

SECTION 6

POTATO (*SOLANUM TUBEROSUM* SUBSP. *TUBEROSUM*)

1. General Information

This consensus document addresses the biology of the potato (*Solanum tuberosum* subsp. *tuberosum*). It contains general information on the taxonomy, morphology, and centre of diversity of the species which can be of importance during a risk assessment (for example, information on reproductive biology, the possibility of crosses, and ecology). In regard to intra- and interspecific crosses, emphasis has been given to the conditions which make a cross possible rather than listing all successful crosses. Such a list would be very long and subject to frequent changes. Only hybridisation events not requiring human intervention are considered.

The Netherlands served as lead country in the preparation of this document, in collaboration with the United Kingdom.

2. Taxonomic Status

The family *Solanaceae* contains several well known cultivated crops such as tomato (*Lycopersicon esculentum*), eggplant (*Solanum melogena*), tobacco (*Nicotiana tabacum*), pepper (*Capsicum annuum*) and potato (*Solanum tuberosum*). The potato ranks, on a world scale, fourth in food production for starch crops. Around 300,000 metric tonnes are produced (FAO, 1985). About 95 countries produce potatoes, with a total value of around \$US 13 billion (Horton *et al.*, 1985).

Within the genus *Solanum* over a thousand species have been recognised. According to Burton (1989), there are “well over two thousand species”. This genus is subdivided into several subsections, of which the subsection *potatoe* contains all tuber-bearing potatoes. The subsection *potatoe* is divided into series, one of which, *tuberosa*, is relevant to this document. Within the series *tuberosa* about 54 species, both wild and cultivated, are found. One of these is *S. tuberosum* (Hawkes, 1990).

S. tuberosum is divided into two subspecies: *tuberosum* and *andigena*. The subspecies *tuberosum* (Table 1.7) is the cultivated potato widely in use as a crop plant in, for example, North America and Europe. The subspecies *andigena* is also a cultivated species, but cultivation is restricted to Central and South America (Hawkes, 1990; Hanneman, 1994).

Table 1.7 Taxonomic position of *S. Tuberosum* subsp. *Tuberosum*

| Taxonomic rank | Latin name |
|----------------|--------------------------|
| family | <i>Solanaceae</i> |
| genus | <i>Solanum</i> |
| section | <i>petota</i> |
| subsection | <i>potatoe</i> |
| series | <i>tuberosa</i> |
| species | <i>Solanum tuberosum</i> |
| subspecies | <i>tuberosum</i> |

3. Centre of Diversity

The centre of diversity for wild tuber-bearing potatoes (subsection *potatoe*) lies in Latin America, which is also considered the centre of origin. For the series *tuberosa* (to which *S. tuberosum* belongs) and most other series within the subsection *potatoe*, there are two centres of diversity. One is a long-stretching Andean area in Venezuela, Colombia, Ecuador, Peru, Bolivia and Argentina. The other is in central Mexico. The distribution area of these wild potatoes is much larger: from the southwestern United States to southern Argentina and Chile (Child, 1990; Hawkes, 1990).

Generally the cultivated *Solanum* species are also found within the centres of diversity for wild potatoes. The exception is the cultivated diploid form of *Solanum tuberosum* subsp. *tuberosum*, which is only found in a constricted area of southwestern Chile.

The cultivated tetraploid *Solanum tuberosum* subsp. *tuberosum*, as known in Europe and most other parts of the world, is considered to be a selection from a small introduction of *S. tuberosum* subsp. *andigena* potatoes from Colombia and Peru, and as such has a very narrow genetic basis. The arguments for this thesis are that plants of the original introductions into Europe are known to have been late flowering and tuberising, and that the morphological description of these potatoes matches the *andigena* type (Howard, 1970). Through selection, this introduction was adapted to the longer day lengths and different environmental conditions of Europe. Simmonds (1966) has shown that such transition can take place in a fairly short period of approximately ten years of selection. From Europe, this new type of potato has spread all over the world as a cultivated crop. An alternative theory is that, after the potato blight epidemic in Europe, new germplasm of *S. tuberosum* subsp. *tuberosum* originating from Chile (Hawkes, 1990) was introduced into Europe.

4. Identification Methods

A. Morphology and somaclonal variation

The subsection *potatoe* is distinguished from all other subsections within the genus *Solanum* by "true potatoes whose tubers are borne on underground stolons, which are true stems, not roots" (Hawkes, 1994).

