Phytophthora species of Switzerland.

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Summary – The first part of this paper gives an inventory of *Phytophthora* spp. in Switzerland. Until end of 1995, the following 15 species have been identified: *P. cactorum, P. cambivora, P. cinnamomi, P. citricola, P. citrophthora, P. cryptogea, P. drechsleri, P. erythroseptica, P. fragariae, P. fragariae* var. *rubi, P. infestans, P. megasperma, P. nicotianae, P. porri,* and *P. syringae*. They occurr on a total of 57 host plants belonging to 27 different botanical families.

After a short history of the genus, the host plants for each fungal species, the typical disease symptoms and the geographical distribution within the country are described. The inventory is based on literature reports and investigations of the authors.

In the second part the results of ecological field studies over a period of 25 years are described. They comprise a survey of the occurrence of *Phytophthora* spp. in fallen apples from 33 orchards all over Switzerland and, more detailed studies on their distribution in soils of the region of Basle. Using apple baiting techniques, a total of 161 soil samples were taken at altitudes between 250 and 1050 m, including apple orchards, agricultural fields, pastures, woodland and the banks of two streams. We isolated *Phytophthora* spp. from 93 samples, i.e. 58% of the total number.The species detected were (in order of descending frequency): *P. citricola (44 times), P. cactorum,* (32), *P. cryptogea,* (8), *P. drechsleri* (6), *P. megasperma* (2) and *P. cinnamomi* (1). *Phytophthora* spp. occurred not only in the vicinity of their host plants, but also in permanent woods, and on the sandy banks down to the water level of the two streams. Most surprising was the occurrence of *P. cinnamomi* in a pasture soil. This is the first record of this species in the open nature in this country. There was no correlation between occurrence of the fungi and type or pH of the various soils.

Zusammenfassung – Im ersten Teil dieses Artikels wird ein Inventar der in der Schweiz vorkommenden Pilze der Gattung *Phytophtora* aufgelistet. Bis En-de 1995 wurden 14 Arten und eine Varietät identifiziert: *P. cactorum*, *P. cambivora*, *P. cinnamomi*, *P. citricola*, *P. citrophthora*, *P. cryptogea*, *P. drechsleri*, *P. erythroseptica*, *P. fragariae*, *P. fragariae* var. *rubi*, *P. infestants*, *P. megasperma*, *P. nicotianae*, *P. porri und P. syringae.* Diese Arten parasitieren eine oder mehrere von 57 verschiedenen Wirtspflanzen, die ihrerseits 27 botanischen Familien angehören.

Für jede *Phytophtora* sp. werden die Wirtspflanzen, das Schadbild und die geographische Verbreitung angegeben. Die Angaben basieren auf Literaturhinweisen sowie auf eigenen Beobachtungen.

Im zweiten Teil dieser Arbeit präsentieren wir die Resultate der ökologischen Studien der letzten zwanzig Jahre. Wir fanden verschiedene *Phytophthora* spp. an auf dem Boden liegenden Äpfeln aus 33 verschiedenen Obstanlagen in verschiedenen Regionen der Schweiz.

Aus Erdproben von Obstanlagen, Wiesen, Wäldern und zwei verschiedenen Bachufern der Region Basel (250–1050 m ü. M.) konnten mehrere *Phytophthora* spp. nachgewiesen werden. Sechs verschiedene Arten konnten isoliert werden. 93 aus 161 Proben (58%) erwiesen sich im Labortest als positiv. Es handelt sich um folgende Arten, nach Häufigkeit angeordnet: *P. citricola* (44×), *P. cactorum* (32×), *P. cryptogea* (8×), *P. drechsleri* (6×), *P. megasperma* (2×) und *P. cinnamoni* (1×).

In den Obstanlagen konnten die *Phytophtora* spp. nicht nur unter den Bäumen, sondern auch in den Grasstreifen zwischen den Reihen festgestellt werden. Diese Pilze konnten auch aus Erdproben aus Wäldern und sandigen Bachufern (2 Bäche) isoliert werden. Überraschend war ein Isolat von *P. cinnamomi* aus einem Wiesenboden. Diese Art wurde somit im Freiland zum ersten Mal in der Schweiz beobachtet. Im weiteren konnte keine Korrelation zwischen dem Vorkommen der diversen *Phytophthora* spp. und dem Boden-Typ nachgewiesen werden.

Résumé – La premiere partie de cette publication dresse un inventaire des champignons du genre *Phytophthora* présents en Suisse. Jusqu'à la fin de 1995, 14 espèces et une variété y ont été identifiées, soit: *P. cactorum*, *P. cambivora*, *P. cinnamomi*, *P. citricola*, *P. citrophthora*, *P. cryptogea*, *P. drechsleri*, *P. erythroseptica*, *P. fragariae*, *P. fragariae* var. *rubi*, *P. infestans*, *P. megasperma*, *P. nicotianae*, *P. porri* et *P. syringae*. Ces espèces parasitent 57 plantes hôtes appartenant à 27 familles botaniques.

Pour chaque *Phytophthora* sp., on indique le ou les hôtes, la nature des symptômes occasionnés et la répartition géographique des cas constatés. Cet inventaire est basé tant sur les indications de la littérature que sur nos propres observations.

Dans la deuxième partie nous présentons les résultats des études écologiques effectuées pendant une vingtaine d'années. Elles mettent en évidence la présence de plusieurs espèces de *Phytophthora* dans des pommes tombées ramassées dans 33 vergers répartis dans différentes régions de Suisse. Dans la région de Bâle, plusieurs *Phytophthora* spp. sont isolés d'échantillons de sols récoltés entre 250 et 1050 m d'altitude, dans des vergers, des champs, des prés, des forêts et sur les rives de deux rivières. En les piègeant avec des pommes au laboratoire, six espèces de *Phytophthora* sont isolées de 93 des 161 échantillons de sols prélevés, soit dans 58% des cas. Les espèces identifiées sont, par ordre décroissant: *P. citricola* (*44 fois*), *P. cactorum* (32), *P. cryptogea* (8), *P. drechsleri* (6), *P. megasperma* (2) et *P. cinnamomi* (1).

Dans les vergers, les espèces du genre *Phytophthora* sont décelées non seulement sous les arbres, mais aussi dans l'espace les séparant. Ces champignons sont également identifiés du sol de diverses forêts et des rives sableuses de deux rivières, jusqu'au niveau de l'eau. Un résultat surprenant de ces études est l'isolation de *P. cinnamomi* du sol d'un pré. Il s'agit de la première observation de cette espèce en plein air en Suisse. En outre nous n'avons pas constaté de corrélation entre la présence des *Phytophthora* et le type ou le pH des différents sols.

1. Introduction

Amongst the plant parasitic fungi, the *Phytophthora* species hold a special position by their virulence and epidemic potential, their broad geographic distribution and by their array of host plant species. Surveys of their biology, genetics, taxonomy, ecology and pathology were compiled recently by Erwin et al. (1983) and Lucas et al. (1991). Certain species cause considerable losses in a number of crops of worldwide economic importance, such as cacao, rubber, pineapple and several palm species in the tropics, as well as citrus, avocado, deciduous fruit trees, strawberry, berry, potato, tobacco, several legume crops and ornamentals in mediterranean and temperate climates.

Some species also attack forest trees, such as *P. cinnamomi* which recently killed thousands of hectares of natural forests in Australia. It is difficult to observe *Phytophthora* fungi as soil saprophytes or as parasites in plant tissues. Tsao (1990) states that many of them have not yet been recognized as parasites on various host plants and in vast regions of the globe. He assumes that a large number of root rots are still wrongly attributed to other microbial parasites or abiotic factors, respectively. In his view in many cases the observation and isolation techniques for *Phytophthora* species are insufficiently known or incorrectly used. In the saprophytic stage, they are very weak competitors (Gregory 1983). During isolation from soil or from necrotic plant tissues they easily suffer from competition by other fungi.

In contrast to the majority of soil-borne pathogens *Phytophthora* spp. attack only healthy tissue. They only infect organs which have not yet been colonized by other microorganisms, i.e. they never occur as secondary parasites. If *Phytophthora* spp. are isolated from diseased tissue one can be sure that they are the primary cause of the damage. Their mycelium undergoes autolysis very quickly in the attacked tissue, leaving room for numerous secondary fungi. Due to this situation, microscopic observation or isolation of *Phytophthora* spp. is only possible during a very short period of time after infection. It is for the reasons described above that many diseases caused by *Phytophthora* spp. have been ignored for such a long time in many parts of the world and particularly in Switzerland.

The increase in numbers of *Phytophthora* spp. and their hosts in our country during recent years is not only a consequence of better isolation and identification techniques but also of intensified production methods such as the use of fertilizers and irrigation, which favored the aggressiveness of *Phythophthora* spp. naturally occurring in our soils. In addition the sale of rooted plants in containers and plastic bags as well as the still increasing international trade with plants and planting substrates have facilitated the recent introduction of the following new species into our country:

- *P. fragariae*, causal agent of the red root rot disease of strawberries,
- *P. fragariae* var. *rubi*, causing wilt of raspberry plants,
- *P. cinnamomi* and *P. citrophthora*, causing occasionally root and collar rots of various vegetable and horticultural crops.

This review summarizes work during the past 25 years on the role of *Phytophthora* spp. as causal agents of plant diseases (first author) and on their occurrence and distribution in soils of Switzerland (second author).

2. History

The genus *Phytophthora* was established by de Bary in 1876 with *P. infestans* (Montagne) de Bary, causal agent of late blight of potatoes, as type species. Eighty years later Waterhouse (1956) presented a list of 92 species and subspecies. Her revised list (Waterhouse 1963) retained 42 taxa. Newhook et al. (1978) published a tabular key for their identification covering 50 species and subspecies. This number increased to 67 species in the revised key by Stamps et al. (1990).

The first *Phytophthora* species reported in Switzerland was *P. infestans*. This fungus, originating from Mexico, arrived in Europe in 1830 (Viennot-Bourgin 1949). In Germany, i.e. in the Palatinate it caused significant losses from 1840 onwards. In 1845 the meteorological conditions were so favorable that it spread, between June and October, from Flandres to the England and Ireland (Nelson 1995) and to the Northern slopes of the alps (Semal et al. 1983, Bourke 1991). It can be assumed that the disease reached the Swiss Mittelland during the same season. However it took fourty years until the causal agent of potato blight was mentioned in a Swiss publication. Dufour (1889) refers to it under the name *Peronospora infestans* Casp. The taxon *P. infestans* was not used until 1908 in the annual report of the Federal Research Station Zurich-Oerlikon (Stebler 1908).

In 1904 and 1905 Osterwalder (1906) of the Federal Research Station in Waedenswil, observed a fruit rot on apples and pears which he attributed to *P. omnivora de Bary,* a species synonymous to *P. cactorum* (Leb. et Cohn) Schroet. In the annual report 1911/1912 of the same station, Müller-Thurgau et al. (1915) report infections by *P. omnivora* on pears and strawberries and by *P. infestans* on tomatoes. The latter is the only species mentioned by Faes (1917) in his book «Les maladies des plantes cultivées et leur traitement».

