated variances: $\sigma^2_y=12.32$, $\sigma^2_p=71.30$, $\sigma^2_{b(y)}=0.87$, $\sigma^2_{yp}=2.11$, $\sigma^2_{c(p)}=0.87$, $\sigma^2_{yc(p)}=11.34$, $\sigma^2_e=24.01$

Table 2. Analysis of variance of the general and specific combining ability effects (GCA, SCA), and reciprocal effects (RE) for harvest index (%) in mid-July.

Source	df	Sum of Squares	Mean Squares	Expected Mean Squares
GCA	5	1532.7	306.5**	$5.3\sigma^2_{gca} + 1.43\sigma^2_{sca} + 3.10\sigma^2_{re} + \sigma^2_e$
SCA	9	78.2	8.7**	$1.26\sigma^2_{sca} + 0.86\sigma^2_{re} + \sigma^2_e$
RE	5	17.5	3.5**	$0.79\sigma^2_{sca} + 3.55\sigma^2_{re} + \sigma^2_e$
Error[a]	-	-	0.6	σ^2_e

**) significant at $P<0.01$;
mean=42.15, estimated variances: $\sigma^2_{gca} = 56.19$, $\sigma^2_{sca} = 5.65$, $\sigma^2_{re} = 0$.
[a]) The error variance is calculated in the analysis of variance of the trials of 1986 and 1987 based on the progeny means, df=38.

account (see Table 4). To estimate this rate, the maximum level of the fresh weight harvest index was set at 65%. This was the mean percentage determined for completely mature varieties in the experiments. The fixed maximum level harvest index was used since it was not possible to get proper estimates of HI_m of most genotypes, especially for late maturing ones. Furthermore, deviations of the chosen HI_m from the actual HI_m would have led to only minor (less than 5%) differences in the estimated increase rate.

Time was expressed in day.degrees (d°C) after planting, using the temperature sum calculation, according to the relations given by Ingram & McCloud (1984).

Results

The progeny means of the harvest index estimated in mid-July for the diallel experiments (series 2) of 1986 and 1987 showed a high degree of resemblance; the correlation coefficient between years was r=0.97 for the progeny means and r=0.76 for the individual clones. Despite the high correlation there was a significant genotype x year interaction (Table 1).

However, compared to the magnitude of the genotypical variances, the clones within progenies x year and the progeny x year interactions were only small. This means that the harvest index in a single year provides a good

Table 3. Time of tuber initiation in day.degrees (d°C) of parents (P_1 and P_2) and their progenies (F_1) in 1986 and 1987.

Progeny		Time of tuber initiation					
		1986			1987		
P_1	P_2	P_1	P_2	F_1	P_1	P_2	F_1
Maritta	Alcmaria	545	449	461			
Maritta	Pimpernel	545	585	551			
Alcmaria	Desiree	449	457	431			
Pimpernel	Desiree	585	457	490			
Pimpernel	AM74-602	585	516	514			
MPI49-540/2	Alcmaria	485	449	465			
MPI49-540/2	Pimpernel	485	585	522	448	562	465
Alcmaria	AM74-602	449	516	466	422	447	429
Pimpernel	Alcmaria	585	449	475	562	422	440
MPI49-540/2	Maritta				448	465	449
Desiree	AM74-602				415	447	386
Desiree	Alcmaria				415	422	404
AM74-602	MPI49-540/2				447	448	426
Desiree	Maritta				415	465	430
Maritta	Desiree				465	415	429

estimate of the value of the clone or the progeny.

The analysis of variance of GCA, SCA and RE for harvest index at mid-July reflects that for the determination of the progeny mean, GCA-effects as well as SCA- and RE-effects were significant (Table 2). However, the SCA-variance in comparison to the GCA-variance, was only small and the estimated RE-variance was zero. So, SCA- and RE-effects will have had minor influence on the progeny means and the parental GCA-effects provide a good estimate for predicting the harvest index progeny mean of mid-July.

The course of the harvest index

Tuber initiation Both in 1986 and 1987 (series 1 experiments) the time of tuber initiation of the progenies was associated with the time of tuber initiation of the earliest tuberizing parent, irrespective of whether the late parent was used as female or as male (Table 3). In crosses between early and late tuberizing parents, the progeny was slightly later than the earliest parent; in the crosses between two early parents (e.g. Désirée and Alcmaria) the progeny was earlier than both parents. In general, early tuber initiation dominates over late, however this trend is modified by the other parent.

Also within progenies, there was much variation in tuber initiation. The difference between the minimum and maximum time of tuber initiation was about 150 d°C for most progenies. Selection of genotypes with an early start of tuber growth was possible in all progenies, even in the later ones.

<u>The increase rate of harvest index</u> The mean increase rate of harvest index was estimated from data of the series 1 experiments. The mean increase rate of the progenies was in most cases equal to the mean of the values of their parents (Table 4). Exceptions were found in progenies combining an early maturing mother and a late maturing father, where the progeny mean resembled the maternal value (e.g. MPI49-504/2 x Pimpernel; MPI49-504/2 x Maritta; Désirée x AM74-602; and Désirée x Maritta). The progenies Pimpernel x AM74-602 and Alcmaria x AM74-602 deviated from relations given above. The first progeny did resemble the maternal and not the mid-parent value, the latter progeny equaled the paternal and not the maternal value. These exceptions could not be explained.

For high tuber yield a prolonged period of tuber bulking is favourable, as found in the combination of early tuber initiation and a relative low increase rate of harvest index. Both characters had a weak negative correlation; in general the correlation coefficients were r=-0.37 in 1986 and -0.13 in 1987. The correlation varied for the individual progenies between r=-0.42 and 0.13 in 1986 and r=-0.55 and 0.17 in 1987. So, selection for the combination of an early tuber initiation and a low increase rate of harvest index must be possible, although the number of genotypes with a favourable combination will vary per progeny.

The observed relations between parents and progenies for the tuber initiation and the increase rate of the harvest index were used to estimate the harvest index of the progenies from the parameters of their parents. For this calculations the time of tuber initiation of the earliest parent and the mid-parent value for the increase rate were used in the formula given in Table 4. For crosses of early x late maturing parents, the value of the increase rate of the mother was used. The estimated harvest indices of the 20 progenies in mid-

Table 4. The increase rate of harvest index (proportion tuber weight of total biomass d°C^{-1}) of the progenies and their parents in 1986 and 1987. The rate is estimated from the formula:

$HI=HI_m(1-e^{(-rate(T-T_0)/HI_m)})$, where HI_m=maximal harvest index: set to 0.65, T=time in d°C, and T_0=the time (d°C) of time of tuber initiation (Table 3).

Progeny		Increase rate of harvest index (x 1000)					
		1986			1987		
P_1	P_2	P_1	P_2	F_1	P_1	P_2	F_1
Maritta	Alcmaria	1.96	3.32	2.72			
Maritta	Pimpernel	1.96	1.89	1.82			
Alcmaria	Desiree	3.32	2.45	2.80			
Pimpernel	Desiree	1.89	2.45	2.09			
Pimpernel	AM74-602	1.89	2.79	1.78			
MPI49-540/2	Alcmaria	2.24	3.32	2.86			
MPI49-540/2	Pimpernel	2.24	1.89	2.31	1.72	0.78	1.71
Alcmaria	AM74-602	3.32	2.79	2.58	2.83	2.05	2.09
Pimpernel	Alcmaria	1.89	3.32	2.62	0.78	2.83	1.75
MPI49-540/2	Maritta				1.72	0.96	1.86
Desiree	AM74-602				1.78	2.05	1.67
Desiree	Alcmaria				1.78	2.83	2.21
AM74-602	MPI49-540/2				2.05	1.72	1.78
Desiree	Maritta				1.78	0.96	1.65
Maritta	Desiree				0.96	1.78	1.39

July correlated well with the actual harvest indices: r=0.89 in 1986 and r=0.94 in 1987 (Table 5). This demonstrates that differences in harvest index between progenies can be predicted with a high degree of precision using the harvest index parameters of the parents.

Tuber yield The inheritance of tuber yield as estimated in the mid-September harvests of the series 2 experiments of 1986 and 1987, was determined by both GCA, SCA and reciprocal effects (Table 6). Thus, parental GCA values have only limited value for the prediction of mean tuber yield of progenies.

Table 5. The actual harvest indices -hi_a- on 7 July 1986 (800 d°C) and 15 July 1987 (752 d°C), the estimated harvest indices -hi_e- (both in %) and the correlation coefficient between the actual and the estimated harvest index. The estimated harvest index was calculated with the formula given in Table 4, using the time of tuber initiation of the earliest parent and the mid-parent value of the rate of increase of harvest index. For the progenies 11, 12 and 13 the maternal value of the rate was used.

Progeny			1986		1987	
			hi_a	hi_e	hi_a	hi_e
1	Alcmaria	MPI49-540/2	57.66	50.51	55.82	44.45
2	Desiree	Alcmaria	54.17	51.31	50.38	45.28
3	MPI49-540/2	Alcmaria	54.08	50.51	50.34	44.45
4	Maritta	Alcmaria	52.45	49.38	47.05	40.11
5	Desiree	MPI49-540/2	52.45	46.14	44.30	38.69
6	Desiree	AM74-602	50.82	48.69	39.35	40.87
7	Alcmaria	Desiree	50.61	51.31	50.45	45.28
8	Alcmaria	AM74-602	50.16	52.51	49.76	46.12
9	Pimpernel	Alcmaria	49.60	49.08	41.59	38.93
10	AM74-602	MPI49-540/2	48.19	45.79	42.28	38.08
11	MPI49-540/2	Maritta	46.09	43.05	41.99	35.82
12	Desiree	Maritta	44.73	47.16	41.40	39.12
13	MPI49-540/2	Pimpernel	44.15	45.68	38.12	35.82
14	Maritta	Desiree	41.91	44.70	36.66	33.01
15	Pimpernel	Desiree	37.14	44.32	29.82	31.45
16	AM74-602	Maritta	36.35	41.97	30.59	32.88
17	AM74-602	Pimpernel	34.45	41.62	25.66	31.46
18	Pimpernel	AM74-602	33.75	41.62	26.46	31.46
19	Maritta	Pimpernel	31.80	34.46	20.60	20.66
20	Pimpernel	Maritta	30.71	34.46	22.24	20.66
r(actual,estimated)			.892		.940	

Table 6. Analysis of variance of the general and specific combining ability effects (GCA, SCA), and reciprocal effects (RE) for tuber yield (g per two plants) in mid-September. For the Expected mean squares, see Table 2.

Source	df	Sum of Squares	Mean Squares
GCA	5	1240422	248084**
SCA	9	410074	45564**
RE	5	236840	47368**
Error[a]	-	-	2707

**) $P<0.01$,
mean=2373.2, estimated variances: $\sigma^2_{gca} = 34752$, $\sigma^2_{sca} = 29980$, $\sigma^2_{re} = 5909$.
a) The error variance is calculated in the analysis of variance of the trials of 1986 and 1987 based on the progeny means, d.f.=38.

This is confirmed in Table 7, where the GCA-effects were correlated with the diallel data of 1988. The relation between GCAs of parents and the actual mean progeny yield in 1988 was moderate. Furthermore, for estimation of GCA-effects laborious and time-consuming tests have to be performed and therefore alternative prediction methods are needed. One alternative is the mid-parent tuber yield, the average of the tuber yields of the parents. This method, however, has its drawbacks, since the correlation with the mean progeny yield was poor (Table 7). Also, Brown and Caligari (1989) and Maris (1989) found poor correlation between the mid-parent tuber yield and the mean tuber yield of progenies, although their correlation coefficients were higher than in our experiments.

The harvest index estimated in mid-July showed a better correlation to the tuber yield of mid-September. The estimated harvest index was somewhat better than the actual harvest index. The correlation between the estimated harvest index and tuber yield were substantial for all trial years (Table 7). Moreover, estimated harvest indices are far more easy to obtain than the parental GCAs for tuber yield.

As indicated by the correlation coefficient, progenies with low harvest index at early harvest were not able to produce high tuber yield in September. The low harvest index is the result of a late tuber initiation and a low increase rate

Table 7. Spearman rank correlation coefficients of the mean progeny tuber yield in 1986, 1987 and 1988 with the sum of the GCA-effects of the parents, the mid-parent tuber yield, and the estimated (Table 5) and observed mean progeny harvest index of mid-July.

Correlated characters		Tuber yield in 1986	1987	1988
$GCA_{(mother)}+GCA_{(father)}$		-	-	0.66
mid-parent tuber yield	1986	-0.16	-0.05	-0.06
	1987	0.10	0.24	0.10
estimated harvest index	1986	0.67	0.83	0.68
	1987	0.64	0.82	0.69
observed harvest index	1986	0.55	0.71	0.57
	1987	0.63	0.82	0.61

of harvest index. In these genotypes, the foliage remains an important sink for assimilates, preventing a high tuber yield in mid-September.

For planning a hybridization programme, the estimated parameters of harvest index for both parents can be used as an indication of the mean tuber yield of a progeny in mid-September. Especially for new breeding lines, when no data on GCA are available, the estimated harvest index might provide valuable information. If breeding lines are established and data on the GCA are collected, by diallel analysis or test crosses, an prediction based on the GCAs should be considered as well.

Conclusions

The approach based on harvest index dynamics has shown to be useful for potato breeding. Harvest index is used as a character for identification of the flow of assimilates in the plant, specially the proportion allocated to the tubers and to the foliage. A good estimation of the course of the harvest index of a progeny can be performed based on the parameters of the parents and thus, progenies with a combination of an early tuber initiation and a prolonged tuber bulking period can be selected. Furthermore, the estimated harvest index of mid-July using the parental values of time of tuber initiation and increase rate of harvest index, offers a better prediction of the tuber yield at harvest time of ware potatoes than the mean of the tuber yields of both parents.

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Chapter 4

Early selection for chip* quality and dry matter content in potato seedling populations in greenhouse or screenhouse

A.E.F. Neele and K.M. Louwes

Summary

The possibilities of selecting individual seedlings and seedling progenies for dry matter content and chip colour were examined. Tuber glucose content as measured with Reflocheck Glucose test strips was strongly correlated with the colour of the chips, but Gluko-Test strips were less reliable.

Glasshouse and field determinations of both the dry matter content and the glucose content of the seedling progenies were closely related. Therefore it should be possible to select progenies for both characters on the basis of the progeny performance in the glasshouse.

Individual seedlings could be reliably selected for dry matter content, but such selection should not be rigorous. Individual seedling selection for chip colour is not recommended.

Note: Crisp in UK

Introduction

Because good chip and French fries quality and high dry matter content are important objectives in potato breeding programmes, it is also important to identify progenies with good quality characters at an early stage. Selection of such progenies based on parental performance, however, is possible only to a limited extent. Both the special combining ability, SCA, and the general combining ability, GCA, are thought to determine the hybrid population mean of chip colour (Chitsaz, 1983), and of dry matter content (Killick, 1977; Landeo & Hanneman, 1982).

Since SCA may play an important role for both characters, the progeny mean cannot be predicted by the mid-parent value. Therefore a reliable method of evaluating the progeny mean in the seedling stage needs to be established.

Breeders are not only interested in the mean performance of a progeny but they also would like to identify good genotypes as early as possible in a selection programme. Chip and French fry quality and tests of dry matter content require mature tubers. In a breeding programme, the first and often also the second field generation clones are harvested as seed potatoes. Therefore, selection for chip and French fry quality and dry matter content usually starts in the third clonal generation. Louwes & Neele (1987) demonstrated, however, that the assessment of chip colour and dry matter content, using glasshouse grown plants of 10 cultivars correlated very well with the results of field grown plants. They suggested that seedling tubers produced in the glasshouse could be used to select individual plants with good chip colour and high dry matter content.

This paper describes different methods of testing for dry matter content and chip quality and compares their efficiency for selecting both individual seedlings and seedling progenies.

Materials and methods

Two sets of trials were done, each using different progenies.

Set 1. In 1986, 15 progenies and three standard cultivars (Table 2) were grown during the summer in 11 x 11 cm pots in the glasshouse. For each progeny or cultivar there were 63 seedlings or plants, respectively, assigned to three blocks each of 21 units. After harvest, the tubers were stored for 8 weeks at 10 °C.

Of each tuber the weight was assessed and its the specific gravity, as measure of the dry matter content. The specific gravity was determined with salt solutions ranging from 1030 to 1150 gram per litre in steps of 5 gram per litre. The tuber specific gravity for each plant was calculated as mean of all tubers, relative to the total tuber weight.

Chip colour is determined after frying thin tuber slices in oil. It depends mainly on the content of the reducing sugars glucose and fructose (Hesen, 1983). Of these, glucose is the predominant reducing sugar in potato and chip colour has shown to be related to its content (Louwes & Neele, 1987), which can be measured easily using test strips (Ludwig, 1978; Pfeffer et al., 1984; Louwes & Neele, 1987).

