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The Introduction of Exotic Tree Species with Special Reference to *Pinus Contorta* in Northern Sweden

Review and Background

Introduktion av främmande trädslag med särskild hänsyn till Pinus contorta i norra Sverige

En litteraturöversikt

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Abstract

ODC 174.7 Pinus contorta

The background to the large-scale planting of Pinus contorta in northern Sweden is reviewed with an account of the distribution and characteristics of Pinus contorta within its natural range in western North America. The Swedish Forestry Act of 1979 places restrictions on the planting programme of Pinus contorta. The threats to successful planting of exotics are discussed in relation to the historical background. Attention is also drawn to parasitic fungi which are infecting Pinus contorta in western Canada, and to the potential threat they represent to the indigenous Pinus sylvestris in Sweden.

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1 Introduction

European forests include relatively few coniferous tree species compared to those in the temperate zones of North America and Asia. This poverty of the flora is mainly due to the fact that during the Quarternary glaciations many Tertiary tree species, being unable to retreat southwards because of the east-west barrier of the Alps, died out in Europe. Consequently it is understandable that European foresters became interested in the introduction of foreign tree species. The need to avoid a shortage of raw material for the pulp industry has led to large-scale trials with fast-growing exotics during the past few decades.

Among the variety of conifer species planted in Sweden (see Stefansson 1957, Kiellander 1966, Remröd et al. 1977), the lodgepole pine, *Pinus contorta* Dougl. ex Loudon, has been the most successful. *Pinus contorta* is capable of an approximately 40---70 % higher yield per ha than the native Scots pine (*Pinus sylvestris* L.), depending on site quality (Hägglund et al. 1979). According to Remröd (1977a) the optimum rotation for lodgepole pine is 15----20 years shorter than for Scots pine.

Pinus contorta was first introduced into Sweden from western Canada, in the late 19th century. Several plantations exist from the mid-1920's and the following decade. The increased interest of Swedish foresters in Pinus contorta led to the establishment of a great many trial plantations in the late 1940's, although interest dwindled later and only a few plantations were established in the early 1960's. From 1967 onward, the Pinus contorta planting programme was significantly increased, and at the present time Pinus contorta is planted extensively as a forest tree in Sweden. Hitherto (1980) 150,000 ha have been planted with lodgepole pine, which represents about 50 million plants a year. However, the future percentage of lodgepole pine used in plantations is restricted by the Swedish Forestry Act of 1979, which stipulates that Pinus contorta should be used "in areas difficult to regenerate satisfactorily with indigenous tree species". Thus, until further notice "Pinus contorta may be used only in an experimental scale south of latitude 59°30'N in the counties Värmland and Örebro, and south of latitude 60°N in the rest of the country. North of this border the annual establishment of Pinus contorta must not exceed a total of 0.2% of the productive forest land in the counties Norrbotten, Västerbotten and Jämtland, and 0.1 % in the other counties. On holdings larger than 1000 ha the establishment of stands with Pinus contorta must not exceed 50 % of the total regeneration area each year." (Skogsstyrelsen 1979).

Before 1960 little progress had been made with provenance trials of Pinus contorta. Up to 1963, all seed was taken from trees of provenances growing south of 55°N, i.e. from the northern USA and from the vicinity of the Canadian border. Later on, in the 1960's, the Swedish Cellulose Company (SCA) included an increasing number of northern provenances in its trial plantations in Norrland. Both cones and cuttings were obtained from sites throughout the whole distribution area for Pinus contorta in North America, as far north as 63°N. Hagner & Fahlrot (1974) draw the southern boundary for Pinus contorta provenances which are suitable for use in northern Sweden at 55°N (central British Columbia). Guidelines for the choice of suitable provenances of Pinus contorta in northern Sweden have been drawn up by Hagner & Fahlrot (1974), Remröd (1977b) and the National Board of Forestry (1979).

The provenances of many of the trees used in former trials were either not recorded, or unknown. Frequently they came from regions too far south in North America. A high degree of damage from causes such as windblow, snow-thrust, trunk-forking and breakage, and insect and fungal attack has commonly been recorded in these particular trial plantations (Karlman 1976). Nevertheless, other *Pinus contorta* stands exist, also of southerly provenance, which are well developed and healthy. Favourable soil conditions and a suitable local climate are of vital importance to the success of such plantations.