Table 1: *Phytophthora* spp. in chronological order found in Switzerland until 1995

Species	Year of first observation	First publication
P. infestans	1845	Dufour 1889
P. cactorum	1904	Osterwalder 1906
P. erythroseptica	1912	Mayor 1958
P. cambivora	1942	Faes 1943
P. porri	1964	Rochaix 1966
P. syringae	1975	Bolay 1976
P. megasperma	1976	Bolay 1978
P. cryptogea	1976	Varady and Ducrot 1984
P. citricola	1976	Bolay 1992a
P. drechsleri	1977	Bolay 1978
P. nicotianae	1980	Bolay 1990
P. fragariae var. *rubi*	1980	Bolay and Lauber 1989
P. fragariae	1981	Bolay 1982; Fritsche 1982
P. cinnamomi	1981	Reichard and Bolay 1986
P. citrophthora	1981	Bolay et al. 1991

In 1912, P. erythroseptica was identified on potato tubers with a pink rot in the canton of Neuchâtel (Mayor 1958). The fourth species was detected in 1942 in the Tessin. It was *P. cambivora* (Petri) Buisman, causing the ink disease of chestnut trees (Faes 1943).

In the first edition of their book «La défense des plantes cultivées» Faes et al. (1943) only mention three species: *P. infestans* on potato and tomato, *P. omnivora* (= *P. cactorum*) on pip fruit and strawberries and *P. cambivora* on chestnut tree. The third edition of the same book adds root rot of walnut tree and a damping-off, but without mentioning the causal agents (Faes et al. 1953).

P. porri Foister was identified in 1964 and 1965 in the region of lake of Geneva where the fungus was isolated from leek showing a snow-white bleaching of the leaves (Rochaix 1966).

Between 1964 and 1974 the number of *Phytophthora* spp. in Switzerland did not change. Since 1975, however, their number increased and some ten new species were isolated and identified until 1995. Table 1 gives a survey of all species found in Switzerland so far.

3. Isolation and identification

The numerous isolation techniques described in literature have been reviewed by Ribeiro (1978) and Tsao (1983). Within the limits of this report the following simple techniques were used.

3.1. Isolation from diseased plant organs

When attack by *Phytophthora* was presumed the diseased plant parts were first observed microscopically. We learnt from experience that isolation is not successful if the mycelium cannot be seen in the microscope. Stained with aniline blue/lactophenol (Alt 1980), *Phytophthora* spp. are characterized by their coenocytic hyphae in host tissue. However, they may be confused with *Mucorales* or *Pythium* spp.

The success of isolation depends very much on strict coherence to the following rules:

- Isolate immediately after having collected or received the sample,
- Take tissue samples from the border of the lesion,
- Do not wash the material with water nor disinfect it with alcohol because water favors bacteria and alcohol is not well tolerated by *Phytophthora,*
- Cut the tissue into small pieces and eliminate all parts which were in contact with the exterior. Cut the remaining pieces into small slices and put them into the nutrient agar in Petri dishes. (5–7 pieces/plate),

- Corn Meal Agar Difco (with no antibiotics added) guarantees good growth of most species. For conservation of *P. infestans, P. fragariae, P. fragariae* var. *rubi* and *P. porri*, Oat Meal Agar (Difco) is the preferred medium,
- Incubate at room temperature (20–25° C) and check growth under the binocular after 12, 18 and 24 hours to mark mycelium of *Phytophthora* which usually grows faster than that of other fungi except *Pythium* spp. and *Mucorales*,
- Transfer *Phytophthora* mycelium as soon as it can be identified by its coralliform and sometimes vesicular appearance. If the number of isolations is large enough there are always colonies developing in which *Phytophthora* mycelium is sufficiently distant from bacterial or fungal contaminants to allow transfer to new plates.

3.2. Isolation from soil

In the studies described in the first part of this publication, we used mainly the method described by Schwinn (1961): Soil samples taken one to ten cm deep near the diseased plants in the field, are placed in trays so that they are half filled. The soil is then irrigated with distilled water until the surface of the soil sample is covered by a 1cm layer. Immature apples or pears are then placed in the tray so that they are covered with soil by two thirds of their surface. After 7 to 15 days of incubation, symptoms of rotting appear, usually at the water surface line. From the border of the fruit lesion, *Phytophthora* spp. are easily isolated on agar plates, most times as pure cultures.

The methods used in the studies on the ecology of *Phytophthora* spp. in soils of Switzerland are described on p. 53.

3.3. Identification of species.

In pure culture the isolated strains were identified with the aid of the keys of Waterhouse (1963), Newhook et al. (1978), Ribeiro (1978), Ho (1981), Kröber (1985) and Stamps et al. (1990). To induce the formation of sporangia and oospores, the fungi were cultivated on carrot agar medium as described by Kröber (1985).

4. The species identified in Switzerland

Up to date the following 14 species and one variety of *Phytophthora* were identified:

P. cactorum	*P. fragariae*
P. cambivora	*P. fragariae* var. *rubi*
P. cinnamomi	*P. infestans*
P. citricola	*P. megasperma* var. *megasperma*
P. citrophthora	*P. nicotianae*
P. cryptogea	*P. porri*
P. drechsleri	*P. syringae*
P. erythroseptica	

In this part we describe the history and the phytopathogenic aspects of these species. More specifically, we will indicate for each taxa:

- host plants with typical symptoms and economic importance,
- geographic distribution: site and canton (AG = Aargau, BE = Bern, FR = Fribourg, GE = Geneva, LU = Lucerne, NE = Neuchâtel, SO = Solothurn, TG = Thurgau, TI = Tessin, VD = Vaud, VS = Valais, ZH = Zurich, CH = all Switzerland).
- year of observation,
- bibliography.

4. 1. *P. cactorum* (Leb. et Cohn) Schroet.

Krypt.fl. Schlesien **3** (1): 236, 1886.
Syn: *Peronospora cactorum* Lebert et Cohn
Peronospora sempervivi Schenk
Phytophthora fagi Hartig
Phytophthora omnivora de Bary.

This is the most common species in Switzerland. For example, it represents 50% of all isolations done at the Federal Research Station Changins between 1976 and 1993. It was one of the two the dominating species in the isolations of the second author betweeen 1966 and 1988 all over Switzerland. It causes the following symptoms:

- damping-off,
- fruit rot,
- collar rot, crown rot of pip fruit and several ornamental tree and shrub species,
- collar, stalk, root, bulb rot of numerous herbaceous plants.

In Switzerland *P. cactorum* was identified for the first time in 1904 (Osterwalder 1906) under the name *P. omnivora* de Bary. He isolated the fungus from rotten apples at Waedenswil. He succeeded in inoculating beech seedlings (*Fagus sylvatica L.*) with his isolations from apple. Some years later he observed *P. omnivora* on *Calceolaria rugosa* Ruiz et Pav., on strawberry plants and on apple rootstocks (Osterwalder 1908, 1910a,b, 1912a,b,c). In the second half of our century *P. cactorum* is considered to be the principal cause of apple tree bark rot, either at the collar or at the crown level (Bolay 1992a).

Host plants.

Nienhaus (1960) published a list of 157 host plant species, belonging to some 70 families and having worldwide distribution. In Switzerland we found some twenty host species, four of them not being mentioned in Nienhaus's list, i.e. *Allium ascalonicum* L., *Eryngium alpinum* L., *Eschscholzia californica* Cham. and *Viola x wittrockiana* Gams.

- *Aesculus hippocastanum* L.
  Ink disease found at Aubonne VD, in 1990 and at Dardagny GE, in 1992 (Bolay et al. 1991). The symptoms were the same as those described as bleeding canker in Great Britain by Brasier & Strouts (1976).
- *Allium ascalonicum* L.
  Heavy rotting of bulbs of scallion occurred since 1990 in the region of lake Geneva, particularly on clones of the cultivar 'Milrac' (Corbaz & Bolay 1991).
- *Calceolaria rugosa* Ruiz et Pav. = *C. integrifolia* Murr.
  Rotting of the stalk base described by Osterwalder (1910a,b) at Waedenswil.
- *Callistephus chinensis* (L.) Nees
  Stalk base rot of aster observed at Waedenswil ZH (Osterwalder 1917, Müller-Thurgau et al. 1922, Müller-Thurgau & Osterwalder 1924).
- *Castanea sativa* Miller
  Bark necrosis on chestnut roots at Monthey VS, in 1987. *P. cactorum* was isolated from soil around diseased trees at Monthey and at Mendrisio TI (Bolay et al. 1988).
- *Cydonia oblonga* Miller
  We never observed collar or crown rot symptoms on adult quince trees or on pears grafted on quince rootstocks. In contrast, we isolated *P. cactorum* from necrotic rootlets from a nursery at Chésopelloz FR. (Bolay, unpublished).
- *Dianthus caryophyllus* L.
  Stalk rot of carnation (Chabaud carnation) found at Waedenswil ZH, in 1921 and 1922 (Müller-Thurgau & Osterwalder 1924).

- *Eryngium alpinum* L.
  Collar and root rot of blue thistle cultivated at Bruson VS (Vallée de Bagnes, at an altitude of 1100 m), in 1984 (Bolay et al. 1988).
- *Eschscholzia californica* Cham.
  Collar rot of poppy in a garden at Nyon VD, in 1983. (Bolay, unpublished).
- *Fagus sylvatica* L.
  Damping off of seedlings. Inoculation of beech seedlings by Osterwalder (1906).
- *Fragaria vesca* L.
  Collar, stalk peduncle and fruit rot on four season's strawberries frequently observed. (Bolay, unpublished).
- *Fragaria × ananassa* Duchesne
  Brown core disease, particularly on plants kept in cold store (Bolay 1972). Fruit rot described by Osterwalder (1912a).
- *Glycine max* Merrill = *G. soja* (L.) Sieb. et Zucc.
  Root rot in an experimental field at Changins, Nyon VD, in 1989 (Bolay, unpublished).
- *Malus domestica* Borkh.
  Collar, stem and branch rot on certain susceptible cultivars, such as Cox Orange, Baron Berlepsch, Transparente de Croncels, James Grieve, Ananas and Ontario Reinette (Osterwalder 1912b, Dufour 1954, Gallay 1961, Bolay 1980, 1992a,b).

Bark rot of apple rootstocks except types M9 and M27, reaching from the grafting point to the main roots down to a depth of 20–30 cm (Fritsche 1978, Bolay 1978, 1980, 1992a,b).

Fruit rot of apples fallen on flooded ground or hit by soil particles (Osterwalder 1906, 1908, Bolay 1977).

- *Prunus armeniaca* L.
  Fruit rot of apricots on trees after strong rainstorm or overhead irrigation, shortly before harvest, in Valais and around lake Geneva (Bolay 1962, Rochaix 1966).
- *Prunus domestica* L.
  P. cactorum was isolated once from necrotic roots of a plum tree (cv. Fellenberg) at Cortaillod NE, in 1985 (Bolay, unpublished).
- *Prunus persica* (L.) Batsch
  Collar and stem rot of young peach seedlings in a flooded nursery near Biasca TI, in 1987 (Bolay, Mauri, unpublished).
- *Pyrus communis* L.
  Collar rot on the cultivar 'Général Leclerc', observed at Founex VD in 1987. In inoculation trials at Changins in 1988 this cultivar turned out to be as susceptible as the apple variety 'Cox Orange'. Fruit rot in overhead-

irrigated orchards and on fallen fruit (Osterwalder 1906, 1908, 1929; Fischer 1946; Bolay 1977, 1992a).