The series *tuberosa* is characterised by "imparipinnate or simple leaves, forked peduncle, rotate to petagonal corolla and round berries" (Hawkes, 1990). The species *S. tuberosum* is characterised by "pedicel articulation placed in the middle third, short calyx lobes arranged regularly, leaves often slightly arched, leaflets always ovate to lanceolate, about twice as long as broad, tubers with well marked dormancy period" (Hawkes, 1990).

The differences between the two subspecies within *S. tuberosum* are very small, the greatest difference being the short day dependence of the subspecies *andigena*. The differences are set out in Table 1.8.

Table 1.8 Distinction between *S. tuberosum* subsp. *tuberosum* and subsp. *Andigena* (Hawkes, 1990)

| Characteristic | <i>tuberosum</i> | <i>andigena</i> |
|-----------------|---|------------------------------|
| leaves | less dissected | dissected |
| leaflets | wider | narrow |
| leaf angle | arched | acute |
| pedicel | thickened at the apex | not thickened at the apex |
| tuber formation | long or short days, mostly altitude neutral | short days, higher altitudes |

The general description of the morphology of *S. tuberosum* subsp. *tuberosum* is as follows: Herbaceous perennial with weak stems that grow to a maximum of three feet, long pinnate leaves, ovate leaflets with smaller ones disposed along the midrib. The flowers are white, purple, pinkish, or bluish, in clusters, usually with a five-part corolla and exerted stamens with very short filaments. The fruits are yellowish or green, globose, and less than one inch in diameter. Some lack seeds, but others may contain several hundred. The fruits are inedible by humans due to the presence of toxins (Anonymous, 1996; Hawkes, 1990). Tubers are borne at the end of underground stolons. They are round to long oval. The flesh is generally white or cream to yellow, the skin colour light brownish to red. Tubers can contain high levels of solanine, a toxic alkaloid.

Potatoes are very easily regenerated with the use of *in vitro* tissue culture techniques. This form of vegetative propagation normally leads to genetically identical individuals, but considerable heterogeneity is common after tissue culture in which a callus stage is included. This variation is called somaclonal variation. *S. tuberosum* subsp. *tuberosum* is, like all potatoes, quite prone to this kind of variation (Cutter, 1992; Hawkes, 1990).

A. Molecular identification

It is also possible to distinguish between several *Solanum* species with the use of molecular techniques. Restriction Fragment Length Polymorphism (RFLP) of chloroplast DNA, using eight endonucleases (Hosaka *et al.*, 1984), showed that 33 tuberous *Solanum* species and hybrids and two *Lycopersicon* species could be distinguished. The four different *Solanum tuberosum* subsp. *tuberosum* accessions showed identical patterns.

RFLP analyses of genomic DNA can also lead to species identification within the genus *Solanum*. Debener *et al.*, (1990) showed with the use of 70 probe/enzyme combinations (probes from *S. tuberosum* subsp. *tuberosum*) that 38 accessions representing twelve *Solanum* species and one hybrid could be distinguished. The two accessions from *S. tuberosum* subsp. *tuberosum* were not identical. One of the two accessions was the "true" *S. tuberosum* subsp. *tuberosum* cultivar Bintje, the other was a breeding line in whose pedigree *S. andigena*, *S. demissum* and *S. acaule* were introgressed. It could also be shown that RFLP fingerprinting allows distinction not only between species but also between different cultivars or breeding lines (Weising *et al.*, 1992). The use of probes from other *Solanum* species, mostly repetitive sequences, also led to species and cultivar identification (Schweizer *et al.*, 1993). Also RAPD markers can be used for potato cultivar and clone fingerprinting (Powell *et al.*, 1991; Quiros *et al.*, 1993).

In addition, there are indications that the *Solanum* species can be distinguished with the use of the Amplified Fragment Length Polymorphism (AFLP) technique. One primer can generate up to 120 bands per sample, so that discrimination between *Solanum* species is very easy (Kardolus, in press).

It appears that the potato and tomato genomes are so preserved that probes from one can be used to identify the other (Gebhart *et al.*, 1991). This is especially important for the construction of a genetic map and the development of molecular markers.

5. Genetic Characteristics: The Genome

The basic chromosome number in the genus *Solanum* is twelve. *S. tuberosum* subsp. *tuberosum* can be diploids ($2n=24$) or tetraploids ($4n=48$). The diploids are only found in Chile, while the tetraploids are the most commonly cultivated all over the world. How the tetraploidy originated is unclear. The cultivated *S. tuberosum* subsp. *tuberosum* can be either an autotetraploid (doubling of the chromosomes of a diploid species) or an allotetraploid (doubling of the chromosomes of a diploid hybrid between two related species) (Hawkes, 1990).