During the past five years, a series of *Pinus contorta* plantations in northern Sweden have been investigated annually with respect to different kinds of damage, primarily those by parasitic fungi (Karlman 1976, 1979, 1980a, 1980b). The study has gradually become concentrated on provenance trials made by the College of Forestry (the series is described by Lindgren et al. 1976) and the Institute for Forest Improvement (see Rosvall & Strömberg 1980). Five years of research on the damage

suffered by Pinus contorta have proved that the correct choice of provenance is of the utmost importance if the more serious fungal attacks are to be obviated (Karlman op.cit.). However, an element of uncertainty is always associated with the introduction of exotic species. In Canada Pinus contorta is liable to attack by a series of parasitic fungi and should any of these inadvertently be introduced into Scandinavia the consequences could presumedly be serious. Several of these fungi present a potential threat to the indigenous Pinus sylvestris. Furthermore, some of the pathogenic fungi native to Scandinavia might change in virulence and be more serious to a new host species that has not yet adapted to the environmental conditions prevailing in Sweden.

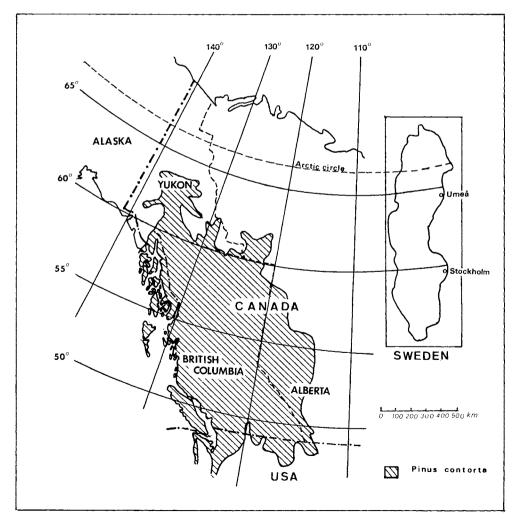


Figure 1. Occurrence of *Pinus contorta* in its northern range of distribution and latitudes in western North America and in Sweden.

2 Distribution and characteristics of Pinus contorta

Pinus contorta exhibits an unusually wide ecological amplitude, with regard to both climate and soil conditions. Its natural distribution area covers a very wide latitudinal zone in western North America. from Baja, California, (31°N) up to the mid-part of the Yukon Territory (Hamilton Creek at 64°15'N). On an areal basis its major occurrence (20 million ha) is in British Columbia and the Yukon Territory. No other species of pine shows such a wide altitudinal range as does Pinus contorta. which has a habitat tolerance from sea-level on the Pacific coast of North America up to 3900 m above sea level in the Sierra Nevada (Critchfield 1966). In view of the above data it is therefore not surprising to find that a large number of highly-differentiated geographical races of *Pinus contorta* have developed, which differ morphologically and ecologically. Critchfield (1978) distinguishes the following subspecies:

1. ssp. latifolia (Rocky Mountain—Intermountain race) has a continuous distributional area extending from the central Yukon to eastern Oregon and southern Colorado, and scattered occurrences from the Caribou Mountains in northern Alberta to the Black Hills in South Dakota. This subspecies is the one which has attracted the interest of Swedish foresters. Its ability to tolerate harsher environmental conditions and poorer soils than *P. sylvestris*, and



Figure 2. Pinus contorta subspecies latifolia. 80-year-old stand north of Fort Nelson, British Columbia. September 1978.



Figure 3. *Pinus contorta* is an aggressive pioneer species on burnt ground. Burnt area 10 years after fire, near Watson Lake, Yukon. September 1978.

yet remain even more productive than that species has made it particularly attractive for planting in the forests of northern Sweden. In Canada, however, this subspecies was of no economic interest before the last few decades. It grows into a tall tree, but with a trunk of no great diameter, because of the density of the stands after natural regeneration. It has a thin bark, like that of the Norway spruce, Picea abies (L.) Karst., and relatively long needles. It produces a large quantity of seed, starting at a relatively early age. The cones are mainly serotinous, i.e. they only open and release their seeds at relatively high air temperatures, e.g. during forest fires, which are quite common, especially in northern British Columbia and the Yukon. This has competitively favoured this subspecies of P. contorta, which, because of its regular and abundant production of seed, its smallsized, readily wind-distributed seeds, and its relatively rapid growth during the first few seedling years, behaves as an aggressive pioneer species on burnt ground.

2. ssp. murrayana (Sierra—Cascade race) occurs in the Cascade Range and the Sierra Nevada, in the mountainous parts of southern California, as well as in the northern part of Baja, California. This subspecies grows only slowly in height, but attains a greater trunk diameter than do any of the other races. Its bark is relatively thin and its needles are short and broad. It does not bear serotinous cones, the seeds instead being shed on maturity, wherefore its distributional area shows no relationship to areas subject to frequent forest fires.