- *Ribes uva-crispa* L.
  Gooseberry rot observed at Waedenswil ZH by Müller-Thurgau et al. (1922).
- *Viola × wittrockiana* Gams
  Frequent decay of whole pansy plants in parks and gardens and on graveyards in the region of lake Geneva and in Fribourg (Bolay et al. 1991).

4. 2. *P. cambivora* (Petri) Buisman

Meded. phytopath. Lab. Willie Commelin Scholten **11**: 4–7, 1927.
Syn: *Blepharospora cambivora* Petri.

Host plants.

- *Castanea sativa* Miller
  P. cambivora is one of the causal agent of ink disease of sweet chestnut. It was described in Switzerland for the first time in the Monte Ceneri region of the canton Tessin by Faes (1943). Arrigoni (1950) and Gäumann (1951) confirmed the presence of the disease in various regions of the Tessin. However, since 1955 it has never been found again there. In 1984, the disease was found in the «Grands Bois» of Roulavaz at Dardagny GE (Reichard & Bolay 1986). In some years it caused the death of more than 15000 trees there.
- *Chamaecyparis* spp.
  Collar and root rot on several species, sold in containers, in a garden center at Assens VD, in 1986 (Bolay, unpublished).
- *Fagus sylvatica* L.
  Ink disease of beech trees in the region of lake Geneva, i.e. at Nyon and Prangins VD, in 1992, at Chigny sur Morges VD, in 1993 (Bolay, unpublished).
- *Malus domestica* Borkh.
  Crown and root rot on apple trees grafted on rootstock M9 in the region of lake Geneva, cantons VD and GE, in 1991 and 1992 (Bolay 1992a,b).
- *Prunus laurocerasus* L.
  Collar and root rot of young cuttings of laurel at Bellinzona TI, in 1991. (Bolay, unpublished).

4. 3. *P. cinnamomi* Rands

Meded. Inst. PlZiekt., Buitenzorg **54**: 412, 1922.

This is the most polyphageous species of the genus. Zentmyer (1980) lists more than 900 host plant species, distributed over the tropical and temperate zones of the globe. It is a dreadful pathogen of many crops and trees. In the 1980ies, it caused the destruction of thousands of hectares of woodland and bushland in Australia. *P. cinnamomi* does not stand temperatures below 5 °C. All strains isolated at Changins or of other provenance were dead after two months of conservation on agar at 5 ± 1°C.

Because of its sensitivity to cold temperatures, this species is not supposed to survive in our country during the dead season in the open nature. However, as shown on p. 57, we isolated it once from soil in grassland. All but one case of diseases by *P. cinnamomi* described in Switzerland so far refer to rooted plants imported in plastic bags. The damage showed up in nurseries or garden centers shortly after importation. The pathogen was able to survive on plants or planting substrates kept over winter in greenhouses or frost-free locations. Only once the pathogen was isolated from a shrub growing in the open air, i. e. from *Taxus baccata*, near Geneva GE (Bolay, unpublished).

On map no 302 of the 1961 edition of "Distribution maps of plant diseases" of the Commonwealth Mycological Institute, the pathogen is recorded from Switzerland, based on Crandall & Gravatt (1967). They mention *Juglans regia* L. and *Castanea sativa* Miller as host species. However, they do not quote the source of their information. We were not able to trace it back.

Host plants.

- *Begonia × tuberhybrida* Voss.
  Collar and stalk rot of potted begonias in Geneva in 1991 (Bolay, unpublished).
- *Chamaecyparis lawsoniana* (A. Murr.) Par.
  Collar and root rot of plants in bags at Versoix GE, in 1992 (Bolay, unpublished).
- *Erica carnea* L.
  Twig rot of potted plants at Renens VD, in 1989 (Bolay, unpublished).
- *Myrtus communis* L.
  Stem and branch rot on plants in bags imported from Spain in a nursery at Taverna TI, in 1981 (Bolay, unpublished).
- *Rhododendron* spp. hort.
  Root and collar rot of potted plants at Avenches VD, in 1982 (Bolay, unpublished).

- *Taxus baccata* L.
  Root rot on yew-tree at Collonge-Bellerive GE in 1992. This is the only case of a disease by *P. cinnamomi* in the open nature. However, the plants were growing at the shore of Lake Geneva in a location well protected from frost (Bolay, unpublished).

4. 4. *P. citricola* Sawada

Rep. Govt. Res. Inst. Dep. Agric. Formosa, **27**: 22–24, 1927.

P. citricola was frequently isolated from soil in pip fruit orchards and near forest and ornamental trees, using the method of Schwinn (1961).

In our ecological studies, it was the most frequently isolated species. In contrast, it was only once isolated from fruit trees.

Host plants.

- *Acer platanoides* L.
  Bark rot and ink disease at the stem base of maple trees at Conches GE, in 1992 (Bolay, unpublished).
- *Chamaecyparis lawsoniana* (A. Murr.)Parl.
  Crown rot on young plants in plastic pots in a nursery at Lausanne, in 1955 (Bolay, unpublished).
- *Citrus* sp.
  Root and collar rot on a single potted plant at Cadenazzo TI, in 1991. (Bolay, unpublished).
- *Ilex aquifolium* L.
  Root and collar rot of holly at Collonge-Bellerive GE, in 1992 (Bolay, unpublished).
- *Malus domestica* Borkh.
  P. citricola was only once isolated from the collar of a Golden Delicious tree grafted on MM 106 at Aigle VD, in 1976. Despite many attempts it was never again isolated from this host plant. Inoculation trials in 1982 and 1983 on twigs and roots of pip and stone fruit trees and on rootstocks clearly demonstrated the pathogenic potential of the strain of *P. citricola* used (Bolay 1992b). In the USA, the susceptibility of pip and stone fruit trees was shown by Wilcox & Mircetich (1985a,b) and by Jeffers & Aldwinckle (1988). In our studies, the pathogen was easily isolated from soil samples from orchards, using the method of Schwinn (1961). However, we were never able to isolate it from rotted fallen fruit.
- *Rubus idaeus* L.
  Isolated once from raspberry roots of a planting heavily infected by *P. fragariae* var. *rubi* at Grandcour VD, in 1987 (Bolay & Lauber 1989).

- *Thuja occidentalis* L.
  Root and collar rot on young thujas in bags at Mannens FR, in 1991. (Bolay, unpublished).

4. 5. *P. citrophthora* (R.E. Smith and E.H. Smith) Leonian

Amer. J. Bot.**12**: 445, 1925.

Similar to *P. cinnamomi* this species is adapted to the tropical and mediterranean climates. Except one case, it was only isolated in Switzerland from rooted plants in bags.

Host plants.

- *Arbutus unedo* L.
  Collar rot of rooted plants imported in bags from Spain in a nursery at Taverne TI, in 1981 (Bolay et al. 1991).
- *Chamaecyparis* sp. and *Cupressus* sp.
  Decay of young plants in bags in a nursery at Avenches VD, in 1982. From *Chamaecyparis*, also *P. cryptogea* was isolated (Bolay et al. 1991).
- *Cucurbita pepo* L.
  Serious decay of a plantation of summer squash at Contone, Magadino plain, TI, in 1989 (Bolay et al. 1991). The origin of the pathogen was never clarified.
- *Fragaria* × *ananassa* Duchesne
  In 1991 *P. citrophthora* was isolated from the collar and roots of some plants (cv. Elvira) of a shipment imported in an air-conditionned lorry from Italy (Bolay, unpublished).
- *Rhododendron* sp.
  Decay of plants in bags in a nursery at Avenches VD, in 1982. *P. cinnamomi* was isolated from the same plants (Bolay, unpublished).
- *Ribes sanguinea* Pursh
  Crown rot on a young shrub of flowering currant shortly after planting in Lausanne, in 1982 (Bolay, unpublished).

4. 6. *P. cryptogea* Pethybridge and Lafferty

Sci. Proc. Dublin Soc. N.S. **15**: 498, 1919.

P. cryptogea attacks a very large number of woody and herbaceous plant species in the open air and under protection. With 17 host species in Switzerland it is ranking second after *P. cactorum (with 19 hosts) and before P. megasperma* (12).

Host plants.

- *Callistephus chinensis* (L.) Nees
  Chinese aster often suffers from a 'black foot'-disease, caused by different fungi of the genera *Fusarium, Rhizoctonia, Pythium* and *Phytophthora. P. cryptogea*, however, was isolated only once from diseased plants at Glion VD, in 1982 (Bolay, unpublished).
- *Chamaecyparis* spp.
  Decay of young plants in bags in a nursery at Chavannes-Renens VD, in 1980, and at Avenches VD, in 1982 (Bolay, unpublished).
- *Cichorium endivia* L.
  Between 1983 and 1992 *P. cryptogea* caused great losses during hothouse cultivation of chicory at Yens, Penthéréaz and Thierrens, VD. The fungus causes a rot of cuttings and roots in hydroponic culture (Varady & Ducrot (1984, 1986, 1988). Temperature and humidity during forced growing of the crop, the presence of soil particles on the roots of the cuttings and the recycling of the nutrient solution create favorable conditions for the development of this rot. The same type of damage was reported from France by Forlot et al. (1966).
  The roots of chicory are contaminated during their growth in the field, but infections are difficult to see at harvest. Despite many checks we found diseased plants only once at St.-Prex VD, in August 1990, in a field which had been repeatedly irrigated during summer time. The losses were reduced by lowering by some degrees Celsius the hothouse temperature and by abandonning the recycling of the nutrient solution which had carried the propagules of the pathogen from one container to the other. Strains of *P. cryptogea* from chicory were also pathogenic to spinach (*Spinacia oleracea* L.), *Callistephus chinensis* (L.) Nees and *Senecio maritima* L.
- In a few isolated cases, the following six plant species were attacked by *P. cryptogea*, causing root and collar rot and subsequent wilting:
  – *Chrysanthemum indicum* L. at Vullierens VD, in 1990,
  – *Dianthus caryophyllus* L. at Geneva in 1986,
  – *Eschscholzia californica* Cham. at Nyon VD, in 1979,
  – *Gypsophilla paniculata* L. at Geneva, in 1982 and at Lullier GE, in 1993,
  – *Petunia × hybrida* Hort. at Loèche VS, in 1980,
  – *Senecio maritima* L. at Nyon VD, in 1984 (Bolay, unpublished)
- *Gerbera jamesonii* Hook
  Collar rot affecting 10 to 30% of plants in greenhouses at Geneva, in 1970 and 1981, at Puplinges GE, in 1980, at Conthey VS, in 1986, and at Yvorne VD, in 1988 (Bolay, unpublished).
- *Ilex aquifolium* L.
  Crown rot of holly at Collonge-Bellerive GE, in 1992 (Bolay, unpublished).

