

Breeding and physiological aspects of potato cultivation in the Mediterranean region

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Summary

In the Mediterranean area the potato is a very important crop and can be cultivated throughout the year. However, tuber yields are generally much lower than those in Northern European countries. This is because the environmental and agro-economic conditions are different from those of Northern countries where most cultivars were developed. We feel that the objective for the “new Mediterranean potato” must be the availability of potato cultivars for each environment and for each planting season. Breeding programmes should focus on improving potato production within a specific agro-ecological Mediterranean area rather than improving crop production across areas. This paper reports aspects of potato breeding and physiology related to resistance to stress conditions in the Mediterranean area, with particular emphasis given to resistance to abiotic (heat, drought and frost) as well as biotic stresses. We also discuss the potential to produce seed tubers suitable for potato cultivation in the Mediterranean area.

Introduction

In countries surrounding the Mediterranean sea the potato is a very important crop. Due to favourable climatic conditions, it can be cultivated throughout the year and planting and harvesting dates depend on the specific area of cultivation. The Mediterranean region includes 17 countries and can be divided into three main areas, Northern, Eastern and Southern. At present, about one million hectares of potatoes are grown in the Mediterranean region, producing around eighteen million tonnes. For both planted area and total production these figures represent about 5.8% and 6.6% of those for the world. Approximately 47% of the potatoes grown in the Mediterranean region are produced in the Northern part, while 25% and 28% are produced in the Eastern and Southern regions respectively. The Northern and Southern areas have similar tuber yields (15.6 and 15.0 tonnes/ha respectively in 1997), whereas the Eastern area gives a higher yield (24.5 tonnes/ha in 1997) (Table 1).

In the last 10 years potato cultivation in the Mediterranean area has undergone a 16.2% reduction in area (Table 2). This has occurred exclusively in the Northern region (32.8%) while in the other two areas there has been an 8% increase. By contrast, there has been a 7.0% yield increase which has left total production unaltered (down by only 4%). Countries showing the largest decrease in area of potato cultivation are Spain and Italy in the Northern region, and Algeria in the

Table 1. Area and yield of potatoes grown in the Mediterranean region (1989-91 and 1997).

	Harvested area (1000 ha)		Yield (t/ha)	
	1989-91	1997	1989-91	1997
North	746	501	15.1	15.6
East	246	266	22.7	24.4
South	279	298	13.4	14.9
Total	1271	1065	17.1	19.3

Table 2. Variation (%) in area and yield of potatoes grown in the Mediterranean regions in 1997 compared with mean areas and yields in 1989-91.

	Area (1000 ha)	Yield (t/ha)
North	-32.8	+3.3
East	+8.1	+7.5
South	+6.8	+11.2
Total	-16.2	+7.0

South. By contrast, Egypt has recorded the largest increase in land area used for potato cultivation. The sharp reduction in cultivated area in several countries has been accompanied by a considerable increase in yields.

Compared with Northern European countries, tuber yields in the Mediterranean area are much lower. This is because the environmental and agro-economic conditions are different from those of Northern countries where most cultivars were developed. In particular, temperatures and water availability are probably the factors which differ the most from growing conditions of Northern Europe, thus causing the lower yield in this area. Furthermore, there is a relatively small number of cultivars some of which were selected several years ago (Ross, 1986). This means that the genetic potential of the potato has been little used by breeders and then only for a limited number of conditions. Thus, breeding programmes based on the exploitation of genetic variability may still offer potential for developing new genetic material suitable for cultivation in the Mediterranean area.

Breeding and physiology

It is well known that the cultivated potato (*Solanum tuberosum* L., $2n=4x=48$) is a polysomic polyploid with tetrasomic inheritance patterns (Howard, 1970). Breeding work is time-consuming due to the necessity to combine in the same genotype several target traits and to eliminate deleterious recessive alleles.