3. ssp. contorta (coastal race) is also known as the Shore pine. It occurs along the Pacific coast of North America from Yukatat Bay in Alaska south to the northern part of California. Throughout this area it is restricted to the most marginal, least favourable, habitats, where it is a lowgrowing, heavily-branched tree, with a spreading crown on top of a short, thick and often twisted trunk. Whether this stunted growth is due to environmental factors has been discussed e.g. by Krajina (1969) and Illingworth (1971). The needles are short and very narrow, and possess relatively more stomata than the needles of the inland races. Along the coast it produces non-serotinous cones, but further inland serotinous ones. Alaska provenances of this subspecies are included in Swedish provenance trials. 4. ssp. *bolanderi* (Mendocino White Plains race) occurs rather locally and only within a rather restricted area of soils of low pH (2.8—3.9) near to the northern Californian coast. Within its natural distribution area it is a low-growing tree, but when planted elsewhere it grows to quite a reasonable height. It bears short, narrow needles and produces abundant pollen. The cones are often serotinous.

5. Del Norte race has a very limited distribution in the coastal mountains of north-west California.

3 The threat of internationally dangerous forest tree diseases

3.1 Historical review

Within international forestry research circles, there has always been an interest in the introduction of fast-growing exotics. Many trial plantings have been made in many countries. Nevertheless, history bears witness to the often disastrous consequences of taking a tree species from one continent and introducing it into another while paying no attention to suitable provenances of seed. The classic example is the case of Pinus strobus L., the Weymouth pine, a five-needle pine species which was introduced into France from North America in the mid-16th century and into England 150 years later (1705). As regards productivity, the Weymouth pine was a very interesting conifer, growing much more rapidly than the native coniferous tree species. In Germany large-scale planting of Pinus strobus commenced during the early part of the 19th century, followed by plantings in both France and Austria (Schmitt 1972).

In the mid-19th century the European plantations were suddenly attacked by the pathogenic fungus Cronartium ribicola J. C. Fisch. ex Rabenh. From an initial outbreak in the Baltic States in 1854, the epidemic spread over the entire continent in the course of a mere 30 years. The effects were catastrophic. Pinus strobus possessed no inherent resistance against this fungal parasite. Cronartium ribicola is a rust fungus with host-alternation, which is able to infect five-needled pines and a large number of Ribes species. The original host of this pathogen is usually considered (Peace 1962) to be Pinus cembra L., the indigenous European populations of which, now restricted to relatively small areas in the Alps, are considerably resistant to infection. The Pinus sibirica populations in Asia are more

susceptible (Gäuman 1950), however, and *Pinus strobus* is thought to have been infected by a pathogen strain which had spread westwards into Europe from Siberia (Macek 1976) or possibly from a small relict area of *Pinus cembra* in the Carpathians (Peace 1962).

Unfortunately Cronartium ribicola was later introduced between 1906 and 1910 on seedlings imported from Germany into the northeastern United States, whence it successively spread throughout the natural range of Pinus strobus. At about the same time (1910) it was introduced from France to Vancouver and advanced at a rate of about 25 miles a year (Van der Plank 1975), causing heavy losses to other species of White pine, e.g. Pinus monticola Dougl., P. lambertiana Dougl., P. flexilis James and P. albicualis Engelm. Despite 50 years of extensive resistance work, progress has been slow (Ziller 1974). During the past few years the most promising control has been selection and breeding of resistant trees (Agrios 1978).

A further example of the world-wide spread of a serious fungal disease is Dutch elm disease (Ceratocystis ulmi (Buisman) C. Moreau). This insect-borne parasitic fungus was first discovered in France in 1918, and had soon spread across western Europe into Russia and the Balkans. The marked resistance shown by some Asiatic elm species led to the assumption that the pathogen had been introduced to France from Asia (Peace 1962), presumedly by Chinese labourers employed in trench digging during the war. They used baskets made of Chinese elm with residual pieces of bark containing the vector beetles (Horsfall & Cowling 1978). Dutch elm disease was noticed in England in 1927 and already three years later had been carried across the Atlantic



Figure 4. The correct choice of provenance is of utmost importance for the success of an exotic. Seven-year-old *Pinus contorta* of suitable provenance at Moskosel, 400 m above sea level, Norrbotten province, northern Sweden. June 1980.

to the USA, probably on infected elm logs imported for the manufacture of veneers (Spaulding 1957), reaching Canada by the mid-1940's. In the 1960's the Dutch elm disease again crossed the Atlantic, now in the opposite direction, and appeared in Great Britain in a much more aggressive and virulent strain eradicating 5 million elms (Wilkinson 1978). Today *Ceratocystis ulmi* is still the most severe shade tree disease in the USA (Agrios 1978).