The phenomenon of unreduced gametes is common in *Solanum* species. In most *Solanum* species, next to the normal haploid gametes (n), unreduced gametes ($2n$) can be found, greatly extending the possible number of natural crosses (see section on crosses) (Hanneman, 1995). Watanabe *et al.*, (1991) reported that most of the 38 tuber-bearing *Solanum* species examined produced $2n$ pollen. The frequency varied from 2 up to 10 per cent.

It is also fairly easy to produce dihaploids from cultivated tetraploid *S. tuberosum*. This can be done by pollinating with, for example, *S. phureja*, which leads to the formation of parthenogenetic diploid plants. Anther culture is also in use to produce dihaploids (Howard, 1970; Caligari, 1992). It has been shown that, where *S. phureja* is used to produce dihaploids, minor chromosomal fragments are found in these dihaploids originating from *S. phureja* (Clulow *et al.*, 1991).

The great value of these diploids is in breeding programmes: species that do not cross readily with the tetraploid potato can cross with a dihaploid (see section on crosses below). These dihaploids are often ovule fertile but pollen sterile.

6. Reproductive Biology

A. Sexual reproduction

Diploid *S. tuberosum* and the other diploid species within the section *petota* are self-incompatible (Kirch *et al.*, 1989). This incompatibility is of a gametophytic, multi-allelic nature based on the occurrence of S alleles. In general these species are insect-pollinating, cross-breeding species

The cultivated tetraploid *S. tuberosum* subsp. *tuberosum* is self-compatible. The S alleles occur in this species, but somehow the incompatibility system is weakened. The mechanism behind this is not known. Plaisted (1980) has shown that under field conditions selfing is most likely for tetraploid *S. tuberosum*, with 80-100 per cent of the seeds formed due to selfing.

To facilitate cross-breeding and selfing, the appearance of insects is necessary. In particular, bumblebees (*e.g.* *Bombus funebris* in Peru and *B. impatiens* in the US) are good pollinators for potatoes (White, 1983). Pollen dispersal is mainly limited by the distance pollinating insects fly. Bumblebees and bees do not fly much further than three kilometres (Reheul, 1987). Normal honeybees (*Apis mellifera*) and *Bombus fervidus* are not pollinators of potato, as the flowers are without any nectar (Sanford and Hanneman, 1981). White (1983) carried out some experiments to determine the importance of pollination by wind for potatoes. Flowers were emasculated, and therefore of no interest to insects. The seedset on these flowers was assessed. No seeds were found, and therefore it was concluded that pollination by wind was of no importance.

Conner *et al.*, (1996) collected outcrossing data from several field experiments with genetically modified potatoes, performed in New Zealand, the United Kingdom and Sweden. In each study the outcrossing rate was reduced to 0 per cent where the receiving plants were separated by more than 20 metres from the genetically modified ones.

Although many *Solanum* species are fertile, it appears that a large number of the tetraploid cultivated *S. tuberosum* subsp. *tuberosum* cultivars have a reduced fertility (Ross, 1986). Most cultivars show a reduced pollen fertility or even pollen sterility. Amongst them are well known cultivars like Bintje and King Edward. Although reduced female fertility is not so common, it is noticed that a lot of cultivars flower less profusely than wild material. Another observable phenomenon is that flowers are dropped after pollination, so that no berries are found. The result is that on most *S. tuberosum* subsp. *tuberosum* cultivars few berries and seeds are formed.

Potato seeds cannot be disseminated by birds, but dissemination by small mammals is possible (Hawkes, 1988). Lawson (1983) showed that in Scotland potato seeds could be stored in the ground for up to ten years without losing viability. Love *et al.*, 1994 report that potato seeds can survive and germinate for periods of time in excess of seven years.

B. Asexual reproduction

The potato can also multiply vegetatively. Tubers are formed under the ground. As the tuber is the product for which potatoes are cultivated, an extensive selection has taken place for good tuber production and quality. These tubers can remain viable for long periods of time as long as there is not a major frost period. The stolons on which the tubers are formed are generally not very long for *S. tuberosum* subsp. *tuberosum* cultivars. Stolons of wild tuber-bearing *Solanum* species are much longer (Hawkes, 1990).

7. Crosses

A. Intraspecific crosses

Solanum tuberosum subspecies *tuberosum* and *andigena* are fully cross-compatible (Plaisted, 1980). Hybrids can occur in nature. The incidence of this cross is not clear, as the morphological distinction between the two subspecies is very small. As both subspecies only occur in southern North America and some parts of South America, natural crosses are only likely to be found there.