A sample of three tubers per plant was used to determine chip colour and glucose content. The tubers were cut from rose to heel end. One half was used for chip frying, the other half was pressed and juice collected for glucose determination.

Chips were produced by frying thin tuber slices in soya bean oil at 180 °C for about three minutes. Their colour was scored, using the colour cards of Agriculture Canada, on a scale from 1, dark, to 9, very pale, although no scores of 8 or 9 were obtained.

Glucose content was measured with the Reflocheck Glucose test strips and the Gluko-Test strips, both manufactured by Boehringer (Mannheim, Federal Republic of Germany). The Reflocheck Glucose test strips were developed for quantitative measurements of glucose in human blood in the range 1.1 to 25 mmol/l. For contents over 25 mmol/l the Reflocheck Glucose test strips enable glucose contents to be estimate in two classes: 33 mmol/l and 44 mmol/l. The Gluko-Test strips were developed to determine glucose in human urine, and distinguish (in urine), (1) a trace; (2) below 5.5 mmol/l; (3) between 5.5 and 27.5 mmol/l; and (4) above 27.5 mmol/l.

Simple correlation coefficients were calculated between the chips colour scores and the glucose test strip measurements. In addition, the phenotypic within progeny variance was calculated for all progenies and related to the error variance as determined with the standard cultivars. The between progeny genetic variance was determined from the analysis of variance, with the sub-progeny means of the blocks as experimental units, to examine the possibility of progeny selection.

Set 2. During the summer of 1987, 10 progenies (Table 3) and three standard cultivars, namely Alcmaria, Desiree and Maritta, were grown in the glasshouse, in the screenhouse and in the field. The same progenies had also been grown in the field in 1986.

Fifty six seedlings or plants for each progeny or cultivar, respectively, were grown in the glasshouse and in the screenhouse, where they were assigned to two blocks of 28 plants each. Within each block, the plants of each progeny or cultivar were kept together and as a unit randomized over the two blocks. The mean value for each unit was used in the analysis of variance. To avoid competition, seedlings and the standard cultivars, grown from tubers, were separated in space. The plants were grown in 11 x 11 cm pots.

For each progeny, 30 third-year clones were grown in the field in two replicates and with two plants per experimental unit; plant spacing was 35 cm within and 75 cm between the rows. In this experiment, seven standard cultivars were included, Bintje and the parents of the progenies. A split-plot design was used with progenies as the main plots and the clones and standard cultivars as the sub-plots.

After harvest, the tubers were stored for 8 weeks at 10 °C.

Dry matter content was assessed as underwater weight (UWW), which can be converted into specific gravity (SG) by the formula: $SG=5000/(5000-UWW)$ (Meijers & van Veldhuisen, 1972). Underwater weight was determined for each experimental unit, standardized to an underwater weight of 5 kg tubers in air. Because there was no hollow heart, the largest tuber of each plant could be used to determine the underwater weight for each sub-progeny. Subsequently, juice was extracted and the glucose content measured with the Reflocheck Glucose test strips.

In the field experiment in 1986 only the underwater weight was determined.

Simple correlation coefficients were calculated between the mean values of the progenies for each growing condition. For the analysis of variance the mean values of the sub-progenies were used as experimental units. The underwater weight of the field grown progenies was also analyzed with genotypes as experimental units.

The accuracy of the two test strips was tested. In 1986 three samples were measured five times with the Reflocheck Glucose test strips and in 1987 40 samples were measured in duplicate. For the Gluko-Test strips twelve juice samples were measured in triplicate.

Results and discussion

Test strips. We concluded that the Gluko-Test strips are very reliable because the replicated measurements of each juice sample all gave the same classification of glucose concentration.

Measurements of glucose concentrations by the Reflocheck Glucose test strips varied between replicates and we found a 95% confidence interval of ± *1.0 mmol/l for unreplicated measurements and an interval of ± 0.7 mmol/l for* duplicate determinations was found. For breeding purposes, these intervals would be satisfactory.

Table 1. Comparison of the Gluko-Test assessments with chips colour determinations (A) or the glucose content (mmol l^{-1}) as measured with the Reflocheck test strips (B).

Chips	Gluko-Test					Glucose	Gluko-Test				
A	4	3	2	1	Sum	B	4	3	2	1	Sum
7	24	26	50	14	114	0 - 2	0	0	1	3	4
6	76	72	18	1	167	2 - 4	0	1	37	12	50
5	162	43	7	0	212	4 - 6	3	77	37	0	117
4	189	12	2	0	203	6 - 8	51	76	2	0	129
3	198	3	0	0	201	8 -10	122	4	0	0	126
2	117	1	1	0	119	10 -12	81	2	0	0	83
1	55	0	0	0	55	>12	574	1	1	0	576
Sum	821	157	78	15	1071	Sum	831	161	78	15	1085

There was only a limited relationship between the results of the Gluko-Test, the Reflocheck Glucose scores, and the chip colour scores (Table 1). Of the 281 seedlings with a satisfactory colour score of 6 or 7, only 181 had a Gluko-Test score of 3 or less. Thus, by using the Gluko-Test an important proportion of the seedlings with good chip colour will fail to be selected. Furthermore, the Gluko-Test discriminates only between glucose contents of less than 8 mmol/l and higher levels (Table 1). Glucose content requirements for French fries, 0.5% of total weight, are less strict than those for chips,

Table 2. The means and phenotypic within progeny variance (var(p)) of the hybrid progenies and cultivars in the 1986 experiment. Chips colour is expressed on a scale 1 to 7. The values of the glucose concentrations were discontinuously distributed (see Materials and Methods) and no phenotypic within progeny variance is presented. For each character the total variance, the genetic between progeny variance, the error variance and the heritability are listed. Differences between the total variance and the sum of the genetic and error variance are due to the block effects.

	Specific gravity (gl^{-1})		Chip colour		Glucose conc. (mmol l^{-1})
Within Progenies	Mean	Var(p)	Mean	Var(p)	Mean
Estima x Ausonia	1087	243.4	3.1	1.85	25.3
Estima x Désirée	1079	134.6	3.4	1.88	23.0
Estima x Hertha	1089	166.4	4.4	2.43	16.7
Estima x Saturna	1101	196.0	4.6	2.16	14.8
Désirée x Ausonia	1074	110.3	3.3	2.16	25.6
Désirée x Hertha	1092	228.0	4.7	2.92	13.0
Multa x Ausonia	1090	198.8	4.0	1.72	19.5
Multa x Désirée	1082	193.2	3.7	1.77	23.0
Multa x Hertha	1098	256.0	5.1	1.61	10.4
Hertha x Estima	1080	146.4	4.4	1.23	17.0
Hertha x Multa	1089	213.2	5.3	1.72	10.1
Saturna x Ausonia	1097	259.2	4.4	1.59	12.6
Saturna x Désirée	1085	125.4	4.6	1.99	15.0
Saturna x Multa	1103	228.0	5.7	1.06	9.6
Saturna x Hertha	1098	219.0	5.3	1.30	9.9
Saturna	1100	118.8	5.6	0.88	11.0
Désirée	1091	100.0	3.1	1.85	24.2
Estima	1093	82.8	2.2	0.85	39.9
Between Progenies					
Total variance	99.7		0.750		38.03
Genetic variance	53.4		0.556		30.11
Error variance	18.6		0.208		7.38
Heritability	0.74		0.73		0.80

0.25% (Hesen, 1983), and seedlings with glucose contents unacceptable for chips but acceptable for French fries cannot be identified.
Therefore, the Gluko-Test strips should not be used in seedling selection for chip or French fry quality.

The results obtained with Reflocheck Glucose test strips were well correlated with the chip colour scores, for both seedlings (r=-0.74) and for progenies (r=-0.96). These results are similar to those previously reported by Louwes & Neele (1987) and confirm the reliability of the Reflocheck Glucose test strips for determining chip quality.

Selection in the seedling generation. Breeders may choose between progeny selection, or individual seedling selection irrespective of progenies. For identification of genotypes that perform well, individual seedling selection is the better choice. However, it is to be preferred only when the observed variance within the progenies is larger than the error variance, otherwise differences between seedlings within progenies might be due to environmental factors and it is better to select the progenies. The standard cultivars were used to determine the error variance of specific gravity and chip colour, since seedlings could not be planted in replicates.

Individual seedling selection. For specific gravity, differences were found between the within progeny variances and the error variances of the cultivars (Table 2). Only for 4 progenies did the variances not differ from those of the cultivars ($P<0.05$). So, selection of individual seedlings is feasible.

Error variance is an important determinant for selecting or rejecting seedlings. To compare the effect of the environment on the variance of measurements on individual clones in 1986 with that in 1987, the specific gravity of 1986 has been converted to the equivalent underwater weight, 1 g l^{-1} specific gravity equaling 4.58 gram underwater weight. Since the between genotypes error variance of 1986 was 100.5 g^2 l^{-2}, this equals 2108 (=100.5×4.58^2) gram^2 underwater weight. This is not significantly different from the variances of 1987, namely 1715 gram^2 and 1741 gram^2 for glasshouse and screenhouse material respectively (Table 3). Hence in both years about the same confidence intervals for each evaluation could have been used in selection.

The error variances of the glasshouse and screenhouse conditions in 1986 and 1987 indicated large 95%-confidence intervals for each determination of ±20 g l^{-1} specific gravity or ±90 gram underwater weight, for 1986 and 1987

Table 3. Underwater weight (g) mid-parent values (MP) and the progeny means for the field (F) experiments of 1986 and 1987 and for the glasshouse (GH) and screenhouse (SH) experiments of 1987. The total, genetic and error variances of the progenies are listed. Differences between the total variance and the sum of the genetic and error variance and the total variance are due to the block effects.

Progeny	1986		1987			
	MP	F	MP	F	GH	SH
AM74-602 x Pimpernel	517	556	446	473	545	528
AM74-602 x Maritta	512	550	439	460	476	486
AM74-602 x MPI49-540/2	471	527	372	424	498	486
MPI49-540/2 x Pimpernel	500	498	414	400	477	455
Pimpernel x Alcmaria	485	488	409	397	456	445
Maritta x Alcmaria	480	479	403	404	479	442
Maritta x Désirée	489	478	423	387	462	450
Désirée x Maritta	489	474	423	384	459	457
Désirée x Alcmaria	432	452	351	359	408	401
MPI49-540/2 x Alcmaria	438	455	336	356	410	389
Between genotypes						
Total variance		2639		3505		
Genetic variance		2030		3003		
Error variance		615		496	1715	1741
Between progenies						
Total variance		1206		1402	1723	1689
Genetic variance		1119		1342	1465	1619
Error variance		91.5		56.8	244	66.2

respectively. These results suggests that seedling selection should not be stringent. For example, underwater weight could be assigned to one of four groups: low (<350 gram), medium (350-440 gram), high (440-530 gram) and very high (>530 gram).

The determination of the error variance for chip colour is difficult, since the three standard cultivars differed significantly in their error variance. The influence of the glasshouse environment seems to depent on the genotype; those genotypes with good or poor chip quality showed less variability than those with a moderate quality (Table 2). Such dependence of the error variance on genotype has been observed by Colon et al. (1989). Compared to Désirée, only the progeny Désirée x Hertha had a significantly higher within progeny variance ($P<0.05$). However, all but three progenies had higher variances than the cultivars Saturna and Estima. So it is not clear, whether the variation within the progenies is due to genotypic effects or to the environment. *Since seedlings of the same progeny cannot be distinguished* from each other, selection should focus on progeny selection rather than on individual seedling selection.

Table 4. Correlation-coefficients between underwater weight of the mid-parent-values and the progeny means.

	Mid-parent 1986	Field 1986	Mid-parent 1987	Field 1987	Glass house 1987	Screen house 1987
Mid-parent 1986	1.00					
Field 1986	0.76	1.00				
Mid-parent 1987	0.96	0.63	1.00			
Field 1987	0.81	0.98	0.71	1.00		
Glasshouse 1987	0.81	0.85	0.71	0.88	1.00	
Screenhouse 1987	0.85	0.93	0.77	0.93	0.95	1.00

Progeny selection. Progeny underwater weight was correlated between field and glasshouse experiments and the coefficient was found to be higher than that between the mid-parent value and the progeny mean. (Table 4). We therefore concluded that the results of a seedling test are better for evaluating

dry matter content of a progeny than the mid-parent value.
Progeny selection is likely to improve the overall dry matter content, since in both experiments the heritability was found to be rather high, $h^2=0.74$ in the 1986 experiment (Table 2) and $h^2=0.86$ (=1465/(1465+244)) to 0.96 (=1619/(1619+66.2)) in the 1987 experiment (Table 3).

The underwater weight of a progeny can be determined simply by sampling the largest tubers of each seedling and the values of such samples were found to be well correlated with the calculated progeny mean of the individual plants ($r=0.95$). For the evaluation of the underwater weight, the experimental procedure followed here, using two subsets of 28 seedling tubers, should suffice. Since most breeders would use such samples for next year's seed tubers, extra costs would be mainly the labour costs of the underwater weight determinations.

The mid-parent value for glucose content has not been calculated, since it was not measured on all parents. It was not possible to determine the glucose content of the screenhouse grown progenies with the Reflocheck Glucose test strips. The total level of the content was higher in the screenhouse experiment than in the field and the greenhouse experiments. Only a few of the sub-progenies had a glucose content within the range of the Reflocheck reflection meter. Perhaps differences in the environment, or agricultural practice prior to storage, induced higher glucose levels in this experiment. The influence of environments and agricultural practices is indicated in Table 5, where the glasshouse grown progenies had lower glucose levels than the field progenies.

The correlation between the glucose content of the field grown progenies and that of their glasshouse grown equivalents was good, $r=0.91$ (Table 5). Seedling progenies with low glucose contents could be discriminated from those with high contents, making it possible to select for chip or French fry quality by discarding progenies with high glucose contents.

The Reflocheck Glucose test strips were quick and easy to use. Determinations carried out on the juice of two samples of 28 tubers of different seedlings sufficed to evaluate a progeny satisfactorily. In contrast, chips colour evaluations are much more laborious because colour determinations of many chips samples per progeny are needed.

Table 5. Glucose contents (mmol l^{-1}) of ten hybrid progenies after growth in the field or in the glasshouse in 1987 and the total, the genetic and the error variances of each growing condition. Differences the total variance and between the sum of the genetic and error variance are due to the block effects.

Progeny		Field	Glass-house
AM74-602	x Maritta	8.8	4.8
AM74-602	x Pimpernel	9.8	5.1
Désirée	x Maritta	11.0	3.2
Maritta	x Désirée	11.3	6.4
Maritta	x Alcmaria	14.0	13.5
Désirée	x Alcmaria	16.6	11.5
AM74-602	x MPI49-540/2	17.3	7.4
Pimpernel	x Alcmaria	23.8	19.7
MPI49-540/2	x Pimpernel	24.8	16.9
MPI49-540/2	x Alcmaria	24.9	20.7
Total variance		41.2	48.2
Genetic variance		40.0	39.4
Error variance		1.15	7.51
Heritability		0.97	0.84

Conclusions

Selection for dry matter content in the seedling generation was shown to be feasible, both for progeny performance and for individual seedlings. Seedling selection, however, should not be rigorous. We suggest that seedlings scores be categorised into four groups; for example, underwater weight may be categorised as: low (<350 gram), medium (350-440 gram), high (440-530 gram) and very high (>530 gram).

For chip quality selection, only progeny selection seems to be practicable. The error variance is genotype dependent, and os it is not clear whether differences between individual seedlings are due to genetic or environmental effects.

For both dry matter content and chip quality, the determination on two samples of about 30 seedling tubers, containing one tuber per seedling, were found to correlate closely with the true progeny mean. Chip quality can be determined measuring the glucose content with Reflocheck Glucose test strips. The tuber samples were found to be easy to use and quick to process for the determination of both dry matter content and chip quality.

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Chapter 5

Effects of plot size and selection intensity on efficiency of selection in the first clonal generation of potato.

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Summary

To improve efficiency of selection in first year clones, investigations were carried out on the use of two-plant plots instead of one-plant ones. Increased plot size did reduce the environmental variance of characters connected with tuber yield, but had only a slightly positive effect on the selection result, as was concluded from a comparison between the first and the second clonal generation. Only lowering selection pressure in the first year clones seems to be a solution for optimising selection efficiency, as could be concluded by comparing simulated selection percentages of about 5%, 20% and 50%.

Owing to genotype x harvest time-interaction for the majority of traits important to either seed or ware potatoes, assessments at both harvest times are necessary for proper evaluation.