- *Lycopersicon esculentum* Miller
  Decay of some plants in a greenhouse at Marin NE, in 1985, and at Geneva in nutrient solution culture, in 1990 (Bolay, unpublished).
- *Malus domestica* Borkh.
  Root and crown rot on young apple trees grafted on rootstock M9, in three orchards at Etoy, La Chaux and Tannay VD, in 1993 (Bolay 1994).
- *Prunus avium* L.
  Root rot on cherry trees cv. 'Bigarreau de Hedelfingen' grafted on rootstock F 12/1 at Nyon VD, in 1977. From the same trees *P. megasperma* was also isolated (Bolay, unpublished).
- *Solanum tuberosum L.*
  Tuber rot with reddish discoloration of diseased tissue, at Chesalles sur Moudon VD, in 1990 (Gindrat, unpublished).
- *Spinacea oleracea* L.
  Partial decay of a spinach field at Suscevaz near Yverdon VD, in fall 1976. The symptoms, similar to those described by Kröber & Beckmann (1973) appeared after excessive watering of the soil (Bolay, unpublished).
- *Thuja* spp.
  Decay of young trees in a field at Conches GE, in 1960, and at Mannens FR, in 1991 (Bolay, unpublished).

4. 7. *P. drechsleri* Tucker

Res. Bull. Mo. Agric. Exp. Sta. **153:** 188, 1931.

Since 1977 we have isolated regularly two species of *Phytophthora* from roots and collar of stone fruit trees and apple trees grafted on rootstock M9. One of them is *P. megasperma*, the other one, so far unknown on fruit trees in Switzerland, is provisionally named *Phytophthora* "A" (Bolay 1978, 1992a, b). Both species are found in the same orchard, on the same tree and are often isolated from the same bark sample. In vitro, they can be distinguished by their mycelium and the production of oospores, readily formed in *P. megasperma*, lacking in *P.* "A". After several years of observation and in vitro tests with some twenty strains of P. "A" isolated from cherry, plum, apricot, peach and apple trees grafted on M9, we consider this fungus to belong to *P. drechsleri*. Whilst most characteristics of the *P.* "A" strains fit, there is one difference: our strains all stop growing at a temperture of 34 °C. However, their identity has been confirmed by Dr. Hall of CMI, UK.

P. drechsleri is unevenly distributed on all continents (Stamps 1985). In Europe, the fungus was reported from Bulgaria, Cyprus, France, Great Britain, Ireland and Greece. Ribeiro (1978) presents a list of 25 host plant species, among them the genera *Malus* and *Prunus*. Duncan (1990) isolated it from raspberry plants in Great Britain, and Kouyeas & Chitzanidis (1968) found it on almond trees in Greece.

Host plants.

- *Malus domestica* Borkh.
  Isolated in orchards at the following locations from roots and collar of apple trees on M9, showing root and crown rot symptoms: Duillier VD on 'Golden Delicious' (=GD) in 1978; La Chaux VD on GD in 1984, on 'Gala' in 1993; Collex-Bossy GE on GD in 1991, on 'Gala' in 1993; Etoy VD on 'Summerred' in 1991 and 1993; Founex VD on 'Gala' in 1993.
  The symptoms on apple tree were described by Bolay (1992a). Inoculation trials on roots of rootstocks M9, M26 and MM106 clearly showed the pathogenic character of the strains of *P. drechsleri* isolated from apple or stone fruit trees, respectively (Bolay 1992b).
  Attacks by *P. drechsleri* on apple trees were reported from the USA by Matheron et al. (1988). When investigating decaying apple trees in 36 orchards of Arizona the authors isolated 43 times *P. cactorum*, 7 times *P. cambivora*, 3 times *P. drechsleri*, once *P. nicotianae* and twice unidentified *P.* species. In inoculation tests on potted apple seedlings all five species turned out to be pathogenic.
- *Prunus armeniaca* L., *P. avium* L., *P. domestica* L., *P. persica* (L.) Batsch
  The decay of these stone fruit trees, showing crown and root rot, in the region of lake Geneva, are generally caused by *P. megasperma* and *P. drechsleri*, acting together or separately. *P. drechsleri* was isolated from cherry trees grafted on F 12/1 and from prune trees (cv. 'Fellenberg') grafted on Myrobolan, at Nyon VD, in 1977, from apricot trees at Nyon and Prangins VD, in 1977 and 1979, and from peach trees at Prangins, in 1980 (Bolay 1992a).
  Similar symptoms are reported from California on cherry trees grafted on 'Mazzard' and on *Prunus mahaleb* L (Mircetich & Matheron 1976, Mircetich et al. 1976) as well as on almond trees (Mircetich et al. 1974). The fungus is associated with *P. megasperma* and *P. syringae* on almond and with *P. cambivora* on cherry trees. Inoculation trials on roots of rootstocks F 12/1 (cherry), 'Myrobolan' (prune, apricot) and GF-305 (peach) at Changins in 1982 and 1983 showed the high virulence of *P. drechsleri* (Bolay 1992b). In the USA, Wilcox & Mircetich (1985a, b) proved the aggressiveness of the fungus on cherry and *Prunus mahaleb* seedlings.

4. 8. *P. erythroseptica* Pethybridge

Sci. Proc. R. Dublin Soc. NS. **13**: (35) 547–548, 1913.

Pink rot of potato was first described from Ireland, in 1909. In 1913, the causal agent was named *P. erythroseptica* by Pethybridge (1913). According to Stamps (1978b) the pathogen is spread over all regions of the world in which potatoes are cultivated. It also attacks other host species, such as sugar cane, asparagus, tulip, raspberry, pea, vetch and tomato.

Host plants.

- *Solanum tuberosum* L.
  The first cases of potato pink rot in Switzerland were reported by Mayor (1958). They appeared since 1912 in several regions of the canton of Neuchâtel in the vine-growing area, at Bôle, Boudry and in the Val-de-Ruz. Since 1944 this disease was never detected again in this region. Later, it was found on potatoes at Puidoux VD (Sijak & Gindrat 1969).
  Other *P.* spp. isolated from rotten potato tubers are: *P. megasperma* at Crans VD, in 1980, at Changins/Nyon VD, in 1981, and at Billens FR, in 1982 and *P. cryptogea* at Chesalles sur Moudon VD, in 1990. In some of these cases the tubers showed typical pink rot symptoms, in others not. Thus, only the cultivation of the pathogen in pure culture allowed its identification. (Gindrat, unpublished).
- *Rubus idaeus* L.
  Converse & Schwartze (1968) describe a root and stalk base rot of raspberry from the state of Washington which they attribute to *P. erythroseptica*. In Switzerland, all isolations made since 1980 from similar symptoms revealed a *Phytophthora* different from *P. erythroseptica*, rather resembling *P. fragariae* (Bolay & Lauber 1989). Recently, Wilcox et al. (1993) named it *P. fragariae* var. *rubi*.

4. 9. *P. fragariae* Hickman

J. Pomol. **18**: 89–118, 1940.

This species is specific on strawberry plants where it causes a quick and complete necrosis, known as 'red core disease'. It was first reported in Switzerland in 1981 from strawberry fields planted with imported refrigerated plants (Bolay 1982, Fritsche 1982). It can be assumed that the disease had been introduced already at the end of the 1970 decade. From 1982 onwards the disease spread rapidly inspite of phytosanitary controls at the border of all imported strawberry plants. The contamination of some indigenous centers of plant propagation also contributed to the rapid spread of the disease all over the country, except the central Valais, where the very cold winter temperature and the sandy nature of the soil in the Rhone valley limit the survival of the pathogen. The use of appropriate fungicides is reducing the damage and allows the continuation of growing strawberries in the contaminated regions (Bolay et al. 1984; Lauber 1984 a,b; Lauber & Bühlmann 1984; Lauber et al. 1984).

In the annual report 1963–1965 of the Federal Research Station at Lausanne (Rochaix 1966) a strawberry disease is mentioned which was erroneously attributed to *P. fragariae*. In reality the disease reported in summer 1964 from plants imported from France was caused by *P. cactorum*. The name 'red core disease' is ambiguous. It describes a disease characterized by a reddening of the central cylinder of the roots caused by *P. fragariae*, but not the brownish-reddish discoloration of rhizome tissue caused by *P. cactorum*. In order to avoid any confusion, we call the decay caused by *P. fragariae* 'red root rot' and the one caused by *P. cactorum* 'brown core disease'.

Host plants.

- *Fragaria* × *ananassa* Duchesne
  In diseased fields the red root rot is present on all cultivars yielding big fruits.
- *Fragaria vesca* L.
  The disease was never found on wild strawberry plants. In contrast, several clones of four season's strawberries are highly susceptible and therefore used as test plants for detecting the pathogen in the soil or in plant samples (Duncan 1980).

4. 10. *P. fragariae* Hickman var. *rubi* Wilcox et Duncan

Mycol. Res. **97**: 830, 1993.

The first cases of raspberry decay appeared in Switzerland during the 1970 decade (Fritsche 1978, 1980; Lutz et al. 1980; Bolay et al. 1988).

The disease spread during the same period in other European countries: in France (Lefebvre 1977; Chataigneraie 1981; Nourrisseau & Baudry 1987), Great Britain (Montgomerie & Kennedy 1980; Lovelidge 1988) and in Germany (Blank & Graf 1983; Seemüller et al. 1986). The disease could be of American origin, since it was observed already in 1963 at the West coast of the USA (Converse & Schwartze 1968). This type of decay differs from other diseases of the raspberry plant by its extreme virulence. The whole plant, i.e. two years old fertile stalks and the young shoots of the season, die within a few months. The disease is particularly severe in humid, heavy soils (Bolay & Lauber 1989). The symptoms make one think of a vascular disease. Microscopic checks at the shoot base indeed show often mycelia plugging the vessels of the xylem as well as the phloem. Isolations on malt agar media regularly yield fungi of the genera *Fusarium*, mainly *F. oxysporum*, *F. solani* and *F. avenaceum*. Inoculation trials with potted raspberry plants proved the pathogenicity of *F. oxysporum* and *F. avenaceum*, mentioned above (Lutz & Lauber 1981). Since the summer of 1980, isolations were made on Corn Meal Agar Difco. On this substrate, colonies of a *Phytophthora* species, similar to *P. fragariae*, grew, apart from *Fusarium, Cylindrocarpon, Pythium* and *Rhizoctonia* spp. Since then *Phytophthora* sp. was isolated regularly, and oospores were found in the necrotic tissue. The various *Fusarium* spp. were found in dead plant parts even after several months, however, they do not grow out of tissue samples taken at the border of the lesions.

Whilst they prevail in samples from the plains (lake Geneva and Tessin) the *Fusaria* are rarely or not at all isolated from samples from the highlands (Bruson VS, 1100 m). These observations prove the secondary nature of the *Fusaria*. The isolated *Phytophthora* sp. is the primary cause of the disease.

Abroad, several papers published since 1980 describe one or more *Phytophthora* spp. isolated from diseased plants or soil near them. Inoculations of raspberry plants with contaminated soil or pure cultures showed a high pathogenicity of certain strains. Their identity varies depending on the researchers. Converse & Schwartze (1968) in the USA and Montgomerie & Kennedy (1980) in Great Britain report of *P. erythroseptica*. In Germany, Seemüller et al. (1986) identified it as *P. erythroseptica* var. *erythroseptica*, while in Great Britain Duncan et al. (1987) and Duncan & Kennedy (1988) speak of *P. megasperma*. Nourrisseau & Baudry (1987) in France, and Bolay & Lauber (1989) in Switzerland, consider their isolates to be close to *P. fragariae*.

Finally, after having compared a great number of American and European strains Wilcox et al. (1993) concluded that they all belong to *P. fragariae* var. *rubi*.

Host plant.