Breeding strategies for the genetic improvement of the potato are quite straightforward. They are essentially based on phenotypic recurrent selection,

involving crosses between tetraploid cultivars and/or advanced clones, and then field evaluation and selection. Due to the simplicity with which the Endosperm Balance Number and whole chromosome sets can be manipulated in the potato, breeding at diploid level is also possible. It is based on the use of diploid wild species as source of allelic diversity, haploids of the cultivars and $2n$ gametes (Ortiz, 1998). Of the possible avenues to explore for potato breeding at diploid level, one is particularly interesting, which is linked to the possibility of exploiting the genetic variability found in *S. tuberosum* haploids. However, it is necessary to overcome some difficulties related to 1) the limited number of haploids obtained from a cultivar, 2) the consequences arising from a lowering of ploidy level and 3) the late cycle of most *S. tuberosum* haploids.

Breeding for the Mediterranean area does not need new revolutionary strategies to obtain new cultivars but should use the current strategies with new objectives. In the last few years besides common objectives (i.e. yield stability, resistance traits), breeders have focussed mainly on developing cultivars specifically for aspects of quality which are common for both table use and processing (dry matter, flavour, nutritional values, tuber defects, texture etc.). However, considering that in the Mediterranean Region potatoes can be cultivated throughout the year, we feel that the important objective for the "new Mediterranean potato" may be the availability of potato cultivars for each environment and for each planting season. Three different planting seasons can be identified: winter (tubers planted in November–December), spring (tubers planted in January–March), and autumn (tubers planted in August–September). In some areas two potato crops can be grown in one year (double cropping): in spring and in autumn. There are great differences between and within Mediterranean countries and between the planting seasons in the factors influencing the crop performance. Of these, temperature patterns, water availability, soil conditions, daylength, exposure to pests and agronomic systems are the most important. We believe that the main objectives to achieve are those related to the target Mediterranean environment which a breeding programme intends to serve.

Breeding has been very successful in environments which are either naturally favourable or which can be made profitable through irrigation and fertilization and by the chemical control of weeds, pests and diseases. By contrast, yield improvements have been very elusive in marginal environments to the point that the role of breeding for such environments is often questioned. What is now questioned is why it has not been possible to improve agricultural production simply by transferring into marginal environments cultivars and methodologies which have made breeding for favourable conditions so successful.

The obvious hypothesis is that these cultivars, although defined as "widely adapted", are "specifically adapted" to conditions which are at or near the optimum for crop growth. Therefore, the superiority they have in these environments is not expressed in sub-optimal environments. In this respect, breeders can focus on the goal to improve potato production within a specific agro-ecological Mediterranean area rather than to improve crop production across areas. This philosophy has important implications for the breeding methods and strategies employed. Selection

should start from the first generation in the target environment, in that genetic variation is exposed and available for selection mainly in the early generations (seedling and first clonal stages).

With regard to these points, this paper will discuss aspects of potato breeding and physiology related to resistance to stress conditions.

Resistance to abiotic stresses

Resistance to heat stress. The commercial potato has been bred as a crop adapted to northern latitudes. Optimal growth and yield are obtained in temperate climates with cool temperatures and long days such as those in northern Europe and North America. Growth, tuber yield and quality are adversely affected by high temperatures and water deficit. Heat-stressed plants are less likely to tuberize and exhibit continued foliage production after the initiation of tuberization (van der Zaag, 1984). Even short periods of stress cause malformed and less marketable tubers such as bottleneck shape, secondary growth cracks, heat necrosis and premature sprouting. Despite these problems, potato production and utilization are increasing in hot climates where daily temperatures reach 40 °C. Growers can adopt two strategies: intercropping and the use of heat-tolerant potato clones. Levy et al. (1986) found that intercropping with shade crops can cool the soil temperature by 5–10 °C. This is considered to be important as such a reduction in the root and stolon temperature is sufficient to promote stolon growth, and consequently tuber formation.

Breeding for heat tolerance stress has been more difficult because this stress affects various physiological processes including photosynthetic efficiency and haulm growth, tuber initiation and photosynthate partitioning. Reynolds & Ewing (1989) demonstrated that foliage resistance to heat stress and ability to tuberize under heat stress conditions are not correlated. Thus, when screening for heat tolerance it is necessary to evaluate both traits. Heat tolerant-foliage has been found in many accessions of wild species including *S. berthaultii*, *S. brachycarpum*, *S. bulbocastanum*, *S. chacoense*, *S. kurtzianum*, *S. megistacrolobum*, *S. microdontum*, *S. pinnatisectum* and *S. spigazzini* (Hanneman & Bamberg, 1986). Because molecular and genetic factors underlying the initiation of tuberization and partitioning of photosynthates to the tuber are poorly understood, at present heat stress cannot be addressed in any way other than by empirical selection. Heat tolerance of *S. tuberosum* cultivars has long been associated with early maturity. It is likely that some early maturity cultivars, rather than being truly heat-tolerant, escape the stress conditions by accumulating yield quickly (Levy et al., 1986). Recently, Tawfik et al. (1996) suggested that the negative effects of heat stresses on leaf growth and on stomatal function can be mitigated by application of Ca and N during the stress period.