B. Interspecific crosses: crosses within the subsection *potatoe* (Tuber-bearing Potatoes)

The gene pool for potato is extremely large. Dale *et al.*, (1992) and Evenhuis *et al.*, (1991) state that it is likely that all crosses between the tuber-bearing potatoes within the section *petota* may be possible, although in some cases techniques will have to be applied to establish the crosses.

It appears that there are two groups within this section which are very difficult to cross:

- The diploid species in the series *morelliformia*, *bulbocastana*, *pinnatisecta*, *polyadenia*, *commersoniana*, *lignicaulia*, and *circaeifoli*.
- The diploid species in the other series.

The fertilisation of a diploid plant with normal haploid pollen in fact consists of two fertilisations. The pollen contains two (haploid) generative nuclei; one nuclei fertilises the egg cell, the other fertilises the embryo sac nucleus. The result is a diploid embryo with triploid endosperm.

Den Nijs and Peloquin (1977) reported the existence of a "triploid block" where a tetraploid plant was crossed with a diploid plant. This block is due to the imbalance between the endosperm (5x) and the embryo (3x). The endosperm is not formed, and this is followed by embryo abortion (Jacobsen and Rousselle, 1992).

Johnston *et al.*, (1980, 1982) also found that some species of the same ploidy level could not cross, whereas crosses between species of different ploidy levels were successful. They introduced the concept of the Endosperm Balance Number (EBN), which is a measure to express the "effective ploidy of a genome in the endosperm". To make the normal development of the endosperm after fertilisation possible, the maternal EBN must be twice the paternal EBN (2:1).

The EBN is independent of the ploidy level of the species, and its behaviour is additive. This means, for instance, that by doubling of the chromosome number the EBN also doubles.

Two situations can occur:

- The EBN of two species is the same: natural crosses are possible;
- The EBN of two species is not the same: natural crosses are not possible.

Where the EBN of two species is not the same, several natural or artificial mechanisms are available to circumvent the incompatibility.

Natural mechanisms:

- The occurrence of unreduced gametes makes it possible that species with a lower EBN can cross with species with a higher EBN. For example:

A plant with 4x (EBN=4) cannot cross with a 2x (EBN=2) plant, but if the 2x plant produces unreduced gametes the EBN of these gametes becomes 4, which makes the cross possible. The resulting plant is a tetraploid (4x) with an EBN of 4. It is important to notice that, due to the common occurrence of unreduced gametes in most *Solanum* species, crosses of this kind can occur in nature.

Artificial mechanisms:

- Production of dihaploids makes it possible that species with a higher EBN can cross with species with a lower EBN. For example:

A plant with 4x (EBN=4) cannot cross with a 2x (EBN=2) plant. After dihaploidisation of the 4x (EBN=4) plant a diploid plant with an effective EBN of 2 is formed. This plant can be pollinated by the 2x (EBN=2) plant. The resulting plant is a diploid (2x) with an EBN of 2. It is important to notice that crosses of this kind are not likely to occur in nature, due to the fact that dihaploids are only rarely formed in nature.

- Polyploidisation of plants makes it possible to cross plants with a lower EBN with plants with a higher EBN. For example:

A plant with 2x (EBN=2) cannot cross with a 4x (EBN=4) plant. After polyploidisation of the 2x (EBN=2) plant a tetraploid plant with an effective EBN of 4 is formed. This plant can cross with the 4x (EBN=4) plant. The resulting plant is a tetraploid (4x) with an EBN of 4. It is important to notice that crosses of this kind are not likely to occur in nature, due to the fact that spontaneous polyploidisation rarely occurs; nevertheless, it cannot be excluded.

Despite the EBN system, potatoes of different groups can be combined by somatic fusion *in vitro*. The application frequency of this method is increasing. Fusion products may be fertile, so somatic hybrids may serve as a bridge for combining incompatible genomes.

In Annex I the ploidy and EBN of the most common potato species within the section *petota* are given. These data can be used as an indication of the possibility of formation of hybrids of *S. tuberosum* subsp. *tuberosum* with these species in nature. It is likely that *Solanum tuberosum* subsp. *tuberosum* can cross readily with all *Solanum* species mentioned in Annex I with the same EBN (=4). Also, due to the occurrence of unreduced gametes, the crosses of *S. tuberosum* subsp. *tuberosum* with all *Solanum* species mentioned in Annex I with an EBN of 2 are possible.