- *Rubus idaeus* L.
  In Switzerland, the pathogen attacks all cultivars grown in the country. It has so far not been found on other *Rubus* spp. nor on wild raspberries. Treatments of infected fields with metalaxyl or oxadixyl control the disease and allow a normal yield, but do not eliminate the pathogen (Bolay & Ducrot 1989, 1990).

4. 11. *P. infestans* (Montagne) de Bary

J. R. agric. Soc. **12**, Ser. 2: 240, 1876.

This was the first species of the genus identified in Switzerland. Causing late blight of potatoes, it had invaded our country in 1845 (see p. 24–25). Under favorable conditions the sporangia of the pathogen are disseminated by wind over long distances. It overwinters in diseased tubers from which in the following spring plants will develop with the primary foci of late blight.

P. infestans is heterothallic and thus only forms oospores if the compatible sexual partners A1 and A2 meet. Until the early 1980s the two types occurred only in Mexico. In all other countries only the A1 type was present, so that sexual reproduction could not take place. In 1981 Hohl & Iselin (1984) found strains of the type A2 in the region of Zurich. In double cultures with A1 they obtained oospores. Shortly afterwards A2 strains were isolated in Great Britain on blighted tubers imported from Egypt (Shaw et al. 1985). Other types of A2 strains and oospores of *P. infestans* were found in Great Britain and in Wales (Malcolmson 1985; Tantius et al. 1986).

Host plants.

- *Solanum tuberosum* L.
  P. infestans attacks all plant parts of potato: foliage, shoots and tubers. It became quickly the primary potato disease in Switzerland, causing considerable losses in rainy seasons and in fields not or not sufficiently protected by fungicides.
  Up to now chemical control is the only effective way of controlling late blight. Its development was reviewed by Schwinn & Margot (1991). In Switzerland, pioneering work was done by Dufour (1889), Stebler (1910) and Faes (1917). More recently, Terrier (1954), Aebi (1956), Aebi et al. (1956), Staehelin & Trivelli (1953) and Gindrat et al. (1972) have contributed to updating and improving control methods.
- *Lycopersicon esculentum* Miller
  First informations about attack by *P. infestans* on tomatoes in Switzerland were given by Müller-Thurgau et al. (1915) and Faes et al. (1943). In the open field the disease appears towards the end of summer on green fruits which turn brownish. In greenhouse the pathogen also attacks the foliage on autumn crops.

4. 12. *P. megasperma* Drechsler

J. Wash. Acad. Sci. **21**: 535, 1931.

This species is widely distributed in mediterranean and temperate climates where it attacks a large number of host plants (Schwinn 1966; Waterhouse & Waterstone 1966). It can be easily isolated from soil, lakes and streams. Concerning its morphological characters and pathogenic potential, it varies strongly (Hansen & Hamm 1983). Hildebrand (1959) distinguishes two varieties: *P. megasperma var. megasperma* Drechsler, and *P. megasperma var. sojae* Hildebrand.

Host plants.

- *Asparagus officinalis* L.
  In spring 1983 a severe disease occurred in a field of green asparagus at Etoy VD. The shoots rotted and their upper ends bended (Bolay et al. 1991). The symptoms and the characteristics of the isolated pathogen corresponded to the disease caused by *P. megasperma* var. *sojae* in New Zealand and California (Fallon 1982; Fallon & Grogan 1988).
  So far, in Switzerland the disease occurred only in this single field at E toy, where it caused losses of variable severeness during the following years. Finally, the field had to be abandonned for this reason in 1988.
- *Celtis australis* L.
  So far a single case: In 1988 some trees died in the city of Lausanne in a badly drained soil (Bolay, unpublished).
- *Cichorium endivia* L.
  In chicory hothouses, root rot is mostly due to *P. cryptogea*. During checks in 1982 and 1983 at Penthéréaz VD, *P. megasperma* was also isolated from infected roots. (Bolay, unpublished).
- *Daucus carota* L.
  Isolations from rotted carrots during cold storage often revealed *P. megasperma* as the causal agent, such as at Collombey VS in 1982, at Charrat and Saxon VS in 1983 and 1984 and at Anet/Ins BE in 1984. However, damage by this pathogen is much smaller than that caused by other pathogens like *Alternaria, Fusarium, Pythium, Rhizoctonia* and *Sclerotinia* spp., to name only the most frequent ones.
  In 1981 French growers from the department 'Charente Maritime' sent samples of rotten carrots for investigation to Changins. They were all attacked by *P. megasperma*. In this region of France, carrots are overwintered in the field from where they are only digged out as they can be sold on the market. Under these conditions, the pathogen causes heavy losses during mild and rainy winters (Gindrat, Bolay, unpublished).

- *Juniperus* sp.
  Several bushes of creeping juniper showed chlorotic needles and dry branches in spring 1985 at Etoy VD. From necrotic roots and surrounding soil, we isolated several strains of *P. megasperma* (Bolay, unpublished).
- *Malus domestica* Borkh.
  Since 1978 *P. megasperma* has been regularly isolated from roots and crown of apple trees grafted on M9 and showing crown and root rot symptoms. The disease occurs mainly on young trees in the cantons of Vaud and Geneva, such as at Duillier in 1978, Nyon 1981, Etoy and La Chaux in 1984, Etoy, Dully and Gland in 1991 and1993, Russin near Geneva in 1991. From such samples we also isolated *P. drechsleri*, more rarely *P. cambivora* and *P. cryptogea* (Bolay 1992a, 1994).
- *Prunus armeniaca* L., *P. avium* L., *P. domestica* L. and *P. persica* (L.) Batsch
  Since 1977 our attention was drawn to crown and root rot symptoms on stone fruit trees, occurring particularly in regions with heavy, loamy soils in the cantons of VD and GE (Bolay 1992a). *P. megasperma* was isolated from necrotic bark from crown and roots of apricot trees at Nyon and Prangins VD in 1977, from cherry trees at Suscévaz, Nyon, Grens and Prangins VD in 1977, at Versoix in 1979 and at Meyrin GE in 1984, from prune trees in Nyon in 1977 and from peach trees at Nyon in 1982.
  Inoculation trials with roots of three stone fruit rootstocks were performed in 1982 and 1983 at Changins with 15 isolations of *P. megasperma* from various locations. Strains from stone fruit trees were pathogenic on rootstocks F 12/1 of cherry tree, GF 305 of peach tree and on 'Myrobolan' of apricot and prune tree. Those isolated from apple trees on rootstock M9 were pathogenic on F 12/1, but weakly pathogenic on 'Myrobolan'. Those isolated from vegetables (carrot, spinach, chicory) gave very variable results; lesions were heavy on F 12/1, weak to nil on Myrobolan. Strains from potato tubers were avirulent (Bolay1992b).
- *Solanum tuberosum* L.
  Rotten tubers were collected at Crans-près-Céligny and at Changins VD in 1980 and 1982 as well as at Billens FR in 1982 (Gindrat, Bolay, unpublished).
- *Spinacia oleracea* L.
  In 1977, we also isolated *P. megasperma* from the crown of some chlorotic plants in a field partially destroyed by *P. cryptogea* at Suscévaz VD (Gindrat, Bolay, unpublished).

4.13. *P. nicotianae* van Breda de Haan

Meded. Lands Plantentuin **15**: 57, 1896.
Syn (after Hall 1993):
P. melongenae Sawada
P. parasitica Dastur
P. nicotianae var. *nicotianae* (van Breda de Haan) Waterhouse
P. nicotianae var. *parasitica* (Dastur) Waterhouse
P. parasitica var. *nicotianae* (van Breda de Haan) Tucker
P. parasitica var. *parasitica* (Dastur) Tucker
P. parasitica var. *rhei* Godfrey
P. tabaci Sawada
P. terrestris Sherbakoff.

This species has an unusually long list of synonyma. In their revision, Ho & Jong (1989) considered *P. parasitica* as synonymous to *P. nicotianae*. Hall (1993) compared morphological, physiological and biochemical features of more than 80 isolates from different host plants and all continents. He came to the conclusion that they all belong to one and the same species, i.e. *P. nicotianae*.

This species is found above all in tropical and mediterranean climate. In Switzerland, it occurs mainly on plants in greenhouses. However, some years ago we isolated it from fallen apples in orchards. For details see Table 2 (p. 54).

Host plants.

- *Carica pentagona* Heilb.
  At the end of the 1980 decade, some growers in Valais became interested in the cultivation under protection of the melon tree. Among the pathogens identified on this plant species was *P. nicotianae*, causing crown and stem rot (Bolay 1990).
- *Lycopersicon esculentum* Miller
  Local lesions on the roots of glasshouse tomatoes at Troinex GE occurred in 1980, at Chabray FR in 1983, at Lonay VD and Geneva in 1984, at Yens, St-Prex and Constantine VD in 1986 (Bolay, Corbaz, Gindrat, unpublished). In Valais, Gindrat (1967) isolated from necrotic roots of field grown tomatoes fungi belonging to the genera *Pythium* and *Phytophthora* without identifying their species.
- *Saintpaulia ionantha* Wendl.
  In 1986, crown and leaf stalk rot occurred on young plants grown at Nyon and Borex VD (Bolay, unpublished).

- *Sinningia speciosa* (Lodd.) Benth. and Kook
  In 1985, crown and leaf stalk rot occurred on young gloxinias in a greenhouse at Geneva (Bolay, unpublished).

4.14. *P. porri* Foister

Trans. Proc. bot. Soc. Edinb. **30**: 277–278, 1931.

This species grows at low temperatures. Growing actively still at 5 °C, symptoms show up mainly during winter time in open fields: on leek in Scotland (Foister 1929, 1931), in the Netherlands (van Hoof 1959) and Scandinavia (Semb 1969; Nilsson 1970), on seeded onions in Great Britain (Griffin & Jones 1977) and on winter lettuce in South Australia (Sitepu & Bumbieris 1981). In addition the pathogen occurs in cold storage on white cabbage in Great Britain (Geeson 1976) and carrot in Canada (Ho 1983).

Host plants.

- *Allium porrum* L.
  First attacks in Switzerland were observed on leek in 1964 in several fields between Morges and Nyon VD (Rochaix 1966). Later, other cases were found at Lausanne in 1985, at Geneva in 1982 and at Rennaz VD in 1984. The symptoms are white paper-like spots on the foliage. In Dutch they are called "Papiervlekkenziekte" (van Bakel 1964) and in Swedish "Pappersfläcksjuka" (Nilsson 1970). In Switzerland, the damage was never significant and most times the disease remained undetected.
- *Allium cepa* L.
  Since the 1980s growers at La Côte VD began to grow overwintering onions, starting from seed sown late summer and harvested in late spring of the following year. In April 1983 several of these fields showed disease symptoms in the region of Nyon VD. In the most humid parts of the fields, the plants were dead. Leaves which had developed before winter were necrotic in their lower part. The necrotic parts looked whitish, curved and bended. They occurred on one third to three quarters of the leaves. From necrotic tissue, *P. porri* was isolated (Bolay, unpublished). The disease reappeared in the same region, at Grens, in 1984, and at Trélex, in 1990. It was described from Great Britain by Griffin & Jones (1977) and from the Netherlands by Tichelaar & van Kesteren (1967).

4.15. *P. syringae* (Klebahn) Klebahn

Krankh. d. Flieders. Verlag Gebr. Bornträger, Berlin 1909. 75 pp.
Syn.: *Phloeophthora syringae* Klebahn.