Veilleux et al. (1997) used different potato germplasm in order to develop material tolerant to heat stress. The potato hybrids were derived through unilateral sexual polyploidization between cv. Atlantic and eleven diploid hybrids coming from *S.*

tuberosum, *S. andigena*, *S. phureja*, *S. berthaultii*, *S. chacoense* and *S. microdontum*. The authors reported that the hybrids exhibited heat tolerance and good tuberization potential. In addition, they were also more tolerant to heat necrosis and hollow heart than cv. Atlantic.

Resistance to drought stress. Water stress is the most important physiological stress in potato production in most areas of the world. The potato is very sensitive to soil water conditions and much more sensitive than most other crop species. MacKerron & Jefferies (1988) reported that a one-day stress period can cause visible effects. Thus, water availability is not only an extreme problem in arid regions, but is frequently a problem in prime growing areas (van Loon, 1981; MacKerron & Jefferies, 1988; Karafyllidis et al., 1996; Ranalli et al., 1996). At all stages of growth, water stress reduces photosynthetic efficiency, but drought during the period of tuber initiation and bulking has the most drastic effect on the yield. MacKerron & Jefferies (1988) demonstrated that tuber initiation is blocked when water is deficient. It is generally accepted that there are cultivar differences in susceptibility to water stress, although all potato cultivars are affected to some extent.

The physiological basis for differences in cultivar tolerance is not known. One explanation of the acute sensitivity of potato to drought is its relatively shallow root system and the inability of potato roots to penetrate deep into the soil. Furthermore, the bulking of tubers decreases greatly during drought periods, causing severe losses in the dry matter content of tubers.

Although selection for drought stress is still tied to the use of empirical parameters, the proposal of some researchers to use parameters correlated with drought tolerance (i.e. canopy expansion, canopy temperature, chlorophyll fluorescence, apical cuttings) appears very promising, especially because they may be used in the first generations of clonal selection.

Jefferies & MacKerron (1987) demonstrated that drought conditions reduced total dry matter production and tuber yield, and increased dry matter concentration of various cultivars. Functional differences in canopy growth were revealed in differences in the fractions of incident solar radiation intercepted. Therefore it can be hypothesized that genotypes which maintain canopy expansion and maximum light interception will achieve higher dry matter content, and reasonable yields in the presence of drought.

The light energy absorbed by chlorophyll within the leaf is used to drive photosynthesis, lost as heat or re-emitted as fluorescence. Because these processes are competitive, changes in photosynthetic rate in dissipative heat emission will cause complementary changes in fluorescence emission. In wheat, Havaux & Lannoye (1983) found that damage to the photosynthetic apparatus caused by drought conditions strongly affected the characteristics of chlorophyll *a* fluorescence induction. Also, transpirational cooling decreased and foliage temperature increased.

The results reported by Ranalli et al. (1996) showed that values of the ratio between variable fluorescence and maximal fluorescence and the differences in canopy temperature between irrigated and drought treatments can be used as a selection method for screening drought-tolerant potato genotypes. In Bologna potato

clones were selected which are adapted to stress conditions (Table 3). Clone ISCI 4062 performed better than other genotypes and was characterized by the highest number of tubers per plant. This clone was assumed to possess tolerance to water shortage which was accounted for by the earliness of the cycle and the rapid increase in tuber bulking. Potato clones adapted to stress conditions have already been selected.

Demagante et al. (1995) suggested the use of apical cuttings as a simple method to screen genotypes for drought tolerance in potato, because it is fast, simple and repeatable. They found significant correlations for total yield and dry matter ($r=0.8$) between plants grown from apical cutting in beds and from seed tubers in the field. Drought stress sensitivity based on reduction in tuber and total dry matter at maturity in the beds was similar to the results found in the field at maturity.