The chestnut blight (Endothia parasitica (Murr.) And. & And.) is one of the most destructive forest tree diseases in the world. This pathogen has had disastrous effects on forests of the European chestnut (Castanea sativa Mill.) and has also severely attacked the American species of chestnut (Castanea dentata (Marsh.) Borkh.). Endothia parasitica was endemic to China. Consequently, the Castanea species in Japan, China and Korea have a relatively high resistance to infection (Day 1978).

It has been established (Heald et al. 1915) that the ascospores of Endothia parasitica can be spread many miles by the wind and that its sticky conidia can be carried long distances by birds and insects (Heald & Studhalter 1914). Chestnut blight was introduced into the New York Zoological Park in 1904, probably on chestnut plants imported from eastern Asia (Beattie & Diller 1954, see also Diller 1965, Walker 1969, Hepting 1974). It rapidly spread all over the continent reaching the Pacific Northwest by 1929, and did not leave a single tree undamaged. "The loss of chestnut is an outstanding example of the destruction that can be brought by an introduced parasite that finds its new host without any inherent resistance and is a tragic lesson on the danger of introducing living plant material from other countries, particularly when no prior investigation of the diseases that



Figure 5. Seven-year-old *Pinus contorta* of unsuitable provenance. Damage due to unfavourable weather conditions followed by *Phacidium infestans* attack. Moskosel, 400 m above sea level, Norrbotten province, northern Sweden. July 1980.

attack the host in its native land has been made" (Boyce 1961).

Hitherto no resistant chestnuts have been found in America (Agrios 1978). However, a virus-like disease of *Endothia parasitica* has been observed in Italy, weakening the pathogen enough to bring the blight into remission. Strains of the infected fungus have been used successfully by French pathologists to control the blight in French chestnut orchards (Hartline 1980). American efforts have not yet been successful.

After World War I the planting of Douglas Fir, *Pseudotsuga menziesii* (Mirb.) Franco, in central Europe was severely threatened by several pathogens, primarily the fungi *Rhabdocline pseudotsugae* Syd. and *Phaeocryptopus gäumanni* (Rhode) Petrak, both introduced from the natural range of Douglas Fir in western North America and changing into more virulent strains, the former due to the damper climate in Europe during the growing season (Boyce 1954). Both the gray and the blue intermountain forms of Douglas Fir were highly susceptible to Rhabdocline, while the green coastal form has been more resistant (Bergman 1954, MacDonald et al. 1957, Butin & Zycha 1973). The green coastal form was instead attacked by Phaeocryptopus gäumanni and so were the other two forms, which made further planting of Douglas Fir in central Europe dubious for decades. Today, when damage can be controlled by a correct choice of provenance (Kleinschmit 1978), Douglas Fir has become the most important foreign tree species in German forestry.

In Great Britain foresters have a relatively long experience of exotics. A large sector of British forestry is based on nonnative coniferous species, a great many introduced from North America. The fact that at least a dozen species of exotics play a major part in British forestry is of great value in disease control. With a small number of species much larger areas would be involved in any fungal or insect attack of epidemic proportions (Peace 1962).

In North America the introduction of foreign tree diseases, e.g. white pine blister rust (Cronartium ribicola), Dutch elm disease (Ceratocystis ulmi) and chestnut blight (Endothia parasitica) has been both disastrous and has caused tremendous financial losses. Other introduced diseases are larch canker (Lachnellula willkommii (Hart.) Dennis) and Scleroderris canker (Gremmeniella abietina (Lagerb.) Morelet) (see also p. 15). American pathologists have found that about twenty years pass before a new pathogen becomes epidemic, which probably holds true for European conditions as well (Spaulding 1957).

One of the most important examples of an introduced tree species in the Southern Hemisphere is the Monterey pine, *Pinus radiata* D. Don, which is indigenous in only a limited area near the coast in southern California (Dallimore & Jackson 1966, Mirov 1967). *Pinus radiata* has little commercial value within its natural range, but has been extensively introduced as an important timber tree in New Zealand, Australia, Africa and South America, with excellent results. Unfortunately it has gradually become prone to attack by a great many native and introduced pathogens, although *Pinus radiata* is still of great economic importance in the Southern Hemisphere and is a good example of a successful exotic, as are members of the genus *Eucalyptus*, a native of Australia but now successfully introduced into other tropical and subtropical countries.

There is much to learn from these early mistakes in forest history. However, little was known in those days about the transfer of seed. Today we have much more knowlegde about the importance of a correct choice of provenance for the success of an exotic. Concerning pathogens there are still some possible risk factors that must be taken into consideration.