Klebahn (1909) described the pathogen as causal agent of flower and bark rot of lilac (*Syringa vulgaris* L.). Later it was realized that the same species attacks citrus in Mediterranean countries (Kouyeas and Chitzanidis 1968; Laviola et al. 1990; Ricci et al. 1990). *P. syringae* is well adapted to low temperatures. At 2 °C, it causes a serious fruit rot of apples and pears in cold storage. Its optimum is at 20 °C and the fungus is killed at 27 °C (Sewell & Wilson 1964; Bolay 1977). In Switzerland, *P. syringae* is frequent in orchard soils. It is responsible for the rotting of fallen apples and pears. However, it was ignored or mixed up with *P. cactorum* for a long time, which causes the same symptoms. From fallen fruits *P. cactorum* can be isolated between June and early September, and *P. syringae* only towards the end of the season, when the lowering temperature becomes critical for *P. cactorum*.

Host plants.

- *Malus domestica* Borkh.

  In 1975 a severe rot was reported on 'Golden Delicious' apples, harvested in the lake Geneva region and stored at 2 °C under controlled atmosphere (Bolay 1977). The heaviest losses (5–25%) occurred on fruit from orchards in the canton of GE and in La Côte VD. The total loss in cold storage of the 1974 production of 'Golden Delicious' sold by the Fruit Cooperative Lémanique was 1,5%, meaning some 150 000 Swiss Francs. The fruit lots originated from 43 growers. Attack was below 5% in 23 lots, 5–10% in 10 lots, and over 10% in 10 lots.

  This rot did not show up the next winter. During the conservation period 1976–1977, however, several cases were reported, located in the same orchards where it had appeared before. Losses were 0,4%, representing 30 000 sFR. In some lots up to 25% and even 50% of the fruits were attacked. In Vaud, outside the lake Geneva region, the disease was first observed at Mathod near Orbe and at Ollon. Three light cases were detected in Valais, at Conthey and Saxon. The disease occurs mainly on 'Golden Delicious', but also on 'Jonathan' and 'Maigold'.

  Fruits are infected in the orchard shortly before harvest, by soil particles containing propagules of the pathogen during heavy rains or during overhead irrigation. Fruits and boxes are also contaminated with soil particles from the tractor wheels during transport from the orchard to the storage. Growing grass on the soil of orchards was an effective way of controlling the disease. Since 1980 the losses in storage due to *P. syringae* practically disappeared.

Apart from these cases in Western Switzerland, the storage fruit rot, caused by *P. syringae*, is rare. It is known from the British Isles, where it caused damage in 1920 in Ireland (Lafferty & Pethybridge 1922), and in England and in Wales in 1929 (Ogilvie 1931). More recently, this rot caused significant damage in the South of England in 1973 and 1974 (Upstone 1974; Lovelidge 1974).

In addition, *P. syringae* causes collar rot on apple and pear trees in the Netherlands (Roosje 1962) and in Great Britain (Sewell & Wilson 1963, 1964). In Switzerland up to now *P. syringae* has never shown up in this context. In inoculation trials, however, with apple twigs and roots of several different rootstocks, the fungus turned out to be clearly virulent (Bolay 1992b).

- *Pyrus communis* L.

  Attacks by *P. syringae* on pear fruits in the orchard or in storage are rare, despite their high susceptibility. This is due to the fact that pears are harvested earlier than apples, i.e. during a period when the temperature is still too high for the development of *P. syringae.*
- *Prunus avium* L., *Rosa canina* L.

  On both hosts, *P. syringae* attacks nursery material during cold storage. Damages were observed at Yvorne VD in 1983 on rootstocks of roses (*Rosa canina* L), imported from Tunisia, and at Cheseaux-Noréaz VD in 1993, on cherry scions. In both cases the pathogen caused a bark rot leading sometimes to the death of the cherry scions or making rose rootstocks useless for grafting (Bolay, unpublished).

5. List of host plants of *Phytophthora* species

This list is arranged in alphabetic order of the botanical families and species. For every host plant we indicate the canton(s), in which the respective pathogens were found.

Aceraceae

Acer platanoides L.
P. citricola (GE)

Apiaceae

Eryngium alpinum L.
P. cactorum (VS)
Daucus carota L.
P. megasperma (VD, VS)

Aquifoliaceae

Ilex aquifolium L.
From soil with apple bait:
P. citricola (GE), P. cryptogea (GE)
P. cryptogea (GE), P. drechsleri (GE),
P. megasperma (GE), P. syringae (GE)

Asteraceae

Callistephus chinensis (L.) Nees
P. cactorum (ZH), P. cryptogea (VD)
Cichorium endivia L.
P. cryptogea (VD), P. megasperma (VD)
Chrysanthemum indicum L.
P. cryptogea (VD)
Gerbera jamesonii Hook
P. cryptogea (GE, VD, VS)
Senecio maritima L.
P. cryptogea (VD)

Begoniaceae

Begonia × tuberhybrida Voss
P. cinnamomi (GE)

Buxaceae

Buxus sempervirens L.
From soil with apple bait:
P. citricola (GE)

Caricaceae

Carica pentagona Heilb.
P. nicotianae (VS)

Caryophyllaceae

Dianthus caryophyllus L.
P. cactorum (ZH), P. cryptogea (GE)
Gypsophila paniculata L.
P. cryptogea (GE)

Chenopodiaceae

Spinacia oleracea L.
P. cryptogea (VD), P. megasperma (VD)

Cupressaceae

Chamaecyparis spp.
P. cambivora (VD), P. cinnamomi (GE), P. citricola (VD), P. citrophthora (VD), P. cryptogea (VD)
Cupressus spp.
P. citrophthora (VD)
Juniperus spp.
P. megasperma (VD)
Thuja spp.
P. citricola (FR), P. cryptogea (FR)

Cucurbitaceae

Cucurbita pepo L.
P. citrophthora (TI)

Ericaceae

Arbutus unedo L.
P. citrophthora (TI)
Erica carnea L.
P. cinnamomi (VD)
Rhododendron spp.
P. cinnamomi (VD), P. citrophthora (VD)

Fabaceae

Glycine max (L.) Merr.
P. cactorum (VD)

Fagaceae

Castanea sativa Miller
P. cactorum (VS), P. cambivora (GE, TI), P. citricola (VS)
From soil with apple bait:
P. cactorum (TI), P. cambivora (GE), P. citricola (VS)
Fagus silvatica L.
P. cactorum (ZH), P. cambivora (VD)

Gesneriaceae

Saintpaulia ionantha Wendl.
P. nicotianae (VD)
Sinningia speciosa (Lodd.) Benth. & Kook
P. nicotianae (GE)

Hippocastanaceae

Aesculus hippocastanum L.
P. cactorum (GE, VD)

Liliaceae

Allium ascalonicum L.
P. cactorum (VD)
Allium cepa L.
P. porri (VD)
Allium porrum L.
P. porri (GE, VD)
Asparagus officinalis L.
P. megasperma (VD)

Myrtaceae

Myrtus communis L.
P. cinnamomi (TI)

Papaveraceae

Eschscholtzia californica Cham.
P. cactorum (VD), P. cryptogea (VD)

Rosaceae

Cydonia oblonga Miller
P. cactorum (FR)
Fragaria vesca L.
P. cactorum (CH), P. fragariae (VD, ZH)
Fragaria × ananassa Duchesne
P. cactorum (CH), P. citrophthora (VS), P. fragariae (AG, BE, FR, GE, LU, NE, SO, VD)
Malus domestica Borkh.
From fruits: P. cactorum (AG, BL, GE, GR, SH, TI, VD, VS, ZH), P. citricola (BL, SO), P. syringae (GE, VD, VS)
From rootstocks, except M9 and M27: P. cactorum (CH), P. citricola (VD)
From rootstock M9: P. cambivora (GE, VD), P. cryptogea (VD), P. drechsleri (GE, VD), P. megasperma (VD)
From soil with apple bait: P. cactorum (BL, GE, SO, TI, VD, VS), P. cambivora (VD), P. cinnamomi (SO), P. citricola (BL, SO, VD), P. megasperma var. *megasperma (BL, SO, VD), P. syringae (VD)*
Prunus armeniaca L.
From apricots: P. cactorum (VD, VS, ZH)
From roots: P. drechsleri (VD), P. megasperma (VD)
Prunus avium L.
From roots: P. cryptogea (VD), P. drechsleri (VD), P. megasperma (VD).
From twigs of scions: P. syringae (VD)
Prunus domestica L.
From roots: P. cactorum (NE), P. drechsleri (VD), P. megasperma (VD)
Prunus laurocerasus L.
From collar: P. cambivora (TI)
Prunus persica (L.) Batsch
From twigs of seedlings: P. cactorum (TI)
From roots: P. drechsleri (VD), P. megasperma (VD)
Pyrus communis L.
From pears: P. cactorum (GE, TI, VD, VS, ZH), P. syringae (GE, VD, VS)
From collar: P. cactorum (VD)

From soil with appple bait:
P. cactorum (GE, TI, VD, VS),
P. cambivora (VD), P. citricola (VD),
P. megasperma (VD), P. syringae (VD)
Rosa canina L.
P. syringae (VD)
Rubus idaeus L.
P. citricola (VD), P. fragariae var. *rubi (CH)*

Rutaceae

Citrus sp.
P. citricola (TI)

Saxifragaceae

Ribes sanguineum Pursh
P. citrophthora (VD)
Ribes uva-crispa L.
P. cactorum (ZH)

Scrophulariaceae

Calceolaria rugosa Ruiz et Pav.
P. cactorum (ZH)

Solanaceae

Lycopersicon esculentum Miller
P. cryptogea (NE, GE), P. infestans (CH), P. nicotianae (FR, GE, VD)
Petunia × hybrida hort.
P. cryptogea (VS)
Solanum tuberosum L.
P. cryptogea (VD), P. erythroseptica (NE, VD), P. infestans (CH),
P. megasperma (FR, VD)

Taxaceae

Taxus baccata L.
P. cinnamomi (GE)
From soil with apple bait: P. cactorum (GE), P. citricola (GE),
P. cryptogea (GE), P. megasperma (GE)

Ulmaceae

Celtis australis L.
P. megasperma (VD)

Violaceae

Viola wittrockiana Gams
P. cactorum (FR, VD, VS)

6. List of host plants by *Phytophthora* species

P. cactorum: *Aesculus hippocastanum, Allium ascalonicum, Calceolaria rugosa, Callistephus chinensis, Castanea sativa, Cydonia oblonga, Dianthus caryophyllus, Eryngium alpinum, Eschscholzia californica, Fagus sylvatica, Fragaria vesca, Fragaria × ananassa, Glycine max, Malus domestica, Prunus armeniaca, Prunus domestica, Prunus persica, Pyrus communis, Ribes uva-crispa, Viola × wittrockiana.*

P. cambivora: *Castanea sativa, Chamaecyparis* spp., *Fagus sylvatica, Malus domestica, Prunus laurocerasus.*

P. cinnamomi: *Begonia tuberhybrida, Chamaecyparis lawsoniana, Erica carnea, Myrtus communis, Rhododendron* spp., *Taxus baccata.*

P. citricola: *Acer platanoides, Chamaecyparis lawsoniana, Citrus* sp., *Ilex aquifolium, Malus domestica, Rubus idaeus, Thuja occidentalis.*

P. citrophthora: *Arbutus unedo, Chamaecyparis* sp., *Cucurbita pepo, Cupressus* sp., *Fragaria × ananassa, Rhododendron* sp., *Ribes sanguineum.*

P. cryptogea: *Callistephus chinensis, Chamaecyparis* sp., *Cichorium endivia, Chrysanthemum indicum, Dianthus caryophyllus, Eschscholzia californica, Gerbera jamesonii, Gypsophila paniculata, Ilex aquifolium, Lycopersicon esculentum, Malus domestica, Petunia hybrida, Prunus avium, Senecio maritima, Solanum tuberosum, Spinacia oleracea, Thuja* sp.