Introduction

In the Netherlands, in the years 1970 to 1977, 800,000 to 950,000 potato (*Solanum tuberosum* L.) seedlings from true seed were grown yearly (Joosten, pers. comm.). After a period of 10 to 15 years of testing and selection, these seedlings yielded about 5 varieties yearly, i.e. one variety per about 180,000 seedlings tested. Striking differences can be observed in selection intensity between the early days of potato breeding and today. During the period 1849 - 1856, Goodrich selected some good varieties, including Garnet Chili, out of 8400 seedlings (Dorst, 1924). Veenhuizen also used a small number of seedlings. He was a very successful Dutch breeder at the beginning of this century, when about half of the Dutch potato acreage was covered with his varieties to the end of the 1920's (Bekius et al., 1957). Veenhuizen bred 94 varieties out of about 15,000 seedlings (Dorst, 1924). This means one variety per 160 seedlings.

The differences in selection intensity between modern breeding and breeding at the beginning of this century might partly be explained by an increase in the requirements for a new variety. New requirements are for instance endurance of mechanical harvesting, resistance to cyst nematodes and viruses, adaptation to a wide range of climates in connection with the export of seed potatoes and the suitability for production of French fries. However, most testing for these requirements starts in the third clonal generation (Table 1), since only then is sufficient testing material available. As can be seen from Table 1, at present the most rigid selection takes place in the first two clonal generations. The clones are selected for the appearance of the foliage and the immature tubers of one to a few plants per clone, leaving about 1.1 percent of the initial seedling population for testing in the third clonal generation. By contrast Veenhuizen (1924) selected at least 1/4 of his field grown seedlings. These field grown seedlings are similar to the first clonal generation, at present the first field generation.

In the current breeding scheme, it is noteworthy that rigorous selection in the first and second clonal generations is based upon plant appearance of a few immature plants per genotype.

Plant appearance is a character composed of all visually assessable traits, and its score mainly depends on the component character(s) with the poorest performance. Component characters include traits such as skin and flesh colour, eye depth, tuber shape, stolon length and characters concerning tuber

Table 1. The general selection scheme of potato populations by the Dutch potato breeders. (Data kindly provided by Joosten, Governmental Institute for Research on Varieties of Cultivated Plants, RIVRO).

Generation	Numbers of plants per clone	Proportion selected (%)	Remarks
Seedlings	1	59	Plants grown in small pots in the greenhouse. Selection only on skin colour and tuber formation and sometimes for extreme resistance to virus X and Y.
First year clones obtain	1	10	First field-grown generation, harvested immature (July) to virus-free seeds. Selection on plant appearance.
Second year clones	4-8	18	All plants are harvested immature for multiplication of seed potatoes. Selection on plant appearance.
Third year clones tests	16-32	31	Both harvested as seed and as ware potatoes. Performance of on yield, quality characters and resistances.
Fourth year clones and up	32 or more	30-50	Selection for yield over different locations, quality characters and resistances.

yield. The aim of selection is to obtain breeding material with an acceptable level for each component. However, rigid selection on plant appearance in the first two clonal generations is unreliable, since plant appearance is strongly influenced by the environment (Maris, 1962; Tai, 1975; Caligari et al., 1986; Brown et al., 1987).

Therefore, current selection procedure needs a re-examination and has to be optimised on the basis of estimates of the selection efficiency taking into account not only genetic but also the economic aspects of the selection procedure.

Improvement of the selection response can be achieved by reducing the environmental variance. One of the possibilities for diminishing the environmental variance might be the use of larger plots and more replicates. The use of replicates for first year clones is difficult since seedlings grown in pots produce few tubers. Furthermore, replicated testing is time and labour consuming when handling many thousands of first year clones annually. For second year clones, replicated tests are more practicable, because of the lower number of clones to be tested and the greater number of seed tubers available.

For the first year clones, enlarging the experimental plot size is possible, but is limited by several factors. Firstly, plot size is limited, by the low number of seed tubers produced by seedlings. Secondly, increased plot size requires either more land for field trials, or a reduction of the number of first year clones tested, if land is the limiting factor. Thirdly, a trial using larger plots is more time consuming.

The disadvantages of increased plot size are minimized when two-plant plots are used. Therefore in the present study the efficiency of selection in two-plant plots is compared with that of one-plant plots.

Selection in immature plants is efficient only if there are no large genotype x harvest times-interactions for the selection criteria used or if distinct characters are important at each harvest times. Rigid selection in immature plants should only be applied if the criteria selected for are of major importance to the production of seed or ware potatoes and the selection is reliable. Otherwise many potentially good clones at ware potato harvest are eliminated before testing as mature plants.

The most important character for seed potatoes is tuber yield, a trait known for its variability. Therefore, yield evaluations of first year clones, based on one plant, have limited value. Since seed tuber yield can not be determined reliably in the first year clones, there is scope for selection for other traits not showing genotype x harvest-time interactions. This article reports also the results of a study on the identification of such traits.

Materials and methods

Two series of trials were performed, each consisting of a first and a second clonal generation. The first series was carried out during the growing seasons of 1984 and 1985, the second during 1985 and 1986. All trials were executed in the Flevopolder. Plant distances were 35 cm in and 75 cm between rows.

During the first clonal generation two plot sizes were used: a one-plant plot and a two-plant plot. From each seedling grown in the glass-house a set of three tubers was composed, one was assigned randomly to the one-plant plot and the other two to the two-plant plot. As in normal breeding practice, harvest took place in July.

The second clonal generation was grown in four replicates using two-plant plots; two replicates were harvested as seed potatoes in July and two as ware potatoes in September.

In the first series (1984/1985) 185 genotypes were grown out of ten cross populations, typical of those used in breeding programmes. The first year clones were planted on 16-4-84 and harvested on 6-7-84, the second year clones were planted on 23-4-85 and harvested on 18-7-85 and on 19-9-85. The second series (1985/1986) consisted of 162 genotypes, originating from the same ten cross populations. The first year clones were planted on 26-4-85 and harvested on 11-7-85, the second year clones were planted on 26-4-86 and harvested on 11-7-86 and on 23-9-86.

The trials of the first year clones had a randomized block design. For the experimental designs of the trials of the second year clones the split-plot model in two replicates was used, with the harvest times as main factor and the genotypes as splitting factor.

The following characters were observed: tuber shape, eye depth, plant appearance, stolon length (July harvest), leaf maturity (September harvest), tuber yield and tuber number under and above 30 mm diameter. Tuber shape was assessed on a 1 to 5 scale, 1 for round and 5 for long tubers. Eye depth, plant appearance, and stolon length were assessed on a 1 to 9 scale, 1 for a poor performance (deep, undesirable and long) and 9 for an excellent performance (shallow, desirable and short). Leaf maturity at September harvest was also determined on a 1 to 9 scale, 1 for dead foliage and 9 for green foliage. Furthermore in the series 1985/1986, the number of stems was assessed and the foliage yield in July was measured in order to determine the fresh weight harvest index.

Relations between the determinations at early and late harvest, as well as the relation between first and second year clones were expressed by

Table 2. Means and phenotypic coefficients of variation (cv%) for several traits of plants from the first clonal generations (1984 and 1985) in experiments with two plot sizes.

Character	1984				1985			
	one-plant plot		two-plant plot		one-plant plot		two-plant plot	
	mean	cv%	mean	cv%	mean	cv%	mean	cv%
Tuber shape	2.56	43.8	2.53	41.8	3.00	42.6	3.14	37.1
Eye depth	7.13	28.4	7.00	29.0	5.42	34.6	5.83	31.7
Plant appearance	4.48	52.0	4.53	53.1	3.96	48.7	4.13	52.4
Number of stems	3.73	48.5	7.00	42.8				
Stolon length	5.95	44.4	6.25	41.5	4.45	64.5	4.71	60.7
Tuber number <30 mm	3.67	117.0	3.11	104.5	7.69	85.2	6.95	74.5
Tuber number >30 mm	5.29	59.5	5.65	57.1	6.25	67.7	6.40	54.4
Total tuber number	8.92	54.6	8.75	50.1	13.9	53.9	13.4	40.1
Tuber yield >30 mm	36.4	127.3	31.4	105.6	79.9	83.5	73.5	75.1
Tuber yield >30 mm	324	70.7	329	61.2	254	72.2	281	61.9
Total tuber yield	360	61.1	360	54.7	334	54.0	354	46.1
Perc. yield <30mm	36.6	84.6	33.8	76.2	51.7	51.6	49.4	48.1
Total biomass	1403	35.0	1384	27.3				
Harvest index	23.6	42.9	25.4	36.4				

correlation coefficients. For this, the assessments of the second year clones were averaged over the replications.

Coefficients of variation of the phenotypic values were calculated to compare the environmental influence in one-plant plots with that in two-plant plots.

The efficacy of mild, moderate and rigorous selection on plant appearance in the first year clones was determined by calculating the number of first and second year clones needed to obtain a fixed number of excellently performing second year clones.

Results and discussion

Effect of plot size on selection efficiency

The coefficients of variation for all characters assessed visually were hardly affected by plot size, whereas the characters connected with tuber yield had a slightly lower coefficient of variation for the two-plant than for the one-plant plots (Table 2). The reduction of the variation of the characters determined on a continuous scale was caused by a lower frequency of extreme values in the two-plant plots.

The coefficients of variation include both the genetical and the environmental variation. In each trial, both plot-size treatments had equal genotypic variation and differences in the coefficients of variation were due to environmental effects. Since for most traits these differences are rather small, it can be concluded that increasing the plot size from one to two plants will lead to a minor reduction the environmental variance.

For most traits the correlation coefficients between the performance of first year clones in one- and two-plant plots are low (Table 3), indicating a strong influence of the environment. Only for tuber shape, weight of tubers above 30 mm diameter, total tuber yield, harvest index and total biomass, all with a correlation coefficient over 0.65 in both 1984 and 1985, is the environmental effect moderate.

Furthermore, the selection efficiency was hardly improved by using two plants per plot instead of one (Table 4). The coefficients of correlation between the first and the second year clones are generally higher for the two-plant plots, but the extra effort is not justified. Compared with the one-plant plots, the two-plant plots demand twice as much land for the same number of clones. In terms of labour, planting two-plant plots using paper bags, takes

Table 3. Correlation coefficients between one- and two-plant plots for various traits of plants from the first clonal generation assessed in experiments of 1984 and 1985.

Character	1984	1985
Tuber shape	0.68	0.70
Eye depth	0.31	0.58
Plant appearance	0.64	0.44
Number of stems	0.45	
Stolon length	0.57	0.57
Number of tubers <30 mm	0.67	0.33
Number of tubers >30 mm	0.47	0.64
Total number of tubers	0.57	0.56
Tuber yield of tubers <30 mm	0.62	0.33
Tuber yield of tubers >30 mm	0.67	0.71
Total tuber yield	0.65	0.70
Prop. yield by tubers <30 mm	0.58	0.46
Total biomass	0.73	
Harvest index	0.76	

about 4 to 5 times as much time as planting one-plant plots out of a tray. Harvest takes less than twice as much time. Since the increased plot size has only slight effect on both environmental variance and selection efficiency, but demands much more land and labour, the use of two-plant plots in the first clonal generation is not advised.

Relations between early and late harvest

Correlation coefficients for all characters studied were calculated between the early and late harvests in 1985 and 1986, using the means of the two replicates of the second year clones (Table 5). The relations were generally weak, only for tuber shape was a fairly strong correlation of 0.72-0.74 established. Weak relationships are either caused by a predominant variance of the genotype x harvest time-interaction or by a high environmental variance. In the case of characters with a relatively low interaction variance, as for

Table 4. Coefficients of correlation between the first and second clonal generation of both series for all characters determined. The evaluations of the one- and two-plant plots of the first year clones are correlated to the mean performance of the corresponding second year clones. The first year clones were harvested early only, the second year clones early as well as late.

Character	1984/1985				1985/1986			
	Early harvest 1985		Late harvest 1985		Early harvest 1986		Late harvest 1986	
	one-plant plot 1984	two-plant plot 1984	one-plant plot 1984	two-plant plot 1984	one-plant plot 1985	two-plant plot 1985	one-plant plot 1985	two-plant plot 1985
Tuber shape	0.72	0.67	0.61	0.61	0.69	0.74	0.63	0.66
Eye depth	0.31	0.42	0.23	0.37	0.51	0.45	0.61	0.50
Plant appearance	0.58	0.60	0.28	0.38	0.50	0.59	0.30	0.44
Number of stems	-	-	-	-	0.31	0.39	0.34	0.39
Stolon length	0.57	0.60	-	-	0.48	0.55	-	-
No. tubers <30 mm	0.30	0.39	0.08	0.20	0.36	0.26	0.22	0.10
No. tubers >30 mm	0.42	0.42	0.23	0.25	0.54	0.58	0.34	0.32
Total number tubers	0.22	0.33	0.18	0.27	0.34	0.29	0.28	0.27
Tuber yield <30 mm	0.27	0.41	0.06	0.25	0.39	0.34	0.25	0.19
Tuber yield >30 mm	0.66	0.67	0.34	0.40	0.64	0.65	0.40	0.29
Total tuber yield	0.63	0.65	0.36	0.40	0.59	0.61	0.37	0.28
Prop. yield <30 mm	0.47	0.55	0.19	0.31	0.43	0.53	0.12	0.08
Total biomass	-	-	-	-	0.48	0.51	-	-
Harvest index	-	-	-	-	0.65	0.76	-	-

r>0.18 significantly different from zero at P<0.01

Table 5. The genotypic coefficients of variation, cv(g), the coefficients of variation of the genotype x harvest-time-interaction, cv(gxh), the environmental coefficients of variation, cv(e), the character means of the second clonal generation of 1985 and 1986 and the correlation coefficients between character means of the second year clones harvested in July and September.

Character	1985					1986				
	cv (g)	cv (gxh)	cv (e)	mean	r	cv (g)	cv (gxh)	cv (e)	mean	r
Tuber shape	28.8	9.3	21.0	3.18	0.74	36.2	15.0	22.6	2.18	0.72
Eye depth	25.2	17.1	22.8	5.37	0.60	14.2	6.3	10.8	7.09	0.60
Plant appearance	37.5	27.8	29.8	4.33	0.51	23.9	14.8	19.0	5.38	0.55
Tuber number < 30 mm	87.9	83.6	59.5	7.71	0.41	43.6	28.8	45.7	11.5	0.45
Tuber number > 30 mm	28.9	33.4	21.5	22.1	0.17	25.3	13.9	19.5	27.7	0.58
Total tuber number	35.1	17.6	22.4	29.8	0.56	25.4	10.5	21.1	39.3	0.64
Tuber yield < 30 mm	96.1	89.7	65.4	84.0	0.41	46.5	28.7	47.7	102	0.52
Tuber yield > 30 mm	34.6	43.8	25.5	1885	0.17	26.1	24.4	17.1	1838	0.38
Total tuber yield	32.5	41.0	24.4	1969	0.17	24.8	23.0	16.4	1941	0.39
Proportion yield < 30 mm	107	137	81.2	11.3	0.39	66.2	73.6	67.0	7.90	0.34

$r>0.18$ significantly different from zero at $P<0.01$

instance tuber shape, eye depth and total tuber number, a good estimate of the performance as ware potato can be established at the seed potato harvest taking account of the environmental variance. In all other characters the interaction variance is, at least in one series, larger than the environmental variance (Table 5). The use of more replicates for these characters will not lead to a significantly better estimate of assessments at another harvest time.

The genotype x harvest time-interaction makes accurate selection impossible for most traits essential to ware potatoes at seed potato harvest. Therefore, for proper evaluations of traits important to either seed potatoes or to ware potatoes, assessments at both harvest times are required.

The results indicate that selection in the first and second year clones on the appearance of immature plants will not result in a marked improvement of the mean performance of the selected plants when harvested mature. The correlation coefficients in Tables 3 and 5 indicate that only mild selection for characters important to seed potato harvest, such as tuber yield and tuber number over 30 mm diameter and stolon length, should be applied. Rigid selection will result in an unjustified reduction of the genetic material.

Relations between the first and second clonal generation

Coefficients of correlation between the two clonal generations were in general poor to moderate and somewhat lower for the late harvest than for the early one (Table 4). This agrees with the results shown in Table 5. The highest values were found at the early harvest for tuber shape and harvest index. Of all characters assessed the harvest index was the best predictor of the leaf maturity of a clone, r=-0.57 (not in Table 4). Therefore, when the selection only takes place at seed potato harvest time, visual rating of the fresh harvest index might be a manageable extension of the evaluation of the maturity class of the clone.

The correlation coefficients between the first and second year clones for plant appearance ranged from 0.50 to 0.60 at early and from 0.28 to 0.44 at late harvest of the second year clones. This indicates a limited utility for selection for this compound character. However, plant appearance is still among the characters with the highest correlation coefficients and therefore, despite its limitations, assessment of plant appearance can be useful in selection. In order to investigate this, the effect of the selection pressure in the first clonal generation on the selection efficacy is evaluated.

Table 6. Contingency tables of plant appearance assessments at the first (A) and second (B) clonal generation.