Resistance to cold stress. Most *S. tuberosum* cultivars are very susceptible to temperatures below -3°C . Broad genetic variability for the resistance to "freezing" trait is reported in the *Solanum* genus. Chen & Li (1980) divided the *Solanum* species into five classes according to their ability to withstand cold. The species also differed in their ability to acclimate or increase their tolerance after exposure to sublethal temperatures (above 0°C).

It has been demonstrated in *S. commersonii*, a species able to withstand up to -12°C after acclimation at 2°C for two weeks, that acquisition of cold tolerance by means of abscisic acid (ABA) is due to changes in genetic expression, which leads to the activation of ABA-inducible gene transcription, of which the most widely studied and characterized are the *lea* rab genes (Chen et al., 1995). These genes encode highly hydrophilic proteins, whose supposed function is to associate with cellular and

Table 3. Performance of ISCI clones in a field trial carried out on the island of Sardinia.

Genotype	Tuber grading			Tuber yield (t/ha)	Dry matter content (%)	Tubers/ plant (no.)
	$\varnothing < 40$ mm (t/ha)	$\varnothing 40-60$ mm (t/ha)	$\varnothing > 60$ mm (t/ha)			
ISCI A9	24.1	14.3	0	38.4	20.3	11.7
ISCI B31	15.3	16.7	0	31.9	21.0	10.0
ISCI C60	7.2	29.2	0.8	37.2	19.2	9.5
ISCI 67	18.5	32.5	0	51.1	17.7	12.0
ISCI 83	13.5	23.4	0	36.9	18.2	9.7
ISCI 4052	12.4	45.7	0.3	58.4	19.4	15.8
Arinda	13.5	33.8	0	47.3	20.0	11.5
Nicola	25.0	4.6	0	29.5	20.7	14.5
Spunta	18.4	28.6	0.3	47.2	20.2	10.6
Timate	16.5	12.8	0.4	29.6	21.2	8.1
Mean	16.4	24.2	0.2	40.8	19.7	11.3

subcellular constituents and keep their structure unaltered and operational in conditions of dehydration connected with freezing. This shows that stresses of different kinds, such as drought, freezing and excess of salinity have a common physiological basis tied to the non-availability of water. The degree of tolerance of *S. commersonii* has also been associated with a higher level of unsaturation of cell membrane phospholipids (Palta et al., 1993; Leone et al., 1996), as membranes with more unsaturated fatty acids maintain membrane fluidity unaltered at low temperatures, an essential condition for maintaining membrane functionality. By contrast, heat tolerance is associated with a lower level of unsaturation. Genes which encode two different desaturases, enzymes which regulate the level of unsaturation, were recently cloned from a cDNA library of *S. commersonii* (Grillo et al., 1996).

Although the genetic and molecular basis of frost resistance is still partly unclear, studies by Stone et al (1993) demonstrated that resistance to frost and capacity to cold acclimate have a different genetic control, and that the two traits are regulated by relatively few genes. At the University of Naples, the wild 1EBN species *S. commersonii* is being widely used in breeding programmes to introgress frost resistance and capacity to cold acclimate into cultivated forms (Cardi et al., 1993; Carputo et al., 1997a). Triploid sexual hybrids and tetraploid somatic hybrids with good agronomic characteristics and resistance to low temperatures have been identified (Cardi et al., 1993; Carputo et al., 1998). Results showed that, especially in terms of capacity for acclimation, resistance was transmitted into the *tuberosum* gene pool. Particularly interesting was a triploid genotype whose killing temperatures (-4.1 °C and -7.4 °C in non-acclimated and acclimated conditions, respectively) were very similar to those of *S. commersonii*.

Resistance to biotic stresses

Although serious diseases and pests occur in the Mediterranean region, in this paper only some of them will be discussed. For late blight and tuber moth, specific lectures and symposia have been organized during the 14th Triennial Conference of the EAPR, and readers are referred to reports elsewhere in this issue.