3.2 Transmission of pathogens

Pathologists all over the world agree that an element of uncertainty is always associated with the introduction of exotic species. Relatively few fungi have a world-wide distribution. Many pathogens have not yet invaded every corner of their host species' natural geographical range, nor have they yet penetrated all parts of the world into which the host species has been introduced.

Aerobiological studies of the fungal and bacterial flora in the atmosphere over the Atlantic Ocean have proved that viable fungal spores can be spread from one continent to another in the air masses (Meier 1935). During his famous North Atlantic— Greenland flight in 1933, Charles Lindberg made spore collections for Meier. It was then established that some of these fungal spores belonged to pathogenic species (Meier l.c.).

According to Stover (1962) spores of the banana leaf spot fungus (*Mycosphaerella musicola Leach.*) were spread by the wind from eastern Australia to the Caribbean area in 1933, where they caused a disastrous epidemic.

Pady & Kelly (1954) proved that polar air masses contain many fewer fungal spores than do tropical air masses. Nevertheless, impressive numbers of spores have been found in polar air masses. Up to 137 fungus spores per m³ in an air mass of polar origin at 9000 feet over the North Atlantic. and a total of 530 fungus spores per m³ in a tropical air mass were recorded. Pady and Kelly also proved that there was no evidence of a gradual reduction in spore numbers with increasing distance from land. However, such spore dispersal is probably unimportant to the spread of forest tree diseases. Man appears always to be the chief agent for the intercontinental transmission of such pathogens (Orton & Beattie 1923).

Fungi can be carried from one continent to another on imported timber, plants and seed. Tree seed importation offers the least risk (Peace 1962), with the exception of Castanea seed, which may already be infected with chestnut blight (Endothia parasitica), thus making seed disinfection vital. Cronartium ribicola is an example, though not the only one, of a tree disease introduced on imported nursery plants. Unbarked timber, however, represents a far more serious risk for the transmission of pathogens (Morgan & Byrne 1957). Quarantine regulations intended to inhibit the spread of tree diseases have generally applied to the importation of living plants, rather than to imports of seed or timber (Peace 1962). For economic reasons a complete embargo on the import of timber is impossible in most countries.

A few years ago, *Pinus contorta* scions could be imported into Sweden for grafting purposes, a procedure which obviously involved a serious risk factor.

Sherman (1957) discusses another very interesting method of spore dispersal, viz. that spores may be carried inside aircraft, and that passengers may, unknowingly or deliberately, carry diseased materials in their luggage. In 1956, in a check made on all passengers arriving by air in the USA from overseas, 38% were found to be transporting unauthorized plant material.



Figure 6. Both in 1979 and 1980 *Pinus contorta* plantations at higher altitudes in northern Sweden have suffered from bending damage, caused by the weight of a heavy coating of ice after days of rain followed by temperatures below freezing point. Stensvattnet, Västernorrland province, northern Sweden. October 1980.

Nowadays, the introduction of more stringent quarantine regulations has presumedly reduced that percentage, although in the jet age the speed-up of intercontinental journeys must have increased this risk factor considerably.

3.3 Other threats to successful planting of exotics

Pathogens are not the only threat to a successful planting of exotic species. Other factors of importance are:

1. Low tree vigour in the new habitat will naturally increase susceptibility to pathogens and may be fatal for exotics.

2. Unfavourable short-term meteorological conditions may spoil initially successful plantings of non-native tree species, e.g. plantations of *Abies alba* in Norway were

successful for 20—30 years, but were then totally destroyed following a year of severe frost and drought (Børset 1976).

Severe icing affects *Pinus contorta* more severely than *Pinus sylvestris* (Karlman 1980a) owing to the great length of the needles of the former species. Both in 1979 and 1980 *Pinus contorta* plantations at higher altitudes in northern Sweden suffered from bending damage, caused by the weight of a heavy coating of ice, after days of rain followed by temperatures below freezing point.

3. The proper choice of site is of great importance in preventing disease. *Gremmeniella abietina* (Lagerb.) Morelet is generally associated with plantations at high altitudes (Stefansson 1957, Roll-Hansen 1972), *Lachnellula wilkommii* (Hart.) Dennis with frosty sites (Peace 1962), and *Heterobasidion annosum* Bref. with alcaline soils

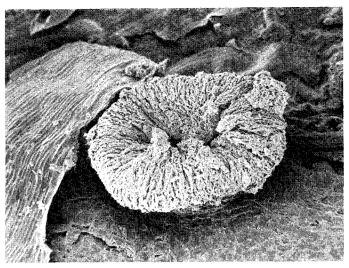


Figure 7. A more virulent European strain of *Gremmeniella abietina* was introduced into the USA in 1964. SEM micrograph × 80.

(Burdekin & Greig 1972). Melampsora pinitorqua Rostr. only attacks mixed plantations of pine and aspen: Populus tremula L., etc.