Series 1

A 1984 early

B		1	2	3	4	5	6	7	8	9	sum
1985	9				1		3				4
early	8						3	3	1	1	8
	7				2	6	1	5	2	1	17
	6		1	1	3	11	4	4	1		25
	5		3	4	4	10	6	4			31
	4	1	2	3	6	12	2	2	1	1	30
	3	3	2	4	3	7	2	4			25
	2	4	5	5	2	3	1	1			21
	1	14	5	1	3	1					24
	sum	22	18	18	23	51	19	26	5	3	185

A 1984 early

B		1	2	3	4	5	6	7	8	9	sum
1985	9				1	1	1	1			4
late	8		1			3	3	1			8
	7			2	3	5	1	3			14
	6	1	4	2	1	9	3	5	1	3	29
	5	1	2	3	5	12	4	6	3		36
	4	2	5	6	7	8	3	2			33
	3	7	4	3	1	5	2	5	1		28
	2	4	2		3		1	2			17
	1	7		2	2	3	1	1			16
	sum	22	18	18	23	51	19	26	5	3	185

Series 2

A 1985 early

B		1	2	3	4	5	6	7	8	9	sum
1986	9			1							1
early	8					2	2	1			5
	7			1	2	4	2	3	1		13
	6		1	2	4	11	9	2			29
	5	2	4	8	12	7	6	2			41
	4	2	5	7	9	5	2	2			32
	3	6	4	6	7	2					25
	2	2	3		3						8
	1	6	1								7
	sum	18	18	25	37	31	21	10	1	0	161

A 1985 early

B		1	2	3	4	5	6	7	8	9	sum
1986	9						3				3
late	8	2		1	1	1	1				6
	7		1	4	2	5	2	1			15
	6	1	2	7	6	13	6	4			39
	5	2	8	11	11	11	3	3			49
	4	6	4	6	10	4	1	1			33
	3	5	3		3		1				12
	2	2			2		1				5
	1										0
	sum	18	18	26	37	31	21	10	1	0	162

note: Given are the numbers of clones per assessment class (score 1-9; 1 = poor appearance, 9 = excellent appearance). Data are averaged over the one and two plant plot (A) or over the replications (B). The first year clones were harvested after a growing season of about 90 days (early), the second year clones both after approximately 90 (early) and 150 days (late).

In Table 6 the relation between the assessments in first and second clonal generations are given for both series of experiments. For the first year clones the assessments of the one-plant plot and of the two-plant plot were averaged, since no clear differences due to plot size were found in correlation coefficients between first and second year clones (Table 4). For the second year clones the assessments were averaged over the replications.

Table 6 shows that 14 to 15% of the clones have scores of 7 or more for plant appearance in the second clonal generation. However only a small number (19.2 to 55%) performed well in the first clonal generation also. Rigid selection in the first year clones would have reduced the number of well performing clones in the second year. For example, on average only 20% of the clones rated 7 or more in the second year clones were retained with selection of 5% best of all first year clones tested. With a selection percentage in the first year clones of 20% the percentage retained is about 50% and with a selection percentage of 50% about 85%. Using the data of Maris (1962, page 156 and 159) similar percentages are found.

These percentages are of major importance in optimising the selection efficiency of potato breeding programmes. In most breeding programmes the number of third year clones and clones in advanced clonal generations is more or less fixed, due to the costs of labour intensive selection trials. So only a fixed number of clones can be selected in the second clonal generation. Combining this fixed number with the percentage of well performing second year clones retained after selection in the first clonal generation, the following can be concluded. If only 20% were retained, the propgenies of the first clonal generation had to be five times larger than when all good clones were retained. As an example, in Table 7 the numbers of clones, as function of 'n', in the succeeding clonal generations are given for the different selection percentages in the first clonal generation.

Table 7 shows that the selection scheme for selection of all well performing second year clones is not the most economic one. Comparing this scheme, without selection in the first clonal generation, to that with 50% or 20% selection, the latter is easier to execute. Although of selection is not practiced fewer clones have to be evaluated in the first clonal generation, about twice as many clones have to be handled in the second clonal generation. Since plot size in the second clonal generation is about four or more, and in the first year clones only one, it is obvious that in all fewer plants have to be handled using a selection scheme with mild selection in the first year clones. The selection scheme with 5% first year clones selected is less preferable. If two

Table 7. The number of clones, as function of 'n', of the first and second clonal generations to be tested to obtain an equal number of well performing clones in the second year, as a result of the selection pressure in the first clonal generation.

Selection in first year clones	Proportion retained of the well performing clones in the 2nd year *)	Number of first year clones	Number of second year clones
no selection	100%	n	n
50%	85%	nx(100/85)= 1.18n	0.59n (=1.18nx0.50)
20%	50%	nx(100/50)= 2.00n	0.40n (=2.00nx0.20)
5%	20%	nx(100/20)= 5.00n	0.25n (=5.00nx0.05)

two-plant plots are used in the second clonal generation, the experimental field contains 5n+(4*0.25n)=6n plants and without selection in the first year clones only 5n plants.

No clear difference in economic efficiency is observed between the selection scheme executing either 20% selection in the first year clones or 50% selection. Rather more first year clones have to be evaluated in the 20%-scheme but fewer in the second year clones. It depends on the mechanization and on the method of working of the breeding station which selection scheme is economically optimal.

Conclusions

The proposed change in the selection procedure by using two-plant plots instead of one-plant plots did not lead to a marked increase in selection efficiency. Furthermore, these experiments confirm that rigid selection for plant appearance in the first year clones is very ineffective, as could already be concluded from the literature (Maris, 1962; Krug et al., 1974; Tai, 1975; Anderson & Howard, 1981; Caligari et al., 1986; Brown et al., 1987). Only milder selection on plant appearance, with an intensity of 20% or more, in the first year clones will improve the selection efficiency. When used in this way, plant appearance is valuable is selection and connot be replaced by single traits.

The optimal selection intensity will differ between breeding stations since it depends on parameters like the equipment available, the number of plants used in the first and second year clones and the time needed in first and second year clones for planting, harvesting, selection and cultivation.

It was shown in this study that the relation of assessments of genotypes harvested both as seed and as ware potatoes was generally weak. Therefore, the determinations at both harvest times should be treated as separate characters. And since the performance of the mature crop is the most important, mild selection in early harvested clones is advisable.

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Chapter 6

Optimising visual selection in early clonal generations of potato based on genetic and economic considerations

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Summary

In 1985, 1986 and 1987, 600 clones were visually assessed at harvest on plant appearance. The clones were harvested 80 days after planting in the first year, in the following years after approximately 80 days as well as after 145 days. The correlation coefficients between years and between harvest times were low to medium. Simulating different selection intensities using the performance of these 600 clones in two successive years, the relation between selection pressure in the first year and the retained proportion of well performing clones in the second year was described. Including the costs of testing, the most economic selection procedure was calculated. This procedure consisted in testing 1,579 first-year clones and 499 second-year clones for every 100 third-year clones required. The optimal period of the main evaluation in the second clonal year is at ware potato harvest time. This selection procedure also provides good selection possibilities for underwater weight and foliage maturity.

Introduction

Potato breeders mainly select clones in the first two clonal generations by visual preference and this preference determines whether the plant is selected or not. The visual preference can be compared to a multiple-trait selection, including traits concerning the smoothness, colour and shape of the tubers, tuber yield and number, stolon length and clinging stolons and the foliage type and will be referred to as 'plant appearance' in this paper. Furthermore, the selection in these generations is rigorous (Neele et al., 1988) and after the second clonal generation only 2% of the initial population is left.

The efficiency of the selection, however, is low (Blomquist and Lauer 1962; Maris 1962, 1966, 1988; Swiezynski 1968; Davies and Johnston 1965, 1968, 1974; Krug et al. 1974; Kameke 1975, 1978; Tai 1975; Anderson and Howard 1981; Brown et al. 1984, 1987; Caligari et al. 1986; Brown and Caligari 1986; Pfeffer et al. 1988; Neele et al. 1988). Despite abundant evidence for low efficiency of rigorous selection on plant appearance, it has not resulted in major changes in the procedures used in potato breeding. The breeders stick to the old method, probably because the economic parameters of alternative selection schemes are unknown. A new scheme must be both genetically and economically attractive, but since the economic advantages of alternative selection schemes are hardly predictable, breeders are not apt to change to another system. This paper gives estimates of economic and genetic parameters of selection for plant appearance at harvest in the first and second clonal generations.

Materials and methods

In the summers of 1985, 1986 and 1987, 600 clones were assessed visually on their performance at harvest. These 600 clones belonged to 20 hybrid populations, equivalent to those used in commercial breeding. Each population was represented by 30 clones. Alcmaria, a very early maturing cultivar, was used as a standard.

In 1985 the clones were planted on 23 April in a trial near Lelystad, in two plant plots. The limited number of seedling tubers excluded replications. Only 80 days after planting, the plants were evaluated and harvested (11 July), in order to obtain virus-free seeds for the next generation.

The 1986 and 1987 experiments were performed on the same farm as that of 1985, and each clone was represented each year by four plots of two plants. In 1986 the plots were planted on 26 April, two plots were harvested after 74 days and the other two after 142 days. In 1987 planting took place on 21 April and two plots were harvested after 86 and the other two after 145 days.

In all field experiments plant spacing was 35 cm within and 75 cm between ridges. A split-plot experimental design was used with the harvests as main plots and the populations as subplots. The clones were randomized in the populations.

In the first, second and third clonal generation, plots were assessed at harvest on plant appearance (1=poor to 9=excellent) and correlations between all generations were calculated. Furthermore, at the late harvest of the second and third clonal generations, the foliage maturity (1=green to 9=dead) and the underwater weight (in grams per 5 kg tubers) were assessed.

For a comparison between first- and second-year clones, first-year clones were simulated by one two-plant plot at early harvest and the second clonal generation by the mean of two two-plant plots at either early or late harvest. Data of single two-plant plots were obtained from the 1985 experiment, and from both replications of the early harvests of the experiments in 1986 and 1987. Six comparisons were made between first-year clones and second-year clones both at early harvest, and between first-year clones at early harvest and the second-year clones at late harvest (See also legend Fig. 1).

Correlations were calculated between years and between harvests within years. For the calculations the means of the replications of each clone were used. For the determination of the genetic variance, the year variance, the error variance and the genotype-year interaction, analyses of variance were performed for the experiments of 1986 and 1987 using the random model.

In the assessment of the economic parameters, special attention was paid to the time involved in activities during the breeding cycle, since labour costs contribute significantly to the costs of a breeding programme. In several large experiments, using either one-plant plots or four-plant plots, the time for each activity was determined over a period of many years by a group of experienced people. For other costs, data of the Dutch Agricultural Economics Research Institute (LEI) and the Netherlands Central Bureau of Statistics (CBS) were used (Anonymous, 1988) as well as those of Noordam and Ham (1988). This means that the calculated economic optimal selection scheme reflects the Dutch situation, and should be interpreted as an example. The method, however, can be applied worldwide.

To identify the selection scheme with minimal costs in the first and second clonal generation, economic parameters were combined with the comparisons between plant appearance of first- and second-year clones.

Assuming that a more or less fixed number of entries are tested in the third clonal generation, the costs of the first and the second clonal generation is described as follows

$$C = c_1 x N_1 + c_2 x N_2 \qquad \text{or,}$$
$$C = c_1 x N_3/I x F + c_2 x(S x N_3/I x F)) \qquad (1)$$

where C is the total costs, c_1 the cost of a first-year clone, c_2 the cost of a second-year clone, N_1, N_2 and N_3 the number of first-, second- and third-year clones respectively, S the selection intensity in the first clonal generation, I the proportion of well-performing clones in the initial population of first-year clones and F the retained fraction of the well-performing second-year clones in the first selection cycle.

Results and discussion

A moderate similarity was found between different years and harvests for plant appearance (Table 1). This agrees the findings of the authors referred to in the introduction. For the calculation of the correlation coefficients, the means of the replications of each clone were used for the 1986 and 1987 experiments. Therefore, compared to breeding practice of the first field generations, where in general small single-field plots are used, the presented coefficients will be higher and breeders should take into account that relationships between years are weaker.

Correlations within years or between years at the same harvest period were moderate, those between years at different harvest times were weak to moderate. Consequently, the appearance of the plants at early harvest of the first year clones predicts poorly the appearance at maturity in the following generations. Therefore, the mature and immature plant appearance should be used independently in the selection.

Moderate correlations between years at early and at late harvesting can be caused by high environmental variances and/or high genotype-environment interactions. As indicated in Table 2, the genotype-year interaction [YC(P)+YP: 0.26 for the early harvest and 0.24 for the late harvest evaluation] was of minor importance; the environmental variance was about four times as high.

Table 1. Correlations for plant appearance between and within years and different harvest times.

	Early vs. early	Early vs. late	Late vs. early	Late vs. late
Between years				
1985-1986	0.69**	0.54**		
1985-1987	0.66**	0.45**		
1986-1987	0.77**	0.46**	0.66**	0.63**
Within years				
1986		0.66**		
1987		0.61**		

**) significant at $P<0.01$

Therefore, an improvement in estimating the value of the clones by using more plants per clones improves the correspondence between years. However, it has already been reported earlier that using more than one plant per first year clone was economically not feasible (Neele et al. 1988). Using two-plant plots instead of one-plant plots resulted only in a minor improvement of the resemblance of the first and the second clonal generation. The heritability for the late harvest was lower than that for the early harvest. Selection for plant appearance at late harvest should, therefore, be carried out with even more caution than at early harvest.

Studying correlation coefficients and heritabilities does not give information on the economically best selection scheme. In such a scheme loss of some potentially valuable material is acceptable if it is compensated for by a reduction of costs. For determining the optimal scheme, the number of third year clones is assumed to be fixed, due to the relatively high costs involved in testing these clones. So in the best scheme, from an economic point of view, a fixed number of clones is retained after two selection cycles at the lowest cost.

In the first selection cycle not all potential clones are recognized, as is shown in Table 3. The data given in contingency tables e.g. Table 3, can be used to optimise the selection in the first and second clonal generation (Simmonds 1985). However, due to the limited number of classes used in the

Table 2. Analysis of variance for plant appearance of 600 clones at early harvest and at late harvest of 1986 and 1987.

Source of variation	abbr.	df	Early harvest		Late harvest		Expected mean squares
			SS	MS	SS	MS	
Year	Y	1	388.0	388.03**	2.1	2.11	e + 2YC(P) + 60YP + 600B(Y) + 1200Y
Populations	P	19	3086.8	162.46**	1141.7	60.09**	e + 2YC(P) + 4C(P) + 60YP + 120P
Blocks within years	B(Y)	2	45.9	22.97**	4.0	2.02	e + 600B(Y)
Years x populations	YP	19	79.2	4.17**	56.9	3.00**	e + 2YC(P) + 60YP
Clones within populations	C(P)	580	3423.2	5.90**	2769.4	4.78**	e + 2YC(P) + 4C(P)
Years x clones within populations	YC(P)	580	738.1	1.37**	825.6	1.42**	e + 2YC(P)
Error	e	1165	1117.5	0.96	1176.7	1.01	e
Mean				4.888		5.441	
Heritability [a]				0.560		0.509	

**) significant at $P<0.01$

estimated variances:

early harvest: error=0.96; YC(P)=0.21; C(P)=1.13; YP=0.05; B(Y)=0.37; P=1.28; Y=0.30

late harvest: error=1.01; YC(P)=0.21; C(P)=0.84; YP=0.03; B(Y)=0; P=0.45; Y=0

[a]) Heritability=(P+C(P))/(error+YC(P)+C(P)+YP+B(Y)+P)

Table 3. Performance at the early harvest of 1986 (one two-plant plot) and at the late harvest of 1987 (mean of two two-plant plots) for the plant appearance character (1=poor, 9=excellent).

		Late harvest 1987									
		1	2	3	4	5	6	7	8	9	Total
Early	9	0	0	0	0	1	2	1	1	0	5
harvest	8	0	0	0	0	1	5	2	3	1	12
1986	7	0	0	0	0	4	13	22	10	2	51
	6	0	0	0	7	16	32	24	11	4	94
	5	0	0	1	18	35	33	36	13	1	137
	4	2	1	4	12	27	22	19	9	0	96
	3	0	1	2	17	18	21	15	2	1	77
	2	0	0	11	20	26	11	4	0	0	72
	1	0	3	5	11	14	8	3	0	0	44
	Total	2	5	23	85	142	147	126	49	9	588

assessment of plant appearance, contingency tables offer a limited number of selection intensities in the first clonal generation. Figure 1 presents the proportion of the selected first year clones performing well in the second year clones (F in Eq. 1) plotted against the selection pressure in the first generation (S in Eq. 1). The relation is continuous and deviates from those expected with random selection, y=x line, and those with perfect selection in the first clonal generation, curve P.