P. drechsleri: *Malus domestica, Prunus armeniaca, Prunus avium, Prunus domestica, Prunus persica.*

P. erythroseptica: *Solanum tuberosum.*

P. fragariae: *Fragaria × ananassa, Fragaria vesca.*

P. fragariae var. rubi: *Rubus idaeus.*

P. infestans: *Lycopersicon esculentum, Solanum tuberosum.*

P. megasperma: *Asparagus officinalis, Celtis australis, Cichorium endivia, Daucus carota, Juniperus* sp., *Malus domestica, Prunus armeniaca, Prunus avium, Prunus domestica, Prunus persica, Solanum tuberosum, Spinacia oleracea.*

P. nicotianae: *Carica pentagona, Lycopersicon esculentum, Saintpaulia ionantha, Sinningia speciosa.*

P. porri: *Allium cepa, Allium porrum.*

P. syringae: *Malus domestica, Prunus avium, Pyrus communis, Rosa canina.*

7. Concluding remarks for parts 4–6

The 15 species and varieties of *Phytophthora* found in Switzerland until end of 1995 have 57 host plants belonging to 27 families. The number of host plant species per *Phytophthora* sp. varies between 19 and 1, as shown here: *P. cactorum* (19), *P. cryptogea* (17), *P. megasperma* (12), *P. citricola* (7), *P. citrophthora (7), P. cinnamomi* (6), *P. cambivora* (5), *P. drechsleri* (5), *P. nicotianae* (4), *P. syringae* (4), *P. fragariae* (2), *P. infestans* (2), *P. porri* (2), *P. erythroseptica* (1), *P. fragariae* var. *rubi* (1).

It is difficult to establish a correlation between the *Phytophthora* species and the families and genera of host plants. Most *Phytophthora* spp. are parasites of host plants belonging to various different families. *P. fragaria* and *P. fragariae* var. *rubi,* however, are only found on *Rosaceae* and *P. infestans* only on *Solanaceae.* This is confirmed by reports of other countries.

P. porri was found in Switzerland only on the genus *Allium*, but abroad it also causes damages on cabbage, lettuce, carotte, tulip and campanula (Geeson, 1976; Sitepu & Bumbieris 1981; Ho 1983; Stamps 1978c).

Likewise *P. erythroseptica*, which here infects only potatoes, was reported by Stamps 1978b) on some ten vegetable and ornamental species. *P. cambivora*, *P. citricola*, *P. drechsleri*, *P. fragariae* var. *rubi* and *P. syringae* attack only shrubs and trees, while *P. erythroseptica*, *P. fragaria*, *P. infestans* and *P. porri* are found only on herbaceous plants.

Most cases of *Phytophthora* diseases in Switzerland are reported from the French speaking part (Romandie) of the country, mainly in the Lake Geneva basin (comprising the cantons GE, VD, VS) and in the Tessin (TI). This concentration of reported cases can be explained first of all by the fact that both regions belong to the area served by the Mycological Department of the Swiss Federal Research Station for agriculture at Changins near Nyon (VD), where the first author, with his special interest in these pathogens, worked. In many other parts of Switzerland the climatic and soil conditions are similarly favorable for the development of *Phytophthora* spp., but the reported cases are rare, except for *P. infestans*. As already said by Tsao (1990), *Phytophthora* spp. are only found where one looks for them. This will be shown in detail in the following chapter 8.

8. Studies on the ecology of *Phytophthora* species in Swiss soils

Most *Phytophthora* species are soil-borne pathogens. It is largely accepted that their majority belongs to the group of soil invaders, i.e. the soil is acting as a reservoir of their inoculum. By way of their dormant structures, i.e. oospores, chlamydospores and encysted zoospores, respectively, they can survive in this substrate for a long time in the absence of suitable host plants or growing conditions (for literature see Waterhouse & Waterston 1964; 1966 b, c, d, Zentmyer & Erwin 1970, Stamps 1978a, b, c, Gregory 1983, Malajczuk 1983, Mitchell & Kannwischer-Mitchell 1983, Weste 1983, Stamps 1985, Coffey 1991). Some species also show active saprophytic growth in the soil. For example, Zentmyer (1980), describes *P. cinnamomi* as a competitive saprophytic soil colonizer. On the other hand, *P. cactorum* and *P. nicotianae* apparently behave rather as typical soil invaders with very limited ability for active growth (for literature see Gisi 1983, Jeffers & Aldwinckle 1988).

Most studies on the distribution, population dynamics and survival of *Phytophthora* spp. in cultivated soils were performed in connection with the occurrence of diseases caused by them. There is a wealth of information showing their survival over many years in soils of diseased orchards. However, there are only few publications on their presence in natural soils in the absence of apparent diseases or in natural habitats (Hendrix & Campbell 1970, Kröber 1980, Jeffers & Aldwinckle 1988, Dilantha Fernando & Linderman 1993).

The objective of our investigations was to study their occurrence

- in the presence and absence of host plants on cultivated land (field crops, orchards),
- in correlation with altitude,
- depending on soil type,
- in natural habitats (woods, grassland and river banks).

These studies were carried out by the second author between 1970 and 1990 assisted by Heide Dahmen, and in the diploma (= 'masters') theses by Ernst (1984) and Jaunin (1985) under his supervision.

8. 1. Methods for isolation from soil

During several years, starting in 1966, naturally infected fallen apples were collected in orchards in the main apple-growing regions of Switzerland. From the lesions, tissue samples were transferred to bean meal agar for identification of the causal pathogen.

All systematic studies were carried out using the apple baiting technique, at first in the field in undisturbed soils, then in trays in climate chambers with soil samples taken from the field (Schwinn 1961). Since the success rate was unsatisfactory in many cases, we studied various alternative methods and eventually favored a modification of the method described by Jeffers & Aldwinkle (1984): we used surface sterilized small apples instead of apple cotyledons. The fruits with their stalk end up were half-covered with water during the phase of incubation in small glass dishes with the soil sample. After 5–11 days lesions were visible from which *Phytophthora* spp. could easily be isolated on V8 agar (amended with 50 ppm Penicillin and 50 ppm Polymixin B sulfate) when the precautions as described on p. 26–27 were followed. With this method we achieved by far the highest success rate, i.e. 60%.

Species identification was done on the basis of the keys quoted on p. 27.

In addition, the identity of critical strains was confirmed by the Commonwealth Mycological Institute, UK.

8. 2. Results

8. 2. 1. Isolation of *Phytophthora* spp. from naturally infected apples

Samples of 5–6 naturally infected fallen apples each were collected during several years between June to September in 33 apple orchards in the cantons of Baselland, Aargau, Wallis, Graubünden (Upper Rhine Valley and Engadin), Emmental, Lake Geneva, and Schaffhausen. Isolations from the lesions yielded the results shown in Table 2.

Table 2: ***Phytophthora*** **spp. isolated from samples of naturally infected apples.**

Total sample number	33	100%
Samples with *P.* spp. of which	30	90%
P. cactorum	23	77%
P. citricola	3	10%
P. nicotianae	2	6%
P. erythroseptica var. *erythroseptica*	1	3%
P. megasperma var. *megasperma*	1	3%

The table shows a high rate of *Phytophthora* infections, the presence of five different species and an apparently wide distribution of *P. cactorum* in orchards with trees which showed no sign and had no history of collar, crown or fruit rot by these pathogens. Unexpectedly, we isolated in 2 samples from one site *P. nicotianae* and at one site *P. erythroseptica* and *P. megasperma*, respectively, from these apples.

It is worth mentioning that *Phytophthora* spp. were not only present in regions of low altitude (Mittelland), but also in more elevated regions, such as the Upper Rhine Valley (ca. 700 m) and, above all, in the Engadin (1500m), an area with very cold winter temperatures (–15 to –20 °C). At the latter site the fruits were collected under single apple trees in house gardens, since there is no commercial apple growing at this altitude in Switzerland.

Of course the results of these preliminary studies are of limited value only since the samples were taken arbitrarily, depending on the presence of naturally infested fallen fruits at the time of the visit. It indicates, however, the broad occurrence of *Phytophthora* spp. in various regions of the country. The following studies were done more systematically and focused on various different ecological aspects.

8. 2. 2. Occurrence of *Phytophthora* spp. in soils at different altitudes

This study was done in the Guldental Valley in the Swiss Jura mountains.In June, apple baits were placed superficially in the soil of natural meadows without history of any fruit trees at 9 different sites from 710 to 1050 m elevation. They were inspected several times and recollected within 20 to 30 days of incubation. Isolations on agar plates from lesions on the fruits revealed *P. cactorum* at 6 out of the 9 sites, up to an altitude of 1010 m (table 3). No other species was isolated from these samples.

Table 3: Occurrence of *Phytophthora* spp. in soil at different altitudes.

Site number	Altitude (m a.s.l.)	Result
1	710	*P. cactorum*
2	750	*P. cactorum*
3	790	*P. cactorum*
4	800	none
5	800	none
6	860	*P. cactorum*
7	950	*P. cactorum*
8	1010	*P. cactorum*
9	1050	none

8. 2. 3. Occurrence of *Phytophthora* spp. in the region of Basle depending on altitude, soil type, presence of host plants and type of land use

The results presented here were obtained in two diploma theses, performed by Ernst (1984) and Jaunin (1985). In these studies, the modified apple baiting technique was used, as described on p. 53. The sampling sites were located West of Basle in the Swiss Jura and its foothills, on a surface of 45 km^2 ranging from 250 to 1050 m above sea-level. The land uses at the sampling sites were:

- grassland with single standard apple, cherry, pear, plum and walnut trees, free of any signs or history of *Phytophthora* attack,
- one commercial orchard with dwarf apple and pear trees, (and single cherry, peach and plum trees), with no signs or history of *Phytophthora* attack,
- meadows and pastures (without fruit trees),
- arable land (with maize, rapeseed, wheat)
- broadleaf woodland and spruce forests,
- the banks of the two small streams, Birs and Birsig (leading to the Rhine river in Basle), respectively.

A total of 161 soil samples was taken during the period of May–June and September–November, respectively. Each sample consisted of 3 subsamples taken within ca.1 qm in the upper 20 cm of the soil, and carefully mixed. From 92 of them, i.e. 57%, a total of 6 different *Phytophthora* spp. was isolated. The occurrence of the various *Phytophthora* spp. at the different sampling sites is shown in table 4.

Table 4: Occurrence of *Phytophthora* spp. in various habitats.