4. It is generally considered that mixed stands are preferable to pure stands. From a pathological point of view, mixed stands are sometimes to be preferred because most pathogens are specific to a host genus or one or a few species in a genus and the spread of infection from one tree to another takes place much more rapidly in a pure stand (Boyce 1961, Peace 1962).

5. Many fungal species have been found to possess numerous races, which vary in their degree of pathogenicity (cf. Kiellander 1976). A more virulent European strain of Gremmeniella abietina, Scleroderris canker, was introduced into the USA in 1964 (Skilling 1977) where it caused heavy losses in pine plantations in New York State and then spread into Vermont, New Hampshire and New Brunswick (Schabas 1979). Agrios (1978) estimated that more than two hundred different races of Puccinia graminis Pers. exist in the world, and that new races are still developing. Although the effects of epidemic fungal diseases on agricultural crops are really severe they cannot be compared to those in forestry plantations or natural regenerations with a 50—100 year rotation. If one cereal crop is wiped out it can be replaced next year by other kinds of crops, e.g. potatoes. If a pine plantation is subject to an attack by a serious pathogen, the results of 10, 25 or 40 years' production are lost.

6. The winter of 1977/78 was a peak year for voles in northern Sweden. Voles appear to prefer Pinus contorta to Pinus sylvestris, presumably because of a thinner and more delicious bark of the former species. However, lodgepole pine has a much higher capacity for recovery from these attacks than the Scots pine. A lateral branch takes over as the leading shoot or adventitious buds are formed. Northern provenances of lodgepole pine appear to be less attacked than southern provenances, although the data are still too limited for any statistical check on whether this tendency is being maintained (Karlman 1979). Nevertheless, during the last winter (1979/80) repeated damage by voles to several Pinus contorta plantations in southern Norrland has been of great concern. Another peak year for voles is expected this winter (1980/81), and severe damage to lodgepole pine has already been reported from the province of Värmland in central Sweden.

Since fungi dangerous to *Pinus contorta*, with special reference to pathogens from northern Europe, have been discussed by Roll-Hansen (1978), this chapter concentrates on pathogens from the natural range of *Pinus contorta* (see also Lindgren 1980).

Within its area of distribution in western Canada *Pinus contorta* is subject to attack by a wide variety of parasitic fungi. However, fungal attack in natural regenerations is not considered to represent a particularly great problem. Such stands are usually far too dense anyway and therefore no serious threat is posed to the future stand when a large number of seedlings are thinned out. This is natural selection at work, a quite necessary process, since it is the most resistant plants which survive (cf. Karlman 1978).

The conditions in forestry plantations are quite different, since the intention is that all transplants shall survive. Attacks by fungi and insects in such cases may have severe effects. Even in Canada, they have scarcely ten years' experience of lodgepole pine plantations and it is stated (Martinsson 1978, 1980, Illingworth 1980—pers. comm.) that the rust fungi, in particular, represent a serious problem in these areas. Many of these fungi also present a potential threat to our native pine, *Pinus sylvestris*, so the consequences would be serious if any of these fungi were introduced into Scandinavia.

4.1 Canker

One of the most serious pathogens of *Pinus* contorta in western Canada is Atropellis canker, Atropellis piniphila (Weir) Lohman & Cash. It causes trunk and stem canker with copious exudation of resin, which are similar effects to those of Crumenulopsis sororia (Karst.) Groves, a closely related ascomycete indigenous to western Europe. The fungus attacks through the undamaged bark, usually at the nodes. The cambial layer is killed off at a multitude of widely separated points, thus leading to a disruption of the tree's transport system. The fungal hyphae then spread vertically, while the host tissues attempt to heal the damage.

Atropellis does not usually kill the host tree, but the attack leads to a reduction in growth increments and loss of timber quality of the tree. The initial sign of infection is a copious exudation of resin down the trunk and from the branches, followed by crack formation. Canker scars gradually become apparent on the trunk and branches, which, when, examined in cross-section, show a dark bluish-black staining of the wood (Hopkins 1963). Atropellis has so far not been found in Europe.