The calculated relationship between the evaluation at early harvest of the first clonal generation and the early harvest evaluation in the second year clones is

$$\ln(1+F) = -1.144+1.847/(1+e^{(-7.147(\ln(1+S)+0.0708)}) \quad (2),$$

that with the late harvest evaluation in the second year clones is

$$\ln(1+F) = -0.804+1.527/(1+e^{(-5.790(\ln(1+S)+0.0220)}) \quad (3)$$

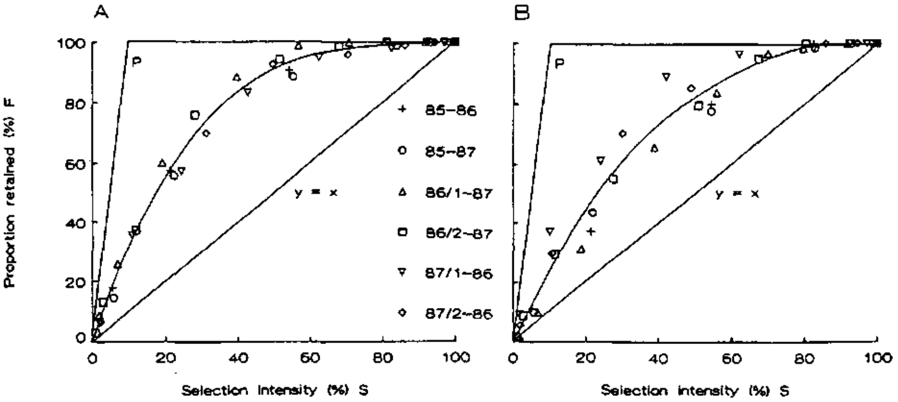

Figure 1 A and B. The proportion of clones performing well in the second clonal generation (*F*, ±10% of the population) recognized at different selection intensities in the first clonal generation (*S*). The first-year clones were represented by the experiment of 1985 and each of the two replicates of the early harvest of the experiments of 1986 and 1987. These were compared to the mean scores of either (**A**) the early or (**B**) the late harvest of the experiments of 1986 and 1987. The y=x-line represents random selection, the P-curve perfect recognition of all well-performing clones in the first clonal

Equations 2 and 3 describe the observed relationship between the selection intensity at early harvest of the first clonal generation and the retained proportion of the well-performing clones in the second clonal generation at early and at late harvests. These formulas agree with the relationship found by Neele et al. (1988) and those calculated with data of Maris (1962). The retained proportion was higher at early harvest than at late harvest. This means that with selection at late harvest, either more first year clones are to be grown or the selection must be milder, if a breeder wants to have equal number of third year clones.

The optimal selection scheme depends not only of the reliability of the assessment, but also on the costs of testing. Costs can be divided into costs that are plot-size independent, like agricultural maintenance and plant protection, and those that are plot-size dependent, such as time required for planting and harvesting. Table 4 shows labour time and costs of relevant activities.

The main costs of field trials with first and second year clones are the loss of commercial harvest and the plot-size dependent costs (Table 4). With respect to the plot-size dependent costs, the costs for planting one seed tuber per clone is considerably less than for planting the same number of

Table 4. Costs of experiments in terms of labour time or in Dutch guilders. The costs are divided into plot size independent (per hectare) and plot size dependent (per 1,000 clones). The plot size dependent costs are separated into costs for growing 1,000 first year clones in one-plant plots or 1,000 second year clones in one four-plant plot (only early harvest evaluation) or two four-plant plots (early and late harvest evaluation) The harvest costs are dependent on the selection intensity S of the first clonal generation, the initial and the retained proportion of well performing clones (I and F).

At harvest all tubers were collected and put into nylon bags. Calculation of the total costs per clone was based on an average wage of a field worker of Dfl 26.50 per hour[1].

Plot size independent (per hectare = 38,000 plants)

Ploughing, harrowing, manuring, etc.			565 minutes[2]
Plant protection (including twelve sprays against *Phytophthora infestans*)			550 minutes[2]
Costs of manure	250 kg N	à Dfl 1.20	Dfl 300.-[2]
	120 kg P_2O_5	à Dfl 0.90	Dfl 108.-[2]
	250 kg K_2O	à Dfl 0.52	Dfl 130.-[2]
Costs of plant protection chemicals			Dfl 1,168.-[2]
Loss of commercial harvest			
- main product	44,000 kg	à Dfl 0.18	Dfl 7,920.-[2]
- rest	4,000 kg	à Dfl 0.05	Dfl 200.-[2]
Land rent			Dfl 580.-[1]
Total plot size independent costs			
- per hectare			Dfl 10,900.-
- per plant (15% border plants and paths)			Dfl 0.337

Plot size dependent (in minutes per 1,000 clones)

	One-plant plot	Four-plant plot
Planting	45	320
Field determinations (3)	540	540
Harvesting		
- Early harvest		
selection independent	465	1565
selection dependent	585xS	1985x(FxI)/S
- Late harvest		
selection independent	675	2405
selection dependent	800xS	2795x(FxI)/S
Total plot size dependent costs per 1,000 clones (Dfl)		
- Early harvest	464+258xS	1,071+877x(FxI)/S
- Early and late harvest	*****	3,151+1,234x(FxI)/S

Total costs per 1,000 clones (Dfl)

	One-plant plot	Four-plant plot
- Early harvest	801+258xS	2,419+877x(FxI)/S
- Early and late harvest	*****	5,847+1,234x(FxI)/S

[1] Anonymous (1988) [2] Noordam and Ham (1988)

seed tubers in four-plant plots. However, harvesting of the four-plant and the relative difference in time exceeds the difference
in planting the seed potatoes.

No differences were found in time needed for the field assessments between one- and four-plant plots. The larger plots were found easier to evaluate, compensating for the extra time used for walking along four-plant plots.

For comparing the economics of one-plant plots versus four-plant plots the total costs for each have been calculated (Table 4). The costs of testing first and second year clones depend on the selection intensity in the first clonal generation (*S* in Eq. 1), the initial proportion of well-performing clones (*I* in Eq. 1) and the retained proportion of well-performing second year clones (*F* in Eq. 1).

In these populations the proportion of well-performing clones (*I*) was found to be approximately 10%. Comparable proportions were also found by Maris (1962) and Neele et al. (1988). Brown (1987) found a proportion of 24% of satisfactorily performing clones, having a score over 5 in a 1-9 scale, and 7% of well-performing clones with a score over 6.

Besides *I*, *F* and *S*, three other parameters are important, namely N_3, c_1 and c_2 (Eq. 1). The number of third year clones, N_3, is taken to be fixed; the costs per first and per second year clone (c_1 and c_2) are calculated in Table 4. The relations between *F* and *S* are described in Eqs. (2) and (3), and by substitution in these formulas and the costs in the cost formula (Eq. 1) the selection procedure with minimal costs can be calculated.

It is calculated that the most economic selection scheme with selection for plant appearance at early harvest in the first and the second clonal generation is obtained by using a selection intensity (*S*) of 32.4% in the first-year clones. Thus, the retained proportion of the well-performing second year clones (=*F*) is 75.8%.

Assuming 10% of well-performing clones in the initial population, the first clonal generation should contain 1,319 [= 100 / (0.758 x 0.10)] clones, the second clonal generation 427 [= 1,319 x 0.342] clones to obtain 100 third year clones. The total number of plants to test is (1,319 x 1) + (427 x 4) = 3027.

For a scheme of visual evaluation at late harvest of the second clonal generation, the most economic selection scheme is obtained by using a selection intensity of 31.6% in the first clonal generation. The retained proportion of potentially well-performing clones at the late harvest is 63.3%.

Table 5. Fourteen alternative selection schemes to obtain 100 third year clones from a population containing 10% well performing clones. For each scheme are listed the selection intensity in the first clonal generation (S), the number of first and second year clones (N1 and N2), the costs of testing a first and second year clone (c_1 and c_2) and the total costs (C). The schemes involve selection in the second clonal generation at either the early harvest or the late harvest.

S(%)	c_1	Selection in second clonal generation at							
		early harvest				late harvest			
		N1	c_2	N2	C (Dfl)	N1	c_2	N2	C (Dfl)
1	0.803	25258	2.766	253	20989	32925	6.222	329	28498
2.5	0.807	11562	2.722	289	10120	15613	6.164	390	15009
5	0.814	6102	2.706	305	5790	8296	6.145	415	9299
10	0.827	3209	2.692	321	3517	4296	6.135	430	6187
15	0.840	2252	2.679	338	2796	2937	6.127	441	5165
20	0.852	1794	2.663	359	2485	2271	6.119	454	4715
30	0.878	1374	2.632	412	2292	1639	6.098	492	4439
40	0.904	1196	2.603	478	2326	1355	6.075	542	4518
50	0.930	1107	2.577	554	2456	1204	6.052	602	4765
60	0.957	1059	2.557	635	2636	1117	6.032	670	5109
70	0.982	1031	2.541	721	2844	1063	6.013	744	5517
80	1.007	1013	2.527	811	3070	1028	5.997	822	5967
90	1.033	1003	2.516	903	3307	1004	5.984	904	6447
100	1.059	1000	2.507	1000	3566	1000	5.972	1000	7033

This implies testing 1,579 [= 100 / (0.633 x 0.10)] first-year clones and 499 (= 1,579 x 0.316) second-year clones, or (1,579 x 1) + (499 x 8) = 5571 plants, to obtain 100 third-year clones. The number of plants is higher than in the scheme involving early harvest evaluation only. This is because the early harvest performance and the performance at late harvest are less well correlated (Table 1), and the extension of the selection scheme to a late harvest evaluation gives additional information.

The most economical selection scheme uses a selection intensity of 32.4% (early harvest evaluation in the second clonal generation) or 31.6% (late harvest evaluation in the second clonal generation) in the first clonal generation. It is also interesting to know what the effects are of different selection schemes on the costs. Costs and plant numbers for alternative selection schemes are listed in Table 5.

Selection schemes involving selection intensities of 20% - 50% in the first clonal generation do not differ much in costs. Therefore, breeders are advised to adjust the selection schemes to a selection intensity in the first clonal generation between 20% and 50%, preferably 32%. Schemes with selection intensities of 10% or less are not recommended, since these are even more costly than the scheme without selection in the first clonal generation.

Table 6. Phenotypic correlation coefficients between plant appearance of the 600 clones at either the early or the late harvest and foliage maturity and underwater weight of tubers, both at the late harvest.

Correlated characters	Early harvest		Late harvest	
	1986	1987	1986	1987
Plant appearance				
- foliage maturity	0.69	0.40	0.38	-0.05
- underwater weight	-0.41	-0.37	-0.28	-0.10

<u>Effects on other traits.</u>Since selection for plant appearance at early harvest might influence the mean of the foliage maturity and underwater weight of the selected population, a measure of the dry matter content, these characters were determined at late harvest.

For foliage maturity, the correlation coefficient with plant appearance at early harvest was moderate (Table 6). This means that selection for plant appearance will favour early-maturing clones. In fact, selection of the best 10% clones at the early harvest in the first clonal generation and 20% in the second clonal generation results in a population containing mainly very early-maturing clones. The mean score of the selected clones for foliage maturity was 8.6 in 1986 and 7.3 in 1987 (Table 7). Since the very early standard variety Alcmaria had a mean score for foliage maturity of 8.9 in 1986 and 7.8 in 1987, a large proportion of the selected clones were even earlier than Alcmaria. Rigorous selection at early harvest of both the first and the second clonal generation will result in a relative early maturing population. A selection intensity of about 35% at early harvest in the first year and 20% in the second year decreased the mean maturity score to 8.3 in 1986 and to 6.3 in 1987. Late harvest evaluation of plant appearance in the second clonal year resulted in a mean maturity of the selected clones of 7.4 in 1986 and 5.2 in 1987. Very early clones were not retained by the latter selection. This shows that high selection pressure at early harvest is not only economically sub-optimal, but also induces a shift of the mean maturity of the selected clones. With milder selection more clones in later maturity classes are retained.

For underwater weight the situation is less critical, as can be concluded from the lower correlation coefficients (Table 6). However, mainly clones with low underwater weight were selected if selection was rigorous in both clonal generations (Table 7). In the starch, French fries or chipping industry a minimum level of the dry matter content is required. So if the major part of the selected population has a low dry matter content, many clones will not be suitable for industrial processing and this will reduce the agronomical value of the breeding material. If a higher proportion is selected, the population mean of underwater weight is higher. This is especially so if the selection is done at the late harvest.

Late harvest evaluation in the second clonal generation does not only improve the total level of the underwater weight and maintain the variation in maturity, but also all clones have a satisfactory plant appearance at late harvest. In selection at early harvest only 50% - 65% of the retained population will perform satisfactorily as ware potato. This means that the number of entries in the third field-year must be 1.5 - 2 times larger than if the main determination occurs at late harvest in the second clonal generation. Increasing the number of third-year clones also implies testing of more first-

Table 7. Effects of selection for plant appearance on the mean scores of the selected clones for maturity and for underwater weight. For the schemes including early harvest evaluation (e) only, the proportion of clones having a plant appearance score over 7 at late harvest is listed. In the scheme marked with (l), late harvest evaluation is included.

	Unselected population	Mean of the population after application of the selection scheme (proportion selected first/second year)		
		10% / 20% (e)	35% / 20% (e)	35% / 20% (l)
1986				
Maturity	5.9	8.6	8.3	7.4
Underwater weight	493	420	450	469
Plant appearance late	21.7%	65%	63%	100%
1987				
Maturity	4.6	7.3	6.3	5.2
Underwater weight	402	337	370	392
Plant appearance late	18.9%	55%	48%	100%

and second-year clones. This will lead to an increase in costs, compared to a scheme including late harvest evaluation. The higher costs of evaluating the second clonal generation at early and at late harvest will be compensated for by a reduced number of entries at the first, second and third clonal generation. For obtaining 100 third year clones in a scheme including late harvest evaluation, 1,579 first year clones have to be tested and 499 second year clones, as mentioned earlier. Total costs are Dfl 4,435 (calculated from data in Table 4). To obtain the same number of third year clones using a scheme with early harvest evaluation only, 1,319 first-year clones and 427 second-year clones must be evaluated. Costs for the first two years are Dfl 2,287. This figure must be multiplied by 1.5 - 2 to obtain an equal number of well-performing third year clones at late harvest. For the costs of the first two field generations this will be within the range Dfl 3,430.50 to Dfl 4,574, equaling the costs of a scheme including late harvest evaluation. However, in the latter scheme the number of the third-year clones is lower and so are the costs of tests. Therefore, a scheme including late harvest evaluation will be more economic.

Conclusions

The commonly used selection scheme with severe visual selection on plant appearance in the first clonal generation and somewhat milder selection in the second is not optimal. To obtain a certain number of third-year clones, the most economic selection procedure is to apply a selection intensity of about 32%. This selection intensity is almost equal to that suggested by Maris (1988). He suggested a selection intensity of 40% for the first clonal generation, but did not support it by economic data. A favourable aspect of milder selection is that later maturing clones with high underwater weight are being retained.

It should be considered that the suggested selection intensity is based on Dutch economic parameters and these parameters differ from those of other countries. However, the approach used in this study can be applied worldwide and by substituting local economic parameters in the model, the economic optimal selection procedure can be adjusted. Furthermore, breeders are advised to include late harvest evaluation on plant appearance in the second clonal generation, since in such a scheme selection can be applied at the lowest relative costs.

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Chapter 7

Components of visual selection in early clonal generations of a potato breeding programme

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Summary

In the first two clonal generations of a potato breeding programme, clones are visually selected for 'plant appearance'. Selection for plant appearance based on unreplicated small plots is unreliable, due to significant genotype x environment interaction and high error variance. In order to improve the selection efficiency, component traits of plant appearance were identified and the effect of selection for these components was studied. Tuber yield was found to be the principal component of plant appearance while stolon length and tuber appearance contributed significantly, but to a lesser extent. Tuber yield had a higher heritability than plant appearance. Characters determining the appearance of stolons and tubers were found to have equal or lower heritabilities than plant appearance at 80 days after planting and somewhat higher heritabilities than plant appearance at 145 days after planting. Hence, since the expected and observed selection responses of the component characters have been found to be equivalent to that of plant appearance, selection for plant appearance cannot be improved upon by separately selecting for characters like tuber yield and tuber appearance.