To determine if a cross really is likely to occur in nature, several factors have to be considered. The most important are:

- The EBN of the crossing partners:

These must be matching, or the EBN of one partner must not be less than half the EBN of the other partner.

- Geographical occurrence of the species involved:

The species involved must occur in the same area and habitat.

- Flowering period of the species involved:

The flowering periods must overlap.

- The presence of stylar barriers that prevent the growth of pollen tubes:

The presence of appropriate pollinators.

In most parts of the world, no *Solanum* species from the section *petota* with an EBN of 2 or 4 will occur next to cultivated tetraploid *S. tuberosum* subsp. *tuberosum*. Crosses are therefore not likely, due to geographical isolation. Only in the southern United States and South America do crossing partners with a suitable EBN occur next to cultivated tetraploid *S. tuberosum* subsp. *tuberosum*. In these areas the characteristics of the species involved and the habitat must be assessed to predict the likelihood of the cross.

C. Interspecific crosses: crosses with species from sections other than *petota*

The occurrence of hybrids with species from sections other than *petota* is not likely, due to strong crossing barriers, although in several areas of the world cultivated tetraploid *S. tuberosum* subsp. *tuberosum* occurs next to indigenous *Solanum* species (not from section *petota*). For instance, *S. nigrum* and *S. dulcamara* occur in the Netherlands. Eijlander and Stiekema (1990) found that the cross of tetraploid *S. tuberosum* subsp. *tuberosum* with *S. dulcamara* did not result in any viable seeds and plants. For the cross of *S. nigrum* with *S. tuberosum* the same is valid. Only after embryo rescue could two hybrids be obtained. These were less vital, male sterile, formed no tubers, and showed less female fertility. After pollination (backcross), no viable seeds were formed.

8. Ecology of *Solanum tuberosum* subsp. *tuberosum*

A. Cultivation

Environmental conditions under which *S. tuberosum* can be successfully grown are very diverse, as can be concluded from the fact that potatoes are cultivated in many parts of the world. A broad spectrum of cultivars are adapted to these different environmental conditions. Some general parameters can be determined for the cultivation of *S. tuberosum* subsp. *tuberosum*:

- The *S. tuberosum* subsp. *tuberosum* tuber cannot survive a temperature of -3°C and lower. The foliage dies at temperatures of -4°C (van Swaaij *et al.*, 1987; Vayda, 1994). Dale (1992) reports that potato tubers are destroyed by a frost period of 25 hours at -2°C or a frost period of five hours at -10°C. Latin American *Solanum* species can be much more frost-resistant.

- *S. tuberosum* subsp. *tuberosum* cannot be acclimatised to lower temperatures, whereas other *Solanum* species (for example, *S. acaule*) can be (van Swaaij *et al.*, 1987; Li and Fennel, 1985).
- Potatoes seem to be very sensitive to soil water deficit (Vayda, 1994).
- A wide range of soil pH can be tolerated by potatoes (normally 5 and higher, but good production at pH 3.7 was observed) (Vayda, 1994).
- *S. tuberosum* subsp. *tuberosum* is a daylight neutral crop, which means that tubers are made at a growth stage independent of the day length. But variation for daylight sensitivity can be found among *S. tuberosum* subsp. *tuberosum* cultivars.
- Extreme low or high temperatures, in particular the night temperature, can obstruct tuber formation.
- Short days (-14 hours) and moderate ground temperatures (15-18°) enhance tuber formation. Longer days (14-16 hours) and higher (day) temperatures (20-25°) enhance flowering and seed formation (Beukema and van der Zaag, 1979; Burton, 1989).
- Germplasm from all over the world has been used to improve potato varieties. The main goal is to develop cultivars with resistance to biotic factors (fungal, virus, bacterial and insect resistance). Other goals are: improved starch content, adaptation to tropical growing conditions, herbicide resistance, stress tolerance, and the introduction of anti-bruise genes (Brown, 1995). The species most used to improve potato are *S. demissum*, *S. acaule*, *S. chacoense*, *S. spegazinii*, *S. stoloniferum*, *S. vernei*. Less used are *S. microdontum*, *S. sparsipilum*, *S. verrucosum*, *S. phureja*, *S. tuberosum* subsp. *andigena*, *S. commersonii* and *S. maglia* (Caligari, 1992). This germplasm has been introduced into many cultivars of *S. tuberosum* subsp. *tuberosum*.

In Annex II the most common diseases (insects, mites, viruses, bacteria and fungi) in potato and their spread throughout the world are shown. This annex is not intended to give a complete list of all potato diseases known. Therefore it should be taken into account that locally other diseases can be of great importance. The national phytosanitary service can best be consulted on this subject. Moreover, Annex II does not give any indication of which sanitary or quarantine provisions have to be applied in a country.