4.2 Rust fungi

Among the variety of rust fungi which infect Pinus contorta, the western gall rust, Endocronartium harknessii (J. P. Moore) Y. Hirat., is considered to be the most common and the most destructive stem rust in western Canada. This rust can spread directly from one tree to another, with no intermediate host stage. The pathogen enters through the needles and the green shoots. Attack leads to gall formation on the pine branches. Teleutospores, which are produced from the galled areas a few years after the infection has occurred, are then spread by the wind to infect other pine trees. The galls increase in size each year, until they finally strangle the branch or stem on which they are situated. This rust fungus seldom kills older, larger pines,



Figure 8. Atropellis piniphila causes stem canker on Pinus contorta, with copious exudation of resin. Vanderhoof, British Columbia. August 1978.

but attacks lead to a reduction in growth increment and infected stems are often more readily broken off by snow or wind. Young pines, on the other hand, as a rule die after an attack (Ziller 1974). Unfortunately, *Pinus sylvestris* is highly susceptible to this rust and forestry plantations of Scots pine in western North America have been severely attacked (Ziller 1967). However the pathogen is still confined to North Amercia, but the consequences would be disastrous if this disease were to be spread to Europe.

A potential threat to both *Pinus contorta* and *Pinus sylvestris* in Sweden is the sweetfern blister-rust *Cronartium comptoniae* Arth., with host-alternation between two and three-needled Pinus species and certain members of the Myricaceae, e.g. Sweet gale (*Myrica gale* L.) and Sweet fern (*Comptonia perigrina* (L.) Coult.). An attack leads to stem girdling close to ground level and causes severe damage in forest nurseries and young plantations, but is not a very important pathogen in natural forests or



Figure 9. Attack by *Endocronartium harknessii* leads to gall formation. Mackenzie, British Columbia. August 1978.

plantations more than ten years old (Ziller 1974).

Myrica gale is fairly common in southern and central Sweden and northwards to Värmland, Dalarna and the south of Norrland into a region which is termed "North Swedish Myrica subregion", (Wahlenberg 1826) "a zone strongly confined to the coast on either side of the Bothnian Bay, extending only about 20—30 km inland", (Ericson 1977). Only isolated Myrica stands have been recorded further inland. Accidental introduction of the pathogen into these regions might therefore have serious consequences.

According to Pawsey (1974) worse epidemics than those produced by *Cronartium ribicola* could occur if *Cronartium comptoniae* were to be introduced into Europe. The disease is not easy to control. For obvious reasons it would be quite impossible to eradicate the alternate host *Myrica gale* from Europe (cf. cereal rusts and the Barberry, *Berberis vulgaris* L.).

Pinus contorta and Pinus sylvestris are also liable to attack by some other species of rust fungi, viz. the pine needle rust, Coleosporium asterum (Diet.) Syd., with species of Aster and Solidago as alternate hosts. Geographical races of Coleosporium are considered to exist and different Pinus species show varying degrees of susceptibility to this pathogen (Browne 1968).

For the Comandra blister rust, Cronartium comandrae Peck, species of Comandra are the alternate hosts. It produces perennial cankers on both Pinus contorta and Pinus sylvestris. Comandra species do not occur in northern Europe and consequently the pathogen represents no impending threat to the northern European pine forests.

The alternate hosts of the stalactiform blister rust, *Cronartium coleosporoides* Arth. f. *coleosporoides*, are American species of *Melampyrum*, *Pedicularis* and *Rhinanthus*, all genera of which other species are very common and widespread in Sweden. Pine seedlings and young plantations are most liable to serious attack and are usually killed off by girdling. Infection of older trees usually results in deformation and retarded growth. Cankers produced by *Atropellis piniphila* are often associated with attacks by this pathogen (Ziller 1974).

4.3 Needle cast fungi

Defoliation of lodgepole pine leading to reduced growth can be caused by the following needle-cast fungi: *Davisomycella* montana (Darker) Darker, *D. medusa* (Dearn.) Darler, *Lophodermella concolor* (Dearn.) Darker, *L. montivaga* Petr. and *Elytroderma deformans* (Weir) Darker. Trees heavily infected by *Elytroderma deformans* are killed off and moderately infected trees are susceptible to subsequent attacks by bark beetles (Childs 1959). So far, none of these pathogenic species have been reported in Europe.

A closely related *Lophodermella* species, *L. sulcigena* (Rostr.) Höhn., however, is a serious pathogen of Scots pine in western Europe and has caused severe reductions in the growth increment of Scots pine in northern Sweden during the past two years. Hitherto the plantations of *Pinus contorta*

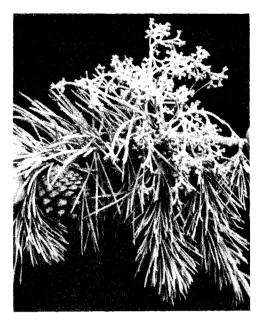


Figure 10. Arceuthobium americanum, the dwarf mistletoe, is a leafless, parasitic, vascular plant, which grows in the crowns of *Pinus* contorta and causes heavy losses in growth increment. Mackenzie, British Columbia. August 1978.

have proved resistant to attack (Karlman 1980).