Site Species	Stream banks	Grass-land/ trees*	Orch-ard**	Arable land+	Past-ure	Woods/ Forest	Total	Rank-ing of species
Total °/positive	32/21	74/45	22/16	10/4	8/2	15/5	161/93	
of which								
P. cactorum	1	21	3	1	1	5	32	2
P. cinnamomi	0	1	0	0	0	0	1	6
P. citricola	11	22	11	0	0	0	44	1
P. cryptogea	3	1	2	2	0	0	8	3
P. drechsleri	6	0	0	0	0	0	6	4
P. megasperma var. *megasperma*	0	0	0	1	1	0	2	5

° = Total number of sampling sites
* = Permanent grassland with single standard (high raising) trees (apple, pear, cherry, plum, walnut), samples taken under canopy or near trees
** = Commercial orchard with dwarf trees (apple and pear; single cherry, peach, plum trees), soil covered by grass (mulch). Samples taken under canopy or between rows
\+ = Arable land planted with maize, rape, wheat, or idle, respectively

Among the six species found, *P. citricola* is largely dominating, not only in apple orchards but also on stream banks. In contrast, it was never isolated from soil of the other habitats.

The second most frequent species is *P. cactorum*. It was isolated from soil of all habitats, mainly in the vicinity of fruit trees, but in addition in a pasture without fruit trees, at a stream bank, in arable land and at 4 sites in natural woods. All in all, it shows the broadest distribution.

The next species in frequency is *P. cryptogea*. It was found at stream banks, under fruit trees as well as in arable soils. *P. drechsleri* was found at 6 sites, all on stream banks.

P. megasperma var. *megasperma* was isolated once from a pasture (at 750 m) and once from an idle field near the Birs stream. Surprisingly, we isolated at one grassland/tree site (Witterswil) *P. cinnamomi*, a species so far not reported from outdoors in Switzerland.

More details about the sampling sites, including their elevation and soil type, and the relative success of isolation of *Phytophthora* spp. are presented in Table 5. In confirmation of the earlier findings, the fungi occurred across the whole range of altitudes.

Table 5: Occurrence of *Phytophthora* spp. depending on land use, altitude, and soil type.

Site/altitude/ soil type	Number° T/pos/%	*P.cac-torum*	*P. cinn-amomi*	*P. ci-tricola*	*P. cryp-togea*	*P. drechs-leri*	*P. mega-sperma*
Stream banks 250 m Sand, gravel	32/21/65	1	0	11	3	6	0
Grassland + trees I 500-620 m Brown earth*							
Under treetop	7/ 6/ 85	6	0	0	0	0	0
Between trees	3/ 1/ 33	1	0	0	0	0	0
*Grassland + trees II** 500-850 m Brown earth/loess/gley*							
Under canopy	25/19/76	6	0	13	0	0	0
Between trees	6/ 0/ 0	0	0	0	0	0	0
*Grassland + trees *** 350-500 m Brown earth, rendzina*							
Under canopy	23/17/74	8	1	7	1	0	0
Between trees	10/ 2/20	0	0	2	0	0	0
Orchard+ 400 m Brown earth/ loess							
Under canopy	17/14/82	3	0	9	2	0	0
Between rows	5/ 2/40	0	0	2	0	0	0
Arable land 250 m (stream) 350-400 m Brown earth/ rendzina	4/ 3/75 6/ 1/17	1 0	0 0	0 0	1 1	0 0	1 0
Pastures 400-750 m Brown earth, Pseudogley	8/ 2/25	1	0	0	0	0	1
Woods/forest 400-800 m Brown earth, rendzina, gley, loess	15/ 5/33	5	0	0	0	0	0

° : T= total number of isolations, pos = isolations yielding *Phytophthora* spp., % = percentage of positive isolations.
* : at Blauen BL, grassland with standard trees
** : at Hofstetten SO, dito
*** : at Witterswil SO, dito
\+ : at Pfeffingen BL

In grassland and in the orchard *Phytophthora* spp. were isolated much more frequently from soil samples taken under the tree canopy than from those outside this zone, i.e. between trees or tree rows, respectively. This underlines the role of fallen fruits (apples, cherries, peaches, pears) as hosts for the fungi during their soil phase. In pastures and in woodland the success rate of isolations was as low as outside the tree canopy in grassland/orchard.

In a preliminary study at Tegerfelden AG, we checked the influence of various soil types (Rendzina, brown earth, gley) on the occurrence of *Phytophthora* spp. We did, however, not observe any correlation between the two factors (Data not shown).

In his thesis Ernst (1984) studied this factor again. As shown in Table 5, the soil types, ranging from sand to brown earth, rendzina, sandy loam, loess and pseudogley, had no influence on the occurrence of *Phytophthora* spp. The same holds true for the pH, which, in these studies ranged from 4,5 to 7,5 (data not shown).

In addition to the above sites, we sampled soils from the banks of the streams Birs and Birsig during two consecutive years. The 27 sampling sites stretched over a distance of 14 km (Birs) and 9 km (Birsig), respectively. They were located in a zone which was temporarily flooded and where the soil was completely sandy. As shown in Table 6, we isolated four different *Phytophthora* spp. from 17 sites with success rates almost as high as in the orchards (63 vs. 73%).

Table 6: Sampling sites and results along the streams Birs (a) and Birsig (b). First line: sampling site numbers; second line: *Phytophthora* sp. isolated.

(a) Birs stream; distance between site 1 and 17 = 14 km.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
B	A	B	–	–	A	A	A	A C	C	–	D	A	A	–	–	–

b) Birsig stream; distance between site 1 and 10 = 9 km.

1	2	3	4	5	6	7	8	9	10
A C	C	–	A	–	–	–	B C	A	A C

– = negative sample A = *P. citricola* B = *P. cryptogea*
C = *P. drechsleri* D = *P. cactorum*

Also in this environment, *P. citricola* was the most widely distributed species (11 findings). It was isolated over a distance of 10 km along the Birs and 9 km along the Birsig stream. In contrast to most of the other biotopes investigated (see Tab. 5), *P. cactorum* was isolated only once on the banks of the Birs stream, whereas *P. drechsleri* (5 times) and *P. cryptogea* (3 times) occurred here quite frequently at both streams.

8. 3. Discussion

The results of our ecological studies show a wide distribution of *Phytophthora* spp. in a broad range of biotopes. In contrast to the majority of publications in which their occurrence was studied in connection with diseases caused by them, our studies were done in a region without history of any *Phytophthora* diseases (except *P. infestans* which was not included in our studies).

With regard to their presence in the soil of fields or orchards with their respective host plants they confirm the numerous earlier findings (for literature see p. 52).

In fallen apples, as expected, *P. cactorum* was the dominating species (Tab 2). In contrast, the presence of *P. nicotianae* and *P. erythroseptica* var. *erythroseptica* was unexpected, since apple so far has not been described as their natural host (Hall 1994, Stamps 1978b). The fact that we never isolated *P. syringae* from fallen apples or soil, respectively, can be explained by two factors:

1) the climatic conditions during our sampling period in the field, i.e. May to September, during which the fungus is quiescent in soil and, thus, difficult to isolate (Harris 1979),
2) the incubation temperature during the baiting period (for details see p. 53) which was too high for this species.

For the first time we report the presence and survival of *Phytophthora cactorum* in soils of mountainous areas. Whereas in the Engadin it had fallen apples as hosts, in the Jura we isolated it from soil samples from a pasture without history of cultivated host plants. In our studies in the region of Basle (Tab. 5) we isolated the fungus from soils of genuine broadleaf and conifer (spruce) forests with scarce or no annual understory. It was isolated from forest soils in the absence of diseases in the Southeastern United States (Campbell & Hendrix 1967), in New York (Jeffers & Aldwinckle 1988) and in Wisconsin (Darmono et al. 1991). To our knowledge it was not found in Europe in forest soils before. In contrast, it was reported as the cause of a seedling blight of *Fagus sylvatica* in nurseries from Germany, Switzerland and other European countries (for literature see Nienhaus 1960). Its occurrence in our genuine forest habitats suggests it to be indigenous in the region of Basle.

The other *Phytophthora* sp. isolated from undisturbed forest soils in the USA is *P. citricola* (Drilias 1989). We did, however, not isolate it from our soils of this origin. This is somewhat surprising, because overall it was the most frequent species in our studies (Table 4). It occurred mainly in soils under the canopy of fruit trees in grassland, much less between tree rows and not at all in arable land.

As the first record for Switzerland, we isolated *P. megasperma* var. *megasperma* from soil of permanent grassland and an idle field in the absence of apparent host plants. Under similar conditions, it was isolated in Germany from soil of an apple orchard by Schwinn (1966). From these findings it can be concluded that also this species can survive in a passive stage in soil.

This is the first report on the occurrence of *P. citricola, P. cryptogea* and *P. drechsleri* in banks near or at the water level of streams (Table 6) in the absence of any potential host plants. The fact that they were isolated from 16 out of 27 sampling sites along the streams stretching over a considerable distance indicates that they were transported with the water flow. The very sandy nature of the soil and the lack of nutrients certainly do not allow an active growth of the fungi. Thus it can be assumed that they survived here in host plant debris as mycelium or in a dormant stage, probably as oospores. The latter are known to be the structures with the highest survival potential (Stack & Millar 1985, Malajczuk 1983). Chlamydospores or sporangia also can survive in decaying plant tissue or in the soil for a considerable period of time (for literature see Zentmyer & Erwin 1970, Coffey 1991). Other *Phytophthora* spp. isolated from natural aqueous habitats are: *P. vignae* on river banks in Sri Lanka (Dilantha Fernando & Linderman 1993) and *P. cinnamomi* in surface water in Hawaii (Kliejunas & Ko 1976) and in surface and in subsurface water in Australia (Kinal et al. 1993).

We isolated *P. cinnamomi* twice during the period of our studies: once as the causal agent of root rot on a yew-tree at the shore of Lake Geneva (see p. 33) and once from the soil of a permanent grassland plot (Table 5). Whereas the first case can be explained by the mild frost-free winter temperature at the lakeside, the second case is surprising, because the species, despite its ability for active saprophytic growth in soil (Zentmyer 1980) is considered not to be able to survive winter temperatures in Central Europe. In laboratory experiments, its minimum temperature is in the range of 5–10 °C (Zentmyer 1980), and its geographical distribution is generally limited to countries with mild winter temperature. As an exception, Kröber (1980), in model survival studies was able to reisolate the fungus from soil after two mild winters.

P. nicotianae, which we isolated twice from diseased fallen apples during our initial survey (table 2) has not been previously described as a pathogen of this fruit species (Hall 1994). We never found it in soil samples taken in the region of Basle (p. 54 ff). The species has a very large range of annual and perennial host plants, mainly in temperate and tropical zones. It is present in soils of citrus groves in Florida (Zitko & Timmer 1994), Italy (Lio & Pennisi 1993), Israel and other Near East countries (Hamdan et al. 1995). Since the pathogen is able to survive frost temperatures in the soil (Kuske & Benson 1983) its occurrence in a Swiss soil is not exceptional. Its origin, however, remains unclear.

In conclusion, our studies show that *Phytophthora* spp. are widely distributed in natural soils without history of corresponding diseases over a wider range of soil types, soil pH, elevations and vegetation.

They are able to survive in these habitats over a long period of time without causing diseases. The high frequency of successful detection in orchard soils in the absence of crown or root rot symptoms underlines the importance of fallen fruits as hosts for active colonization. Running water of streams seems to be a more important means of transportation for dormant structures than generally realized.

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