B. Volunteers and weediness

In the cultivation of *S. tuberosum* subsp. *tuberosum*, plants from seeds from a previous potato crop can act as a volunteer weed. The tubers can also act as a volunteer weed in cultivation. In general these plants (from seeds and tubers) will be eliminated by normal agronomical practices. In addition, tubers will not survive for a long time in most of the areas of cultivation due to unfavourable environmental conditions (low temperatures).

Outside the field, potato seedlings will have difficulty establishing themselves as they cannot compete with other plants. Love *et al.*, 1994 report that these seedlings are limited to cultivated areas for reasons of competition and adaptation. Potato tubers can be spread during transportation and use, but generally these plants will not be established for a long time due to unfavourable environmental conditions.

In general, the potato is not known as a coloniser of unmanaged ecosystems. In climax vegetation it is not able to compete with other species such as grasses, trees and shrubs (Anonymous, 1996).

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APPENDIX I

**Ploidy and EBN of Most *Solanum* Species within the Section *petota*
(Hawkes, 1990; 1992; 1994)**

| SUBSECT. | SERIES | PLOIDY | EBN=1 | EBN=2 | EBN=4 | EBN=unknown |
|----------------------|-----------------------|----------|--|---|-------|--|
| <i>estolonifera</i> | – | Diploid | all species | | | |
| <i>juglandifolia</i> | – | Diploid | | | | all species |
| <i>potatoe</i> | <i>morelliformia</i> | Diploid | | | | <i>S. morelliforma</i> |
| | <i>bulbocastana</i> | Diploid | <i>S. bulbocastanum</i> | | | <i>S. clarum</i> |
| | | Triploid | <i>S. bulbocastanum</i> | | | |
| | <i>pinnatisecta</i> | Diploid | <i>S. branchistotrichum</i> <i>S. jamesii</i> <i>S. cardiophyllum</i> <i>S. pinnatisectum</i> <i>S. trifidum</i> | | | <i>S. tarnii</i> |
| | | Triploid | <i>S. cardiophyllum</i> | | | <i>S. jamesii</i> |
| | <i>polyadenia</i> | Diploid | | | | <i>S. polyadenium</i> <i>S. lesteri</i> |
| | <i>commersoniana</i> | Diploid | <i>S. commersonii</i> | | | |
| | | Triploid | <i>S. commersonii</i> | | | <i>S. calvescens</i> |
| | <i>circaeifolia</i> | Diploid | <i>S. capsicibaccatum</i> <i>S. cicaeifolium</i> | | | |
| | <i>lignicaulia</i> | Diploid | <i>S. lignicaule</i> | | | |
| | <i>olmosiana</i> | Diploid | | | | <i>S. olmosense</i> |
| | <i>yungasensa</i> | diploid | | <i>S. chacoense</i> <i>S. tarijense</i> | | <i>S. arnezii</i> <i>S. yungasense</i> |
| | <i>megistacroloba</i> | diploid | | <i>S. astileyi</i> <i>S. megistacrolobum</i> <i>S. sanctae-rosae</i> <i>S. toralapanum</i> | | <i>S. boliviense</i> |
| | <i>cuneolata</i> | diploid | | <i>S. infundibuliforme</i> | | |

| SUBSECT. | SERIES | PLOIDY | EBN=1 | EBN=2 | EBN=4 | EBN=unknown |
|----------|----------------------|------------|-------|--|---|--|
| | <i>conicibaccata</i> | diploid | | <i>S. chomatophilum</i> <i>S. violaceimarmoratum</i> <i>S. agrimonifolium</i> <i>S. colombianum</i> <i>S. oxycarpum</i> | | <i>S. santolalle</i> |
| | | hexaploid | | | <i>S. moscopanum</i> | |
| | <i>piurana</i> | diploid | | | | <i>S. piurae</i> |
| | <i>ingifolia</i> | diploid | | | | <i>S. ingifolium</i> |
| | <i>maglia</i> | diploid | | | | <i>S. maglia</i> |
| | | triploid | | | | <i>S. maglia</i> |
| | <i>tuberosa</i> | diploid | | wild: <i>S. berthaultii</i> <i>S. brevicaule</i> <i>S. bukasovii</i> <i>S. canasense</i> <i>S. gourlayi</i> <i>S. kurtzianum</i> <i>S. leptophyes</i> <i>S. medians</i> <i>S. microdontum</i> <i>S. multidissectum</i> <i>S. multiinterruptum</i> <i>S. sparsipilum</i> <i>S. spegazzinii</i> <i>S. vernei</i> <i>S. verrucosum</i> cultivated: <i>S. phureja</i> <i>S. stenotomum</i> | | wild: <i>S. alandiae</i> <i>S. hondelmanni</i> <i>S. neocardenasii</i> <i>S. okadae</i> <i>S. oplocense</i> cultivated: <i>S. ajanhuiri</i> |
| | | triploid | | | | wild: <i>S. maglia</i> <i>S. microdontum</i> cultivated: <i>S. × chaucha</i> <i>S. × juzepczukii</i> |
| | | tetraploid | | | wild: <i>S. gourlayi</i> <i>S. oplocense</i> <i>S. surense</i> cultivated: <i>S. tuberosum</i> subsp. <i>tuberosum</i> <i>S. tuberosum</i> subsp. <i>andigena</i> | |
| | | pentaploid | | | | <i>S. × curtilobum</i> |
| | | hexaploid | | | <i>S. oplocense</i> | |