Introduction

After hybridization, the breeding scheme of potato normally consists of two years of visual selection according to the preference of the breeder. In the succeeding generations the selection is generally based on more accurately assessed performance in replicated experiments (Neele et al. 1988). Selection in the first and second clonal generation is based on a visual scoring of foliage, stolons and tubers, in this paper referred to as 'plant appearance'. The aim of this visual selection is to eliminate genotypes with characteristics unacceptable for agriculture, industry and market, such as clinging stolons, irregular tuber shape, growth cracks and deep eyes. Furthermore, selection is carried out for skin and flesh colour, both determined by the preferences prevailing in the country where the resulting varieties are to be marketed. In general, the intention is to select for a combination of characters that can be determined quickly and reliably by eye, and therefore 'plant appearance' can be seen as a selection index. Application of this index in selection of the early clonal generations leads to improved agronomical and commercial value of the selected population and on average breeders are satisfied with the selection results. However, there is much evidence that scoring for plant appearance is not consistent over replicates, locations and years (Blomquist & Lauer 1962, Brown et al. 1984, 1987, Brown et al. 1987, Davies & Johnston 1974, von Kameke 1975, Krug et al. 1974, Maris 1962, 1988, Neele et al. 1988, 1989, Tai 1975). This would suggest that there are possibilities to improve the index. Plant appearance is likely to include characters which are affected by strong genotype-environment interactions and or high error variance, and therefore have low heritabilities. Since the heritabilities of component characters are influencing the selection response when using a selection index (Falconer 1981, Tai 1989), characters with low heritabilities should either not be included in the index or should not carry much weight to optimize the selection response when using the index 'plant appearance'.

This study analyses the importance of several components of 'plant appearance' for the optimal selection decision. In addition, the impact of the environment on phenotypic values is calculated. The results are discussed in relation to breeding methodology.

Materials and Methods

The performance of 600 clones was evaluated in the summers of 1985, 1986 and 1987. The clones were chosen at random from 20 progenies, including reciprocal crosses, resulting from a crossing programme using six unrelated parents. The 20 progenies were comparable to those used in commercial breeding programmes.

All trials were grown on a clay soil near Lelystad in the Dutch New Polders. Plant spacing was 35 cm within and 75 cm between the rows and plots consisted of two plants. Since in breeding practice material is selected independently at the time of seed potato harvest (July) and at the time of ware potato harvest (September), seed and ware potato harvest evaluations were carried out as separate experiments. The harvests in July are referred to as 'early harvests', the harvests in September as 'late harvests'. The clones were randomized within the progenies and in each progeny plots of five standard varieties were included.

In 1985 the clones were planted on April 23 and only an early harvest was carried out, on July 11, to obtain virus free seeds for the next generation. In 1986 and 1987 both the early harvest and the late harvest experiment were carried out in two replicates. In 1986 the plots were planted on April 26, the early harvest took place on July 9 and the late one on September 15. In 1987 planting took place on 21 April, the early harvest on July 16, and the late harvest on September 13.

For visual assessment, clones were compared with the average performance of the standard varieties, to ensure consistency in the determination.

The plots were evaluated for early season growth (1=slow growth to 9=rapid growth), foliage maturity in September (1=green to 9=dead) and number of stems in the middle of June. In 1987 the number of stems could not be counted in the plots of the late harvest, due to adverse weather conditions. During harvest, plant appearance (1=poor to 9=excellent) and, only at early harvest, stolon length (1=long to 9=short) were assessed. Tuber yield and number of tubers under and over 30 mm were determined. Separate visual assessments were made of tuber shape (1=round to 5=long), regularity of tuber shape (1=irregular to 9=regular), skin colour (1=yellow to 4=purple), growth cracks (0=absent, 1=present) and eye depth (1=deep to 9=shallow). In addition the underwater weight (in grams per 5 kg tubers) was determined for the late harvests. Subsequently the average tuber weight, the proportion of the tuber yield by tubers under 30 mm and number of tubers per stem were calculated. All visual assessments were carried out by the second author, an experienced potato breeder.

For every trial, correlation coefficients were calculated between plant appearance and all other characters measured, except growth cracks, since this character was binomially distributed. To identify which characters determined plant appearance, multiple regression analyses were carried out for every year-harvest combination, using the step-up and step-down method (Snedecor & Cochran, 1967). In this analyses a character is selected according to the ratio of the residual mean squares, to be included in or excluded from the regression model. Only the characters that contributed significantly to the variance of plant appearance remained in the regression model.

Analyses of variance were performed for the early and for the late harvest experiments of 1986 and 1987 using the random model (Snedecor & Cochran, 1967). Heritabilities were calculated for two-plant plots without replications in one year, a situation comparable to the first clonal generation.

For the late harvest experiments, correlated responses (*CR*) were estimated for other traits (y) after selection for plant appearance (x) or after selection for tuber yield and average tuber weight. Since the response traits were not only related to the selected traits but also related to each other, the correlated response was calculated by multiplying the matrix of genetic variances and covariances (G) with the inverse matrix of the phenotypic variances and covariances (P^{-1}) and the selection differential (S): $CR_Y=G\ P^{-1}\ S$ (Young & Weiler, 1960), with $S=i\sigma_p(y)r_g$, where i is the selection intensity, $\sigma_p(y)$ the phenotypic standard deviation of trait y, and r_g the genotypic correlation between traits x and y. To evaluate the estimated selection responses, actual responses were calculated.

Results and Discussion

Plant appearance of the clones at early harvest as well as at late harvest was found to be influences by interactions between genotypes and years (Table 1). The interaction components years x progenies and years x clones within progenies were significant at both harvest times. However, the interaction variances were only small compared to the error variance. This indicates that in experiments with small plots and no replicates, the non-genetic variation in

Table 1. Estimates of variance components, mean and heritability for 'plant appearance' (score 1-9, 1=poor to 9=excellent) at the early (mid-July) and at the late harvest (mid-September) of 1986 and 1987.

Source	Abbri-viation	Early harvest	Late harvest
Years	Y	0.30^{*}	0
Progenies	P	1.28^{**}	0.45^{**}
Blocks within years	B(Y)	0.04^{**}	0
Years x Progenies	YP	0.05^{**}	0.03^{**}
Clones within progenies	C(P)	1.36^{**}	0.84^{**}
Years x Clones within progenies	YC(P)	0.16^{**}	0.21^{**}
Error	E	0.96	1.01
Mean		4.88	5.44
Heritability		0.69	0.51

$h^2=(\sigma^2_p+\sigma^2_{c(p)})/(\sigma^2_p+\sigma^2_{c(p)}+\sigma^2_{b(y)}+\sigma^2_{yp}+\sigma^2_{yc(p)}+\sigma^2_e)$ * $P<0.05$, ** $P<0.01$

plant appearance is to a greater extent caused by experimental error than by the genotype-year interaction. The influence of the non-genetic variance on the total variance was relatively large, as is indicated by the moderate heritabilities for plant appearance, particularly for late harvest (Table 1). Since in the early generations of a potato breeding programme the number of plants per clones available for testing is restricted, selection for plant appearance should therefore be mild, to prevent that too many good clones are erroneously rejected.

However, a plant breeder wants to reject unattractive clones as soon as possible, and might be reluctant to reduce selection pressure. Therefore, another option would be to improve the reliability of selection by increasing the heritability of the plant appearance score. As mentioned before, the character can be considered to be a selection index. The only moderate heritability of plant appearance found in the experiments indicates that the index includes characters which cannot be determinated reliably by eye in small plots. To make the selection in the early generations more accurate,

Table 2. Phenotypic and genotypic correlation coefficients (r_p, r_g) between 'plant appearance' and other traits.

Correlated character	Early harvest			Late harvest	
	1985	1986	1987	1986	1987
	r_p	r_g	r_g	r_g	r_g
Tuber yield	0.65	0.83	0.82	0.51	0.67
Average tuber weight	0.62	0.69	0.70	0.28	0.57
Prop. yield tubers < 30mm [a]	-0.51	-0.65	-0.71	-0.34	-0.56
Stolon length	0.51	0.56	0.55	-	-
Early season growth	0.33	0.58	0.60	0.55	0.47
Skin colour [a]	-0.34	-0.34	-0.29	-0.13 [b]	-0.11 [b]
Regularity of tuber shape	0.26	0.64	0.43	0.58	0.34
Tuber shape	0.26	0.30	0.32	0.07 [b]	0.19
Eye depth	0.21	0.32	0.32	0.40	0.25
Total number of tubers	-0.16	0.15	0.07	0.03	0.08
Number of stems	0.03	0.34	0.20	0.25	-
Number of tubers per stem [a]	-0.15	-0.07 [b]	-0.10 [b]	-0.17	-
Maturity	-	-	-	-0.40	0.06
Underwater weight	-	-	-	-0.28	-0.01 [b]

Significance levels of phenotypic correlation coefficients (1985):
$P<0.05$ $r>0.09$; $P<0.01$ $r>0.12$

[a]) Data were log-transformed to obtain a normal distribution.

[b]) correlation coefficient less than twice the standard error.

such characters should be eliminated from the plant appearance selection index. To determine the influence of various characters on plant appearance, phenotypic and genetic correlation coefficients between plant appearance and other traits were calculated (Table 2).

At early harvest, high correlation coefficients were found between plant appearance and tuber yield, and moderate correlation coefficients between plant appearance and average tuber weight, stolon length, early season growth and the proportion of tuber yield from small tubers. At late harvest, tuber yield, average tuber weight, regularity of tuber shape and early season growth were correlated to plant appearance although the correlation coefficients were lower than at the early harvest. Maris (1988) found similar phenotypic correlation coefficients, r_p, between plant appearance and tuber yield or average tuber weight at late harvest, of about 0.5.

At both harvest times, tuber yield was found to be one of the most important characters determining plant appearance. Tuber yield was also moderately correlated with average tuber weight (r_p=0.62-0.67) and early season growth (r_p=0.63-0.73) at early harvest and to average tuber weight (r_p=0.39-0.64) and early season growth (r_p=0.47-0.47) at late harvest. The correlation of plant appearance with these characters can be explained, to a certain extent, by their correlation with tuber yield. To determine this relationship, a multiple regression analysis was performed of all characters measured on plant appearance (Table 3). The percentage of the variance in plant appearance accounted for by component traits, varied from 52.8% to 70.6%. The rather large proportion of unaccounted variance might be explained by inconsequent assessments of plant appearance and by discontinuity in the scoring scale. Moreover, probably not all characters relevant for plant appearance were measured in the experiments. It is not likely that inconsequent observations are responsible for a large part of the unaccounted variation since five standard varieties were included in each progeny-plot and the plant appearance scores for each clone were adjusted to those of the standards.

At late harvest, a smaller proportion of the variation could be explained by the evaluated characters, and it is likely that other characters were important for plant appearance. For example growth cracks were not included in the multiple regression, since it was binomially distributed. Plants with heavy growth cracks always got a low score for plant appearance; plants with one or two tubers with a small crack, however, could compensate this shortcoming with excellent performance of other characters. Therefore, the data were divided into two groups referring to plants with growth cracks, approximately 5% of the population, and plants without growth cracks. In the group without growth cracks the variance in plant appearance accounted for by the other characters and the regression coefficients did hardly differ from those of Table 3. In the group with growth cracks, however, the percentage of variance accounted for was even lower than in Table 3, varying from 41.1% to 58.1%. This illustrates that the character growth cracks had some impact on plant appearance, but could not explain a major part of the unaccounted variance of plant appearance.

The major part of the explained variation in plant appearance could be contributed to five to seven characters (Table 3). Tuber yield explained about

Table 3. Multiple regression analysis by the step-up and step-down method of the characters mentioned in Table 2 on plant appearance evaluated in 1985, 1986 and 1987 at early and late harvest. r.c. is the regression coefficient, s.e. is its standard error. Characters not mentioned did not contribute significantly to the regression.

	Early harvest						Late harvest			
	1985		1986		1987		1986		1987	
	r.c.	s.e.	r.c.	s.e.	r.c.	s.e.	r.c.	s.e.	r.c.	s.e.
Constant	0.23	0.35	-0.02	0.30	1.47	0.26	1.94	0.30	1.39	0.17
Character										
Tuber yield (kg)	3.21	0.17	2.09	0.15	1.85	0.13	1.42	0.08	0.92	0.04
Number of tubers	-0.05	0.01	-0.01	0.00	-0.01	0.00	-0.04	0.00	-0.02	0.00
Regularity of tuber shape	0.30	0.04	0.30	0.02	0.18	0.02	0.38	0.02	0.36	0.02
Stolon length	0.13	0.03	0.11	0.02	0.09	0.02	-	-	-	-
Skin colour [a]	-0.41	0.12	0.36	0.07	n.s.		n.s.		n.s.	
Prop. yield tubers <30mm[a]	n.s.		-0.14	0.05	-0.26	0.05	n.s.		n.s.	
Early season growth	n.s.		0.06	0.02	0.05	0.02	0.04	0.01	-0.14	0.03
Tuber shape	n.s.		n.s.		n.s.		-0.11	0.03	n.s.	
Maturity	-		-		-		-0.12	0.01	n.s.	
Average tuber weight	n.s.		n.s.		n.s.		-0.01	0.00	n.s.	
Percentage variance accounted for	58.7%		70.6%		67.5%		57.7%		52.8%	

n.s.= non-significant

[a]) Data were log-transformed to obtain normal-distribution.

50% of the variation in plant appearance at the early harvest and about 30% of the variation at the late harvest (calculated as squares of the phenotypic correlation coefficients of Table 2). The remaining explainable variance is determined by characters such as skin colour, number of tubers, regularity of tuber shape and stolon length.

Tuber yield showed significant genotype-year interaction variances and a relative large error variance at early and late harvest (Tables 4 and 5). This suggests that misclassifications of potential tuber yield based on the performance of unreplicated two-plant plots are likely to occur. The heritabilities of tuber yield, however, were far better than those of plant appearance (Tables 1, 4 and 5). Other characters than tuber yield might, therefore, have more severely decreased the reliability of the plant appearance scores.

Number of tubers and the regularity of tuber shape had lower heritabilities than plant appearance (Table 4 and 5). This suggests that breeders should take less notion of the number of tubers during the first and second clonal generation in the visual selection, and that only clones with extreme high or low numbers of tubers should be eliminated. Paying less attention to the regularity of tuber shape is also likely to improve the consistency of the plant appearance scores at early harvest. However, since the heritability of regularity of tuber shape was still moderate, the exclusion of this character might only result in a slight improvement of the heritability of plant appearance. The other characters with low heritability (Table 4), such as number of stems and number of tubers per stem, had no substantial influence on plant appearance (Table 3), and therefore their low heritability is unlikely to affect the heritability of plant appearance.

For early harvest selection, plant appearance as indicated by the heritabilities (Tables 1 and 4), offered equal or better conditions for selection than other characters, and selection for separate characters would not have resulted in improved selection responses.

For late harvest selection, in contrast, most characters had higher heritabilities than plant appearance (Tables 1 and 5). In addition, all characters were found to be either weakly correlated with each other or to show a positively correlated response. However, not all of the evaluated characters are normally subject to selection, and some characters cannot accurately be determined by eye. Maturity is generally not a character to select for, only very late maturing genotypes are rejected; it is merely a character for classification. It is not possible to select visually for underwater weight. In the experiments

Table 4. Estimated variance components, means, and heritabilities for traits determined on plants harvested mid-July (early harvest) in 1986 and 1987. For abbreviations see Table 1.

Source	Early season growth (1-9)	Number of stems	Stolon length (1-9)	Skin colour (1-4) ^{a}	Tuber shape (1-5)	Regula-rity of tuber shape (1-9)	Eye depth (1-9)	Number of tubers	Number of tubers per stem	Tuber yield (100 g)	Av. tuber weight (g)	Prop. yield tubers <30mm^{a}
Y	0	4.83**	1.65**	0.001**	0.318**	0.102	0	0.1	2.00**	1.99	7.9	0.013**
P	0.256**	0.59*	1.70**	0.089**	0.298**	0.487**	1.39**	25.0**	0.18*	9.56**	82.3**	0.303**
B(Y)	0.054**	0.05**	0.01**	0	0.004**	0.024**	0	0.0	0.01*	0.49**	5.6**	0.026**
YP	0.066**	0.75**	0.03	0.001*	0.013**	0.118**	0.05**	2.0	0.24**	0.26*	1.8**	0.015**
C(P)	0.655**	3.76**	2.35**	0.116**	0.580**	0.818**	1.68**	85.3**	0.98**	9.83**	77.6**	0.552**
YC(P)	0	1.18**	0.93**	0	0.120**	0.150**	0.14**	68.5**	0.65**	0.64**	14.6**	0
E	0.620	6.51	1.31	0.021	0.290	0.890	1.36	73.8	2.00	5.65	54.5	0.517
Mean	6.694	9.225	6.258	0.3317	2.853	6.281	5.159	39.51	4.286	11.63	31.67	2.154
h^2	0.55	0.34	0.64	0.90	0.67	0.52	0.66	0.43	0.29	0.73	0.68	0.61

a) log-transformed * $P<0.05$, ** $P<0.01$

Table 5. Estimated variance components, means, and heritabilities for characters determined on plants harvested mid-September (late harvest) in 1986 and 1987. For abbreviations see Table 1.