Bacteria of the genus *Erwinia* may seriously hamper potato cultivation in Mediterranean areas, causing losses in the field and during tuber storage. Control of soft rot *Erwinias* is difficult, and the degree of resistance is low in the cultivated potato. Resistant diploid species have been identified which can be used in breeding programmes at diploid level (Hanneman & Bamberg, 1986; Rousselle-Bourgeois & Priou, 1995; Carputo et al., 1996). De,Maine et al. (1998) recently selected long-day-adapted *S. phureja* genotypes that were highly resistant to tuber soft rot and with good tuber yield and quality. At the University of Naples, we have recently produced hybrids between *S. tuberosum* haploids and the diploid 2EBN species *S. multidissectum* and *S. tarijense* resistant to blackleg and tuber soft rot (Carputo et al., 1997b). Some of the hybrids carried both resistances, and through the function of 2n gametes they were used in sexual polyploidization crossing schemes to produce the backcross generations. The resistance to tuber soft rot of selected BC₂ *tuberosum*-

tarijense hybrids is shown in Fig. 1. A number of genotypes with a diameter of rotted area <4 mm (classified as resistant) was identified, and is now used in the backcrosses.

Bacterial wilt caused by *Ralstonia solanacearum* is another important disease in the Mediterranean region as well as in the tropical areas. There is no chemical control and current strategies rely on the integrated use of tolerant cultivars, seed certification, improved crop management and general on-farm hygiene. However, they are usually only partially effective. Improved cultivar resistance remains the most desirable target. Sources of resistances have been identified in *S. phureja* (Rowe & Siquera, 1970) as well as in several other diploid species, including *S. sparsipilium*, *S. chacoense*, *S. microdontum* and *S. raphanifolium* (Schmiediche, 1988). Breeding work is currently carried out at tetraploid (Anguiz & Mendoza, 1997) and at diploid level (Watanabe et al., 1996). It seems that genetic control is specific for each species and no information on the inheritance of resistance from individual species is available in literature. Tung et al. (1990) have demonstrated that the stable expression of resistance, under warm tropical conditions, is enhanced when resistance genes are combined with genes conferring adaptation to that environment.

Verticillium wilt (*Verticillium albo-atrum* and *V. dahliae*) and early blight (*Alternaria solani*) are the most common fungus diseases of potato in the warm growing area. Depending on the presence of inoculum and on environmental conditions, symptoms of both diseases are often seen at about the same time during the later stages of tuber bulking. Most cultivars are susceptible, and management strategies for the control of the pathogens rely mainly on soil fumigation and crop rotation.

With Verticillium wilt, *S. chacoense* seems to be an excellent source of resistance and has recently been used in a number of breeding programmes (Mohan et al., 1990;

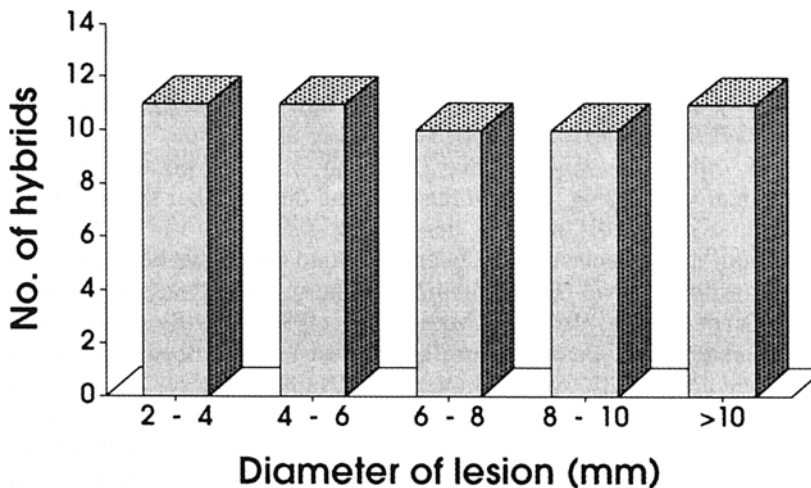


Fig. 1. Resistance to tuber soft rot in BC2 *Solanum tarijense*-*S. tuberosum* hybrids. Genotypes were classified as resistant when the diameter of lesion was <4 mm.