Part 1 – Consensus Documents on Biology of Crops

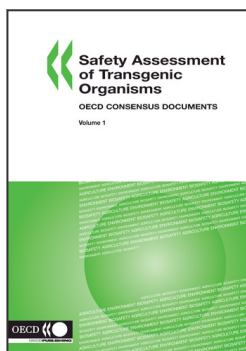
| SUBSECT. | SERIES | PLOIDY | EBN=1 | EBN=2 | EBN=4 | EBN=unknown |
|----------|-------------------------|------------|-------|--|---|-------------------------|
| | <i>aucaia</i> | tetraploid | | <i>S. acaule</i> | | |
| | | hexaploid | | | <i>S. albicans</i> | |
| | <i>longipedicellata</i> | triploid | | | | <i>S. ×vallis-mexci</i> |
| | | tetraploid | | <i>S. fenderi</i> <i>S. hjertingii</i> <i>S. papita</i> <i>S. polytrichon</i> <i>S. stoloniferum</i> | | |
| SUBSECT. | SERIES | PLOIDY | EBN=1 | EBN=2 | EBN=4 | EBN=unknown |
| | <i>demissa</i> | triploid | | | | <i>S. ×semidemissum</i> |
| | | hexaploid | | | <i>S. brachycarpum</i> <i>S. demissum</i> <i>S. guerreroense</i> <i>S. hougasii</i> <i>S. iopetalum</i> | <i>S. scheckii</i> |

APPENDIX II

The most common diseases in *Solanum tuberosum* subsp. *tuberosum* and their distribution: for each pest/disease category a reference to a more extensive review is given (Hide and Lapwood, 1992; Evans and Trudgill, 1992; Raman and Radcliffe, 1992)

| INSECT AND MITE PESTS (review: Hooker, 1986) | |
|---|---|
| Organism | Occurrence |
| <i>Myzus persicae</i> , <i>Phthorimaea operculella</i> , <i>Agriotes</i> spp. | Worldwide |
| <i>Macrosiphum euphorbiae</i> , <i>Aphis fabae</i> , <i>Empoasca devastans</i> , <i>Heliothus armigera</i> , <i>Spodoptera exigua</i> | Worldwide except Africa |
| <i>Plusia orichalcea</i> , <i>Sthenaridea pulsilla</i> , <i>Psylloides plana</i> , <i>Epicauta hirticornis</i> , <i>Anomala dimidiata</i> , <i>Phyllognathus dionysius</i> , <i>Melolontha</i> spp., <i>Odontotermes obesus</i> , <i>Eremotermes</i> spp., <i>Alcidodes westermanni</i> , <i>Mylocerus subfasciatus</i> , <i>Pyrallis farinalis</i> , <i>Nipaecoccus vastator</i> | Asia |
| <i>Empoasca fabae</i> , <i>Paratrioza cockerelli</i> , <i>Hypolithus</i> spp. | North America |
| <i>Diabrotica</i> sp., <i>Epicauta</i> spp., <i>Premnotrypes</i> spp., <i>Phylophaga</i> spp., <i>Scrobipalpula absoluta</i> , <i>Scrobipalpopis solanivora</i> , <i>Symmetrischema plaeseosema</i> , <i>Feltia experta</i> , <i>Stenotycha</i> spp., <i>Copitarsia turbata</i> , <i>Bonthinus mainon</i> , <i>Phenacoccus grenadensis</i> , <i>Liriomyza</i> spp. | Central and South America |
| <i>Shistocerca gregaria</i> , <i>Liriomyza trifolii</i> | Africa |
| <i>Henosepilachna sparsa</i> , <i>H. vigintisexpunctata</i> , <i>Austroasca virigrisea</i> , <i>Listroderes obliquus</i> , <i>Heteronychus arator</i> , <i>Cheiroplatys latipes</i> , <i>Graphognathus leucoloma</i> | Australia |
| <i>Aphis nasturtii</i> , <i>Limonius</i> spp., <i>Ctenicera</i> spp., <i>Conodorus</i> spp. | North America and Europe |
| <i>Aphis gossypii</i> | Central and South America, Asia |
| <i>Aulacorthum solani</i> | North America, Europe and Africa |
| <i>Leptinotarsa decemlineata</i> | North America, Europe and Asia |
| <i>Epitrix</i> spp. | North, Central and South America |
| <i>Epilachna</i> spp., <i>Polyphagotarsonemus latus</i> , <i>Thrips palmi</i> , <i>Gryllotalpa africana</i> | Africa and Asia |
| NEMATODES (review: Hooker, 1986) | |
| Organism | Occurrence |
| <i>Globodera rostochiensis</i> , <i>Globodera pallida</i> | Worldwide |
| <i>Meloidogyne hapla</i> | North America and temperate areas in general |
| <i>Meloidogyne chitwoodi</i> | Northwest America and parts of Western Europe |
| <i>Nacobbus aberrans</i> | Peru and Bolivia |
| <i>Pratylenchus penetrans</i> , <i>Trichodorus</i> and <i>Paratrichodorus</i> spp. | North America and Europe |