Source	Early season growth (1-9)	Maturity (1-9)	Skin colour (1-4) [a]	Tuber shape (1-5)	Regularity of tuber shape (1-9)	Eye depth (1-9)	Number of tubers	Tuber yield (100 g)	Average tuber weight (g)	Prop. of yield by tubers <30 mm [a]	Underwater weight (g)
Y	0.156^{**}	0.85^{**}	0.003^{**}	0.231^{*}	0	0.047	5.9	3.6^{**}	73.9	0.450^{**}	4214.1^{**}
P	0.288^{**}	2.06^{**}	0.098^{**}	0.203^{**}	0.531^{**}	1.796^{**}	21.7^{**}	5.9^{**}	119.5^{**}	0.094^{**}	1217.3^{**}
B(Y)	0.002	0.01^{*}	0	0.006^{**}	0.001	0.023^{**}	1.8^{**}	0.0	7.9^{**}	0.013^{**}	0.0
YP	0.009^{**}	0.11^{**}	0.003^{**}	0.009^{*}	0.045^{**}	0.092^{**}	0	1.5^{**}	15.8^{**}	0.007	26.6^{**}
C(P)	0.542^{**}	4.67^{**}	0.120^{**}	0.530^{**}	0.820^{**}	1.520^{**}	85.1^{**}	48.5^{**}	520.1^{**}	0.655^{**}	968.0^{**}
YC(P)	0	0.57^{**}	0.008^{**}	0.110^{**}	0.135^{**}	0.200^{**}	29.4^{**}	11.4^{**}	94.8^{**}	0.119^{*}	462.7^{**}
E	0.537	1.41	0.025	0.340	0.710	1.130	61.7	19.7	240.8	0.970	536.7
Mean	7.055	5.290	0.3477	2.984	6.499	5.914	35.38	23.71	72.45	0.627	448.08
h^2	0.60	0.77	0.86	0.61	0.60	0.69	0.54	0.63	0.64	0.40	0.68

[a]) log-transformed * $P<0.05$, ** $P<0.01$

Table 6. Estimated and observed selection responses for several characters at the late harvests. The 1987 experiment was used to calculate the response of the selection in 1986 and the 1986 experiment for that in 1987. Selection of the best clones were based on plant appearance (PA) or on a combination of tuber yield (TY) and average tuber weight (ATW). Data is based on plots of two plants.

Character	Selection in 1986, performance in 1987					Selection in 1987, performance in 1986				
	Unselected	Selected for				Unselected	Selected for			
		PA		TY+ATW			PA		TY+ATW	
		Est.	Obs.	Est.	Obs.		Est.	Obs.	Est.	Obs.
Early season growth	6.97	7.48	7.60	7.41	7.60	7.14	7.55	7.64	7.69	7.60
Number of stems	-	-	-	-	-	7.23	-	7.64	-	7.39
Maturity	4.63	5.66	5.12	3.83	3.00	5.95	5.82	5.80	4.47	4.72
Plant appearance	5.48	6.68	6.86	6.33	6.58	5.42	6.58	6.76	6.86	6.20
Skin colour	1.51	1.44	1.51	1.51	1.52	1.75	1.71	1.86	1.68	1.63
Growth cracks	0.06	-	0.04	-	0.09	0.02	-	0.02	-	0.02
Tuber shape	3.33	3.40	3.53	3.49	3.96	2.64	2.81	2.93	2.99	2.91
Regularity of tuber shape	6.48	7.23	7.27	6.44	6.21	6.52	6.93	7.25	6.41	6.48
Eye depth	5.74	6.44	6.75	5.63	5.76	6.09	6.59	7.10	6.05	6.20
Tuber yield (g)	2489	2931	3104	3548	3881	2253	2684	2845	3192	3158
Number of tubers	33.5	34.0	35.0	31.4	31.8	37.3	38.0	38.8	35.7	32.0
Underwater weight (g)	402	389	382	385	405	493	491	482	483	481
Prop. yield by tubers < 30mm	2.8%	1.4%	1.2%	0.7%	0.7%	5.5%	3.8%	4.1%	2.5%	2.2%
Average tuber weight	78.8	87.8	93.5	116.6	126.8	66.1	78.4	80.6	90.7	97.0
Number of clones	600		59		56	600		61		65

described here, the exact tuber yield and the exact average tuber weight were determined. In field evaluations of the first and second clonal generations, however, only a visual estimate is possible, since many clones must be assessed. A visual assessment of yield would be possible when using a 1 to 9 scale. This was simulated by dividing the clones for tuber yield and average tuber weight into nine classes, resulting in h^2 estimates of 0.71 and 0.68 for tuber yield and average tuber weight, respectively. This simulated classification may have resulted in an overestimation of the heritabilities since misclassifications are likely to occur by the visual assessment.

The heritabilities of tuber yield and average tuber weight were considerably higher than that of plant appearance, and putting more emphasis in selection both characters might result in a more consistent selection decision. However, high tuber yield and high average tuber weight are not the only characters of interest in a breeding programme. The main aim of visual selection in early generation is to reject clones with visually perceptible deficiencies for agricultural practice, industry and market. Selection for tuber yield and average tuber weight would only be advised if it would result in an improved population with respect to those characters as well. Therefore, correlated selection responses were estimated and simulated for selection on either plant appearance or on tuber yield and average tuber weight. The estimated and the actual selection responses corresponded very well (Table 6). With a few exceptions the estimated and the actual selection responses were similar and the selection responses can be accurately predicted from the matrices of the phenotypic and genotypic variances and covariances.

Selection for tuber yield and average tuber weight resulted in an improved population for the traits early season growth, proportion of tuber yield by tuber under 30 mm, number of tubers, and of course tuber yield and average tuber weight. Selection hardly changed the population average for skin colour, eye depth and regularity of tuber shape. Selection for plant appearance, in contrast, improved the population average for eye depth and regularity of tuber shape considerably. Since the latter characters are of great economic importance, a population selected for plant appearance has better prospects. Moreover, as argued earlier, it is likely that other unassessed characters were contributing to plant appearance and selection for plant appearance will result in an improvement of these characters as well.

Since there is no justification to rigorously alter the selection traits in the first clonal generations, the only option to improve the gain from selection is to optimize the selection procedure in the first and second clonal generation such as to maximize the expected overall gain. How this might be carried out has been reported earlier (Neele et al. 1989).

Conclusions

Early clonal generation selection using one or a number of characters evaluated in this study instead of 'plant appearance', cannot be recommended. At early harvest, a slight improvement in the consistency of the plant appearance scores might be obtained by paying less attention to the regularity of tuber shape and far less attention to number of tubers. At late harvest the heritability of plant appearance was lower than that of the other characters, but only heritabilities of tuber yield and average tuber weight were considerably higher. Selection for tuber yield and average tuber weight resulted in fast progress for these traits, but is, however, not recommended, since such selection did not improve other important traits. Furthermore, plant appearance includes more characters than evaluated in these experiments. Therefore, by selection for plant appearance shortcomings of every visual character will be integrated in the final selection decision.

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Chapter 8

General discussion

A potato breeding programme can be divided in four main phases, namely parental choice, the seedling generation, visual selection in the first few clonal generations and subsequently selection from the third clonal generation on for a range of individually measured characters to identify potential new varieties. Studies were carried out in order to optimize the breeding programme in the first three phases.

In the selection of parental combinations, the mid-parent value is often used as a selection criterium. This predictor of off-spring performance will frequently generate poor predictions, particularly for ware harvest tuber yield, as was observed in the studies of this thesis (Chapter 2) and in the work of Maris (1989) and Brown & Caligari (1989), As a result, worthless hybrid progenies might be evaluated over a series of years of the breeding programme. A good method of parental evaluation will, therefore, reduce the chance that resources will be spoiled on progenies with low prospects and in this way will compensate for the extra costs involved in parental testing.

Preferably, special tests, such as a diallel, must be carried out to estimate the parental general combining ability (GCA), but such tests are likely to retard the breeding process since specially created hybrid populations must be evaluated. A possible alternative method to estimate the parental GCAs uses data from the normal breeding programme. For this prediction procedure, calculation methods for incomplete diallels or NC II designs of Garretsen & Keuls (1978) and Herdam (1984) are used. However, some caution is required when these methods are applied to data from a normal breeding programme. For visual selection in the early clonal generations the plants are often harvested immature. The Chapters 5 and 6 showed that the immature plant performance correlated poorly with the mature plant performance for many important characters. Prediction of progeny performance, based on performance data of the immature plant, might therefore lead to poor prediction at ware potato harvest. In addition, in a normal breeding programme the genotypes are subjected to selection and this will affect the mean progeny performance of many unselected traits when these traits are genetically or physiologically correlated to the selected ones. In this way, the use of selected progenies for the estimation of GCA and SCA effects will, therefore, result in inaccurate progeny predictions.

The crop physiological approach to tuber yield (Chapter 3) and the 4x-2x test-crosses prediction of characters such as tuber yield (Chapter 2) seemed to offer better prospects to predict the progeny performance than the mid-parent value. Therefore, breeders are advised to use these methods for selection of parental combinations.

In the seedling generation, generally only a mild selection is applied. Fitschen (1984) for instance selected about 70% of the seedlings. Special tests are not common in the seedling generation. However, it might be profitable to invest in seedling tests, since progenies or genotypes with poor commercial prospects could be eliminated before they are brought to the field. For example, in the Netherlands the costs of evaluation of a progeny of 300 first year clones and subsequently 100 second year clones are about Dfl 900,- (see also Chapter 6). If such a progeny has low prospects, the waste of this money could be prevented if a good seedling test is available, such as the tests described in Chapter 4 for chip and French fry quality.

Seedling tests can be used for either genotype or progeny selection. Genotype selection in the seedling generation is profitable if the costs for testing and administration of all genotypes are less than for growing the possible rejected genotypes in the field and instead to select for the character in an advanced field cycle. Progeny evaluation in the seedling generation is an adjustment of the predicted progeny performance. Progeny selection can therefore be carried out for traits that can not be easily predicted out of parental evaluations, such as traits with high non-additive inheritance. In addition, if the parental evaluation method is relatively expensive compared to the seedling evaluation, the latter is to be prefered.

Visual selection in the first clonal generations can be characterized by high selection pressure based on evaluation of a large number of genotypes represented by few a plants each. There are a number of reasons to change the selection methods and selection objectives in this phase.

First of all, intensive selection appears to be not only very inadequate in respect to selection of the better genotypes but also very expensive. Chapter 6 showed that selection of less than 10% of the population of first year clones was more expensive than no selection at all. In addition, it does not seem possible to substantially improve the reliability of the selection by either enlarging the plot size in the first year of clonal selection or altering the selection index 'plant appearance'. Growing more than one plant per first year clone is likely to yield somewhat more constant results, but is very expensive. For the selection index 'plant appearance', the only character that seemed to affect the reliability of the evaluations substantially was found to be number of tubers. Putting less emphasis on the number of tubers will probably make the selection decisions a little more constant over years. Therefore, the only way to optimize selection efficacy appears to be reduction the selection pressure in the first clonal generation to about 30%.

Secondly, the high selection pressure in this phase based on 'plant appearance', indicates that breeders regard the visual performance as one of the most important characters. In fact, it is doubtful whether this trait should be regarded as very important. In selection studies where good commercial varieties were included in a population of unselected hybrid progenies, these varieties were often rejected (Davies & Johnston, 1974, Anderson & Howard, 1981, Brown *et al.*, 1984, Pfeffer *et al.*, 1988). This indicates that the selection aim was not properly defined. The common practice of selecting only 10% in the first clonal generation would only be valid if only varieties with perfect plant appearance would be favoured by farmers, industry and consumers. However, also the rejected varieties are favoured and accepted. Therefore, in the first few clonal generations the breeding aim should be that all genotypes that do not show any deficiency more serious than generally accepted varieties show should be retained. These genotypes have sufficient quality to justify further evaluation in the more expensive experiments of the final phase of the breeding programme. It is thought that a breeder should intent to eliminate all poor performing clones and retain about 30% of the population in the first clonal generation. The contingency tables of Chapters 5 and 6 show that such a procedure is likely to yield more constant selection results.

Proposals for improving the efficiency

The conclusions and recommendations reached in the foregoing chapters have been incorporated in a proposal for an improved model breeding programme, described in Table 1. The part for evaluation of parental choice is new compared to the conventional breeding scheme and helps to identify the most promising progenies in the selection part.

For the practical application of the suggested parental choice programme the following procedure is advised. The parents are test-crossed with two

Table 1. Proposal for an alternative selection scheme for the first three phases of a potato breeding programme.

Year	Parental choice programme	Selection programme
1	Parental tests, involving 15 genotypes, and two diploid 2n FDR pollen producing males. Hybridization programme resulting in 30 progenies of 60 clones each for two experimental years.	Hybridization of potential parents based on mid-parent values, test-cross evaluations of previous cycles and growth analysis.
2	Seedling generation of the 4x-2x test-crosses.	no action
3	First field evaluation of the test-crosses. Second seedling generation.	Seedling generation with various tests. Selection between progenies based on the performance of parents in the parental choice programme, and if necessary production of seeds of additional hybrid progenies.
4	Second field evaluation of the test-crosses.	First clonal generation. One plant per genotype, plants are harvested immature. Selection on plant appearance, with a selection intensity of about 32%. Progeny selection based on the parental choice programme.
5		Second clonal generation. Eight plants per genotype, four plants are harvested immature for seeds and the remaining four mature to evaluate the ware harvest performance. Selection intensity of about 20%.

clones that produce 2n FDR pollen. This is facilitated by the fact that the pollen of these clones can be collected and stored at -18 °C, where it remains viable for some years. About 200 seeds per test-cross are required for the experiments, of which 100 are sown in year 2 to obtain seedling tubers.

In year 3, of each tested genotype a progeny of 60 clones is planted in two replicates of 30. Since the test-crosses provided better predictions only at ware potato harvest, the clones are harvested mature. For the seed potato harvest prediction, the mid-parent value can be used. Visual evaluations for various traits are carried out per plant, while all tubers of a progeny of 60 clones are gathered together for the evaluation of tuber yield and the number of tubers.

The second field evaluation seems also to be necessary, since for many characters a significant yearXprogeny interaction was observed (Chapter 7). A second seedling generation should be grown in year 3 for the year 4 field evaluation at ware potato harvest, since this procedure does not include harvest of seed tubers. The remaining 100 seeds can be used for this purpose.

Table 2. Typical costs and requirements of a parental choice programme involving 15 genotypes, carried out in the Netherlands in the period 1980-1990.

Year 1	40 m^2 glasshouse for 15 genotypes with 3 plants each and 2 diploid pollen males with 15 plants each. The labour requirements are about 6 man days.
Year 2	Of each of the 30 progenies 100 seedlings are grown, requiring 40 m^2 glasshouse space when using 11x11 cm pots. Seeding, transplanting, maintenance and harvesting are likely to ask for labour equivalent to four man days.
Year 3	The field evaluation of 30 progenies with 60 clones each will cost Dfl 600.- (Chapter 6) for the plot-size independent costs. Additional labour requirements are about 5 man days. For the second seedling generation, 40 m^2 of glasshouse and 4 man days of labour are required.
Year 4	The field evaluation costs are equal to the costs in the previous year.

The costs and requirements of the parental choice programme are listed in Table 2. In the Netherlands this scheme would require 120 m^2 glasshouse, 24 days of labour (about Dfl 5000.-) and approximately Dfl 1200.- for the plot-size independent costs. The glasshouse costs are determined by heating and electricity, water, pots and peat and the depreciation of the glasshouse itself. The heating and electricity demands are likely to depend mainly on the period of the year. A summer generation will not require additional heating and electricity, whereas for plants grown during the winter considerable heating and electricity costs must be made. The total costs, however, are not likely to exceed Dfl 8000.- and these costs are about equal to growing 3000 first year clones and 1000 selected second year clones. Therefore, if a parental choice programme of 15 genotypes prevents the breeder to grow 3000 or more first year clones with poor prospects, the costs of this parental choice programme have been justified.

The programme described in Table 1 is still similar to the commonly used breeding scheme, with the exception that due to interaction with the parental choice programme, progenies might be rejected before they are grown in the field. Furthermore, a more economic selection procedure in the seedling and the first clonal generation is proposed. The selection programme starts one year after the start of the parental choice programme, not awaiting the final conclusions of the latter programme. This means that more progenies should be produced than can be handled in the selection programme and in years 3 and 4, the best progenies can be selected.

The option to start the selection programme one year after the start of the parental choice programme and not to wait till the final conclusions can be drawn from the latter programme, is dictated mainly by time-pressure. In comparison to a conventional breeding programme, waiting for the final conclusions would delay the incorporation of new breeding material by four years. It is likely that breeders are not willing to wait for such a long period and would want to start the selection programme earlier. With the seedling generation in Year 3, the ware potato performance of the progeny can be predicted before the second clonal generation is grown in the field, which means that an effective progeny selection can still be carried out.