Concibo et al. 1994; Corsini & Pavek, 1996). The transfer of resistance to *Verticillium* wilt from *S. torvum* to *S. tuberosum* gene pool has been successfully achieved also through somatic hybridization (Jadari et al., 1992). Contrasting results have been reported on the inheritance of *Verticillium* wilt resistance. Lynch et al. (1997) suggested that the resistance in *S. chacoense* is controlled by a single dominant gene, whereas Concibo et al. (1994) hypothesized that the inheritance of resistance may be polygenic and rather complex.

With early blight, the diploid species *S. phureja* and *S. stenotomum* have been identified as good sources of resistance (Ortiz et al., 1993). Inheritance studies by these authors indicated that genes with additive effects were the most important in determining resistance at the diploid level. Breeding programmes have been developed at the tetraploid level by Brandolini (1992), Boiteux et al. (1995) and Love et al. (1997) to enhance the resistance. Recently, a gene encoding an endochitinase from a biocontrol fungus (*Trichoderma harzianum*) was transferred to potato by Lorito et al. (1998). Selected transgenic plants were highly tolerant or completely resistant to *A. solani*, and they did not show any deleterious effect of this gene on plant development.

Seed tuber production

Besides availability of the right genotypes, another problem related to potato cultivation in the Mediterranean area is the availability of seed tubers at the right physiological stage. Because seed tubers produced in the spring and planted in August are physiologically "young", their emergence is often not uniform and continues over a period of 4–6 weeks so that plant establishment and development are not homogeneous and most plants produce few stems. Either cultivars with a relatively short dormancy, or controlled ageing of seed tubers are essential for the success of the autumn crop. Uniform and rapid plant development gives rapid foliage cover which is important for efficient light interception and for high tuber yields. In the Mediterranean region, rapid and uniform growth is especially important in autumn because it maximizes the use of climatic conditions until mid-November when winter starts.

Indigenous seed tubers are required for autumn crops as aged seed from foreign countries is unavailable for planting in August. Usually, ware potatoes harvested in May and June are employed for planting crops in the subsequent autumn season; this material is not health certified and consequently gives low yields. In this situation two questions arise: 1) can Mediterranean countries develop seed production programmes which are able to replace and improve local production of seed required for the autumn crop? 2) can Mediterranean countries develop programmes to produce seed for winter crops?

In Italy, projects funded by the Ministry of Agriculture since 1985 have provided new insights into steps necessary for the production of healthy seed potato. The approach is based on the implementation of *in vitro* techniques (micro and minituber production), husbandry management of the initial disease-free seed stocks to

maximize multiplication rates and avoid disease transmission, and identification of health-certified areas for field multiplication (Ranalli et al., 1994).

For the autumn crop, Giordano and colleagues produced seed tubers from the beginning of February to the end of May (I. Giordano, personal communication). Planting took place from the beginning of August in Campania up to beginning of September in Sicily. On average emergence occurred in 50 days, while the maximum leaf cover occurred in 75 days. At harvest from December, the new genetic material performed well in terms of yield and quality, with a dry matter content 2–3 points higher than the field average. The trial also showed that for autumn cultivation, increase in seed tuber size significantly increased yield in terms of both tuber number per plant and mean weight. Larger seed tubers also appear to break dormancy more readily.

Seed tuber production problems have been tackled initially by research institutes but many problems which are normally beyond the scope or responsibility of the research sector have remained unsolved because a) the producer is not specialized in seed production; b) programmes for seed production have been established by producers of potatoes for consumption who have found neither the economic motivation nor the assistance to become seed potato producers; c) market structures for local seed remain extremely weak when compared with those for imported seed; d) the failure of previous seed tuber production programmes has meant that many local producers are not attracted by new programmes in which to invest their capital.

Conclusion

The availability of potato cultivars for each environment and for each planting season is fundamental for potato cultivation in the Mediterranean area. Here, breeding does not need new revolutionary strategies and should use the current ones but with new objectives. The main objectives should be those related to the growth cycle, which has to be as short as possible to have mature tubers in a short time, and to the resistance to environmental constraints. The availability of seed tubers at the right physiological stage is also felt very important for potato production in the Mediterranean area, especially for the autumn and the winter crops. Seed production programmes able to replace and/or improve local production of seed would be desirable for crop improvement.

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