| | |
|--|--|
| <i>Ditylenchus destructor</i> | North America, Western Europe and the former USSR |
| <i>Ditylenchus dipsaci</i> | Western Europe |
| VIRUSES (review: Valkonen, 1994) | |
| Organism | Occurrence |
| Virus X (mild mosaic), leaf roll virus, Virus Y (severe mosaic), Virus A (mild mosaic), Virus S | Worldwide |
| Virus M | Europe and North America |
| Tobacco rattle virus | Europe, North America, Brazil and Japan |
| Mop top virus | Western Europe and Peru |
| Yellow dwarf virus | North America |
| Spindle tuber “viroid” | North America, former USSR and South Africa |
| Witches' broom (mycoplasma) | Europe, North America, Australia, China |
| BACTERIA (review: Hooker, 1986) | |
| Organism | Occurrence |
| <i>Clavibacter michiganensis</i> var. <i>sepedonicus</i> (ring rot), <i>Erwinia carotovora</i> ssp. <i>atroseptica</i> and subsp. <i>Carotovora</i> (blackleg, soft rot) | Europe and North America |
| <i>Erwinia chrysanthemi</i> (blackleg, soft rot) | Tropics and sub-tropics |
| <i>Streptomyces scabies</i> (common scab) | Worldwide |
| <i>Pseudomonas solanacearum</i> (brown rot) | Tropics and warm temperate zones |
| FUNGI (review: Hooker, 1986) | |
| Organism | Occurrence |
| <i>Alternaria solani</i> (early blight), <i>Botrytis cinerea</i> (grey mould), <i>Collectotrichum coccodes</i> (black dot), <i>Helicobasidium purpureum</i> (violet root rot), <i>Phytophthora infestans</i> (late blight), <i>Pythium ultimum</i> (watery wound rot), <i>Rhizoctonia solani</i> (black scurf), <i>Spongospora subterranea</i> (powdery scab), <i>Verticillium albo-atrum</i> , <i>V. dahliae</i> (wilt) | Worldwide |
| <i>Angiosorus solani</i> (potato smut) | Central and South America |
| <i>Fusarium</i> spp. (wilt) | North America |
| <i>Fusarium solani</i> var. <i>Coeruleum</i> (dry rot), <i>Phoma foveata</i> (gangrene) | Europe |
| <i>Helminthosporium solani</i> (silver scurf), <i>Sclerotinia sclerotiorum</i> (stalk break) | Europe and North America |
| <i>Macrophomina phaseolina</i> (charcoal rot) | North America and India |
| <i>Polyscytalum pustulans</i> (skin rot) | Northern Europe, North America, Australia |
| <i>Synchytrium endobioticum</i> (wart) | Europe, North and South America, South Africa and Asia |
| <i>Phoma exigua</i> var. <i>Exigua</i> (gangrene), <i>Phytophthora erythroseptica</i> (pink rot) | Europe, North America and Australia |



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