In general, this adjusted breeding scheme is expected to be more effective and economic in obtaining breeding material that is suitable for the fourth phase of the breeding programme, the selection based on the assessment of individually measured characters.

Final remarks

This thesis is mainly based on experiments with hybrid progenies of six genotypes, Alcmaria, Désirée, Maritta, Pimpernel, AM74-602 and MPI49-540/2. These six were chosen for low coancestry, good male and female fertility and a diversity in agronomical performance. It is thought that this sample is representative for potential parents used in most commercial breeding programmes, and that therefore the results of this thesis are of value to commercial breeding programmes. However, since only six genotypes were used, the results must be seen as indications and it might be advisable to confirm the conclusions with larger scale evaluations.

A number of new questions have arisen from the studies of this thesis. First of all the apparent contradictory result that ware harvest tuber yield could be predicted accurately by the 4x-2x test crosses in spite of the large proportion of the total genetic variance contributed by the non-additive variance. An explanation of this phenomenon might be that the gametes of the tested genotype were expressed against the more or less constant background of the testers. Additive and non-additive gene-actions present within the 2x-gametes of the investigated genotype could be detected in the test-progeny, and therefore are taken into account in the prediction. Only the non-additive gene-actions caused by the interaction of allels of different parents could not be noticed and are likely to have generated the deviations between the predicted and the actual progeny performance. These deviations, however, might have been not so large that accurate prediction was prevented. The mid-parent value prediction could not account for the segregation of alleles and the demolition of allele combinations that induce non-additive gene-action during the meiosis, which might have resulted in an inadequate prediction of ware potato tuber yield by the mid-parent value. In the selfed progenies, the value of the gamete population of a genotype was evaluated against gametes of itself. In such a case, the non-additive gene-actions for a certain character is not evaluated properly, in case of dominance the value of the genotype as parent will be over-estimated while for instance for complementary genes an under-estimation will occur. The diploids, however, should also show the non-additive gene-action present in the egg-cells and therefore would theoretically produce suitable predictions. The action of sub-lethal genes resulting in poor growing plants, however, might have spoiled the predictive ability of this method and made it unsuitable for breeding practice.

The optimization strategies were designed for a breeding programme for tetraploid potatoes. Nowadays, in commercial breeding programmes more attention is paid to breeding at the diploid level. It cannot be assumed that all strategies described here can be applied directly to diploid breeding programmes as well. At the moment, the aim of the diploid breeding programmes is to yield parental lines for the tetraploid breeding programme. When carrying out parental evaluations at the diploid level some aspects should be investigated; the value of a genotype as parent of diploid progenies and its value in interploidy crosses or somatic hybridization. To evaluate a genotype as parent for diploid progenies, the test crossing as described in Chapter 2 is clearly not suitable. The crop physiological approach, however, might be worth-while to investigate. For interploidy crosses the diploid 2n FDR testers can only be used if the potential parents produce 2n egg cells and if not, other methods should be developed. Maybe tetraploid genotypes can be used as female parents in test crosses. Also for somatic hybridization, parental choice methods should be evaluated. The mid-parent value might predict the performance of somatic fusion products satisfactory, since the non-additive gene-action available within each of the parents remains unchanged. Only new non-additive gene-action caused by fusion of the chromosomes of both parents might result in deviations from the prediction. For the optimization of the visual selection the procedures proposed in Chapter 6 are likely to be valid also for diploid potato breeding. A study of the environmental influence on diploid potatoes in comparison with tetraploids would be of great help.

In this thesis an analysis is presented of many genetic and physiological characterstics of potato clones, both for parents and progenies in the early phases of a potato breeding programme. Hopefully this knowledge will contribute to an increased efficiency of many potato breeding programmes. Clearly, changes in one phase of a breeding programme affect the efficiency of other parts, and changes should not be made without careful considerations of all the effects. A good example is the observed increased number of seedlings in the modern breeding programmes which for economic reasons have not been accompanied by adequated enlargements of the number of clones that can be evaluated in the later stages of the programme, resulting in a very inefficient and high selection pressure in the first clonal generation. The greatest contribution to the efficiency of a potato breeding programme, however, lies in the choice of the potential parents to be included in the hybridization programme. Therefore, I hope that Wilhelm Busch's statement on fathers can be converted for the potato into "Elter sein ist nicht schwer, Elter werden dagegen sehr".

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Summary

A potato breeding programme can be divided in four phases, choice of parents, seedling generation, visual selection in the first and second clonal generation and selection from the third clonal generation based on individually assessed characters. The first three phases were subject of this thesis.

Choice of parents. The choice of the most promising parental combinations is crucial for the success in the subsequent phases of the breeding programme. The identification of a method which predicts the value of a hybrid progeny properly will therefore increase the efficiency of a breeding programme. The value of five predictors was investigated by relating the predicted progeny performance to the actual value of 20 hybrid progenies from an incomplete 6x6 diallel. The five predictors were the 'mid-parent value', glasshouse grown seedling populations, diploid offspring obtained after pollination with *Solanum phureja*, selfed populations, and test-cross progenies using diploid 2n-FDR pollen producing clones as male parent. In addition, for the prediction of tuber yield, the use of a crop physiological approach has been investigated.

Of the five predictors, the mid-parent value gave acceptable predictions of all examined characters at time of seed potato harvest, and for most characters at ware potato harvest. However, this predictor failed for the important character ware potato tuber yield. Better predictors of ware potato tuber yield were obtained using the crop physiological approach and the test-crosses.

For the crop physiological approach, potential parental clones are harvested at intervals during the growing season. Time of tuber initiation and the relative rate of tuber bulking are important parameters in the prediction of tuber yield of the hybrid progenies. The harvests at intervals, however, askes for high labour inputs, but no loss in time occurs for the production and growing additional hybrid progenies. The test-cross method can be incorporated in a breeding scheme, as presented, with relatively low labour inputs. Compared to the traditional breeding scheme this alternative scheme strongly reduces the chance that inferior hybrid progenies will enter the time consuming and expensive third and fourth phase, but also adds an extra year to the breeding programme.

Seedling generation. With the growth of seedlings in the glasshouse botanical seeds are converted to seed tubers. In this phase only a mildly selection in practised and there is need for additional selection traits. Therefore, for a

number of characters the prospects of early-selection were examined.

For tuber yield, number of tubers and the average tuber weight, no relation was observed between the performance in the glasshouse and in the field. Selection for these characters using glasshouse grown seedlings is not to be advised. The glucose content, as a parameter for the chip and French fry quality, of seedling progenies grown in the glasshouse was satisfactorily correlated to the contents of field grown progenies. The glucose content can be determined simply and cheaply with glucose test strips and early selection of progenies in the seedling generation is recommended. For the dry matter content prospects for early selection are even better and a mild direct genotype selection seems to be feasible.

First and second field generation. During the first two field generations, clones are selected for visual characters. A selected clone should meet a number of minimum requirements to be admitted to the last phase of the breeding programme. In the last phase clones are examined accurately for a great number of traits and clones superior to the existing varieties are identified.

Selection in the early field generations is generally severe, while based on only a low number of plants per genotype. Such a procedure is not very efficient, and three methods to increase the efficiency were compared.

Enlarging the number of plants per genotype in the first clonal generation from one to two plants did increase the reliability of selection, but was found to be very expensive.

Analysis of the components of the selection trait 'plant appearance' did not reveal sub-traits with a poor heritability and a large influence on the plant appearance score. Therefore altering the relative weight of the individual components of 'plant appearance' is not likely to improve to selection in the first two field generations.

The best prospect for increasing the efficiency seemed to be offered by manipulating the selection intensity in the first field generation. By decreasing the selection intensity from 10% to about 30% in the first field generation, not only the reliability of the selection decisions improved, also the scheme was found to be more economic, at least for the Dutch situation. In the second field generation, a selection intensity of 20% at ware potato harvest is recommended. The number of first year clones should of course be reduced to one third of the initial number to accomodate the changes.

A detailed scheme of a potato breeding programme incorporated some of the suggested improvements is presented.

Samenvatting

Een aardappelveredelingsprogramma kan in grote lijnen worden onderverdeeld in vier fasen, nl. de ouderkeuze, de zaailingteelt in de kas, de fase van visuele selectie in de eerste en tweede veldgeneratie en de laatste fase waarin gedetailleerd wordt onderzocht om per kloon eigenschappen te evalueren zoals opbrengst, resistentie en kwaliteit. In dit proefschrift zijn selectiemethoden onderzocht die tot verhoging van de selectie-efficiëntie in de eerste drie fasen kunnen leiden.

Ouderkeuze. De ouderkeuze, de eerste fase, is een zeer essentiële stap in het veredelingsproces en bepaalt in belangrijke mate de kans op succes in de volgende fasen. Een goede voorspelling van de gebruiksmogelijkheden van de kruisingsnakomelingschap verhoogt de efficiëntie van een veredelingsprogramma aanzienlijk. Vijf potentiële voorspellers zijn onderzocht en getoetst op de overeenkomst tussen de voorspelde en de actuele waarde van 20 kruisingscombinaties uit een incomplete 6x6 diallel. De vijf methoden waren de 'mid-parent value', de gemiddelde waarde van kruisingspopulaties bij teelt van zaailingen in de kas, populaties van diploiden verkregen na bestuiving met *Solanum phureja*, zelfbevruchtingspopulaties, en testkruisingspopulaties waarbij diploide vader klonen die 2n-FDR gameten vormen, als tester fungereerden. Voor knolopbrengst is daarnaast nog een additionele methode gebruikt, waarbij gebruik is gemaakt van gewas-fysiologische parameters.

Van de onderzochte methoden had de 'mid-parent value' de beste mogelijkheden. De methode lijkt behalve eenvoudig en goedkoop, ook een goede voorspeller te zijn voor de meeste van de eigenschappen, met als belangrijke uitzondering de knolopbrengst bij rijpe rooi. Voor de voorspelling van de knolopbrengst bij rijpe rooi kon beter gebruik worden gemaakt van de gewas-fysiologische aanpak of van testkruisingen. Voor de gewas-fysiologische aanpak moeten de potentiële ouders gedurende het groeiseizoen op onder- en bovengrondse productie worden gevolgd. Het tijdstip van knolinitiatie en de relatieve snelheid van knolvulling zijn daarbij belangrijke parameters en deze worden gebruikt bij de voorspelling van de knolopbrengst van een kruisingspopulatie. Deze gewas-fysiologische aanpak is door het gebruik van tussentijdse oogsten arbeidsintensief, echter er treedt geen verlies in tijd op voor het maken van kruisingen en de teelt van de zaailingen. Indien gebruik gemaakt wordt van testkruisingen, treedt wel tijdverlies op maar de methode is aanmerkelijk minder bewerkelijk dan de gewas-fysiologische aanpak, met name indien de testkruisingen per populatie en niet per kloon worden geanalyseerd.

Zaailingen. In de kasteelt van de zaailingen, de tweede fase van de aardappelveredeling, wordt het kruisingszaad omgezet in knolletjes, waarbij een milde selectie plaats vindt. Voor een aantal eigenschappen is onderzocht wat de mogelijkheden van 'early-selection' zijn.

Voor knolopbrengst, aantal knollen en gemiddeld knolgewicht bleek geen relatie gevonden te kunnen worden tussen de prestaties van de zaailingen van een kasteelt en de klonen in het veld. Zaailing-selectie op deze eigenschappen in de kas wordt daarom sterk afgeraden. Voor het glucose gehalte, een belangrijke eigenschap voor de chips en friet kwaliteit, bleek goede overeenstemming te bestaan tussen zaailingen en in het veld geteelde populaties. Het glucosegehalte kan eenvoudig en goedkoop bepaald worden met glucose-teststrookjes en 'early-selection' op populatie basis kan worden aanbevolen. Voor het droge-stofgehalte waren de uitkomsten zodanig dat er in de zaailingen zelfs overgegaan zou kunnen worden tot selectie op genotype basis. Gezien de te verwachten hoge proeffout lijkt het echter aan te bevelen om niet te scherp te selecteren en alleen de klonen met een zeer laag droge-stofgehalte te verwijderen.

Eerste en tweede veldgeneratie. Gedurende de eerste twee veldgeneraties, de derde fase van het veredelingsproces, worden de klonen geselecteerd op een goede landbouwkundige waarde. Een geselecteerde kloon dient te voldoen aan een serie van minimum eisen, nodig om in een later stadium raswaardig te kunnen zijn. In de vierde fase van het veredelingsproces worden de klonen op een groot aantal eigenschappen nauwkeurig onderzocht en wordt getoetst of klonen zich positief onderscheiden van het bestaande rassensortiment.

De selectie in de derde veredelingsfase is in het algemeen streng en is gebaseerd op een gering aantal planten per kloon. Al vanuit eerder onderzoek was duidelijk dat met een dergelijke aanpak niet efficiënt omgesprongen wordt met de genetische variatie, hetgeen door het onderzoek beschreven in dit proefschrift wordt bevestigd. Drie mogelijkheden zijn onderzocht om de selectie-efficiëntie te verhogen, te weten vergroting van de plotgrootte, aanpassing van de selectie-criteria en verandering van de selectie-intensiteit.

Vergroting van het aantal planten per eerste jaars kloon van één naar twee heeft weliswaar een positieve invloed op de betrouwbaarheid van de selectie, maar dit is onvoldoende om de aanzienlijke extra kosten te dekken.

Het bij de visuele selectie gebruikte selectiekenmerk 'algemene indruk' is opgebouwd uit een groot aantal componenten, zoals oogdiepte, knolvorm, opbrengst, aantal knollen, enz.. 'Algemene indruk' kan derhalve gezien worden als een selectie-index. Verandering van het onderlinge gewicht van de verschillende componenten van de selectie-index 'algemene indruk' leidde niet tot een wezenlijke verbetering van het selectie-resultaat. Optimalisatie van de selectie moet derhalve niet gezocht worden in verandering van de selectie-eigenschap, maar van de selectie-intensiteit.

De samenhang tussen de selectie-intensiteit en de selectie-respons werd bepaald door de prestaties van 600 klonen gedurende drie jaar te volgen. Bij het onderzoek naar het optimale selectieschema is ook een financiële kosten/baten analyse uitgevoerd. Voor de berekening van het financieel optimale schema is ervan uitgegaan dat het aantal derde jaars klonen min of meer vast ligt door de hoge kosten van de toetsen in deze generatie. Voor de Nederlandse situatie bleek een verlaging van de selectie intensiteit van de gebruikelijke 10% naar 32% in de eerste jaars klonen, in combinatie met de nu al gebruikelijke selectie-intensiteit van 20% in de tweede jaars klonen de optimale situatie te vertegenwoordigen. Hierbij werd ervan uitgegaan dat in de tweede jaars klonen de belangrijkste selectie bij rijpe rooi plaats vindt.

Op grond van het hier beschreven onderzoek kan het volgende aardappel veredelingsprogramma worden voorgesteld. Voor de selectie van kruisingspopulaties met de beste perspectieven voor een aantal visueel te evalueren eigenschappen kan gebruik worden gemaakt van een gerichter ouderkeuze met behulp van de 4x-2x testkruisingen. Populatieselectie voor chipskwaliteit en onderwatergewicht kan betrouwbaar uitgevoerd worden aan zaailingpopulaties in de kas. Door deze werkwijze is het waarschijnlijk dat het aantal kruisingspopulaties met onvoldoende perspectieven dat de tweede en derde fase bereikt af zal nemen. De extra kosten nodig voor de uitvoering van de testkruisingen zullen hierdoor waarschijnlijk worden terugbetaald.

Voor de selectie van individuele genotypen op algemene indruk in de eerste twee veldgenerates is het economisch en genetisch gezien ongunstig om streng te selecteren. In vergelijking met de nu gebruikelijke situatie kan beter uitgegaan worden van een geringer aantal eerste jaars klonen, waarin minder streng geselecteerd wordt. De bespaarde fondsen in de eerste jaars klonen kunnen elders in het programma worden aangewend.

Curriculum vitae

Adelbert Ernst Franciscus Neele werd geboren op 23 juni 1957 te Palembang (Indonesië). Na het Atheneum is hij in 1975 begonnen aan de studie Plantenveredeling bij de Landbouw Universiteit te Wageningen. In september 1982 studeerde hij af met het doctoraalpakket plantenveredeling, leer van het grasland en erfelijkheidsleer. In december 1982 is hij aangesteld, in een duobaan met zijn vrouw, bij de Stichting voor Plantenveredeling, het huidige Centrum voor Plantenveredelingsonderzoek, met als onderzoekstaak optimalisering van selectie-methoden bij de aardappelveredeling. Het onderzoek heeft geresulteerd in dit proefschrift.

Per 1 oktober 1990 is hij werkzaam als grassenveredelaar bij Van Engelen Zaden BV in Vlijmen.

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