Scirrhia pini Funk & Parker causes "red band disease, a serious problem of worldwide consequence especially in plantations of fast-growing pine species", (Krebill 1975). This needle cast pathogen is widely distributed both in the Northern and the Southern Hemispheres. It has so far been restricted to damp habitats and has not been found in Scandinavia, where the climatic factors may be unfavourable (Roll-Hansen 1978).

4.4 Root rot fungi

Among the various basidiomycetes which cause root rot of lodgepole pine in western Canada, *Heterobasidion annosum* (Fr.) Bref. and *Armillariella mellea* (Vahl ex Fr.) Karst. are the most serious. Both these pathogens are widely distributed in the North Temperate Zone. They are also widespread in Sweden, where they have led to heavy economic losses in Swedish forestry. In northern Sweden *Pinus contorta* also suffers occasional attacks of *Armillariella mellea*. *Heterobasidion annosum* is predominantly found on *Pinus sylvestris* in southern Sweden, but has recently (1980) also been observed on *Pinus contorta* in the north of the country.

4.5 Mistletoe

Finally, the dwarf mistletoe, *Arceuthobium americanum* Nutt. ex Engelm., Loranthaceae, although not a fungal parasite, ought to be mentioned in this survey. The dwarf mistletoe is a leafless, perennial, parasitic vascular plant, which grows in the crowns of various coniferous species. The decrease in wood volume caused by the growth of this parasite represents a quarter of the entire annual cut of lodgepole pine and western hemlock in British Columbia (Baranyay & Smith 1972). However, the distance of seed dispersal is limited and were dwarf mistletoe to be accidentally introduced into Scandinavia, it could relatively easily be controlled by silvicultural treatment.

5 Conclusions and summary

There is much to be said in favour of the large-scale planting of Pinus contorta in northern Sweden in the future, especially in view of its high rate of production and its superiority to Pinus sylvestris in areas in which regeneration is very hard to achieve. Moreover, Pinus contorta has so far been virtually resistant to both Melampsora rust (Melampsora pinitorqua Rostr.) and Lophodermella needle cast (Lophodermella sulcigena (Rostr.) Höhn.), two parasitic fungi which have caused severe infections in the Pinus sylvestris forests of northern Sweden during the past two years. We need to bear in mind that even our native pine, Pinus sylvestris, is subject to attack by a number of parasitic fungi, although in this case we are relatively familiar with the different kinds of pathogens concerned, thanks to the long-standing mycological research that has been carried out in Sweden during the present century (Lagerberg, Björkman). So far as the resistance of Pinus contorta to the various pathogenic fungi native to Sweden is concerned, our knowledge is still far from complete. We can presume that introduced species possess no specifically selected resistance to the native pathogens of the new country. It is therefore unrealistic to make any prognosis based solely on the knowledge we have of Pinus sylvestris, a tree species which has had many millennia to become adapted to the ecological conditions in Sweden (cf. Karlman 1979). As stated elsewhere, "it is not until at least one rotation has passed that reasonable judgement can be rendered as to the result of an introduction no matter how initially successful it may seem to be", (Boyce 1961).

No simple answer thus exists to the vexed question of whether the introduction of *Pinus contorta* into northern Sweden will be exceedingly favourable, or whether it will present a great risk. Nevertheless, we can learn much from the results of previous forestry experience of the potential threats to successful planting of exotic species. Some of the risk factors that must be considered in regard to potential pathogens are:

1. A pathogen so far restricted to the natural distribution range of *Pinus contorta* might be inadvertently introduced into Scandinavia, leading to severe damage to *Pinus contorta* and to the native species, *Pinus sylvestris.*

2. Pathogens indigenous to Scandinavia might prove more virulent to the new host, not yet adapted to its new environment.

3. A relatively unimportant pathogen, or a saprophyte, introduced from western Canada or native to Scandinavia, might change in virulence under new environmental conditions or on a new host, respectively.

One risk factor of importance is that we introduce a species of the same genus as the native *Pinus sylvestris*. From a phytosanitarical point of view a better policy would in fact be to plant exotics of other genera than *Pinus*, thus avoiding potential threats by pathogens to our native conifers, which are mostly not attacked by the same parasitic fungi as are species of e.g. the genera *Abies*, *Larix* and *Pseudotsuga*. An increase in frequency of vole damage is another risk factor.

Pinus contorta exhibits an unusually wide ecological amplitude and possesses a high capacity of recovery from a wide variety of damage. Moreover, the risks to a successful planting of *Pinus contorta* are presumedly reduced considerably by a correct choice of provenance. However, a continual watch must be kept on the progress of the *Pinus contorta* plantations in northern Sweden, in the knowledge that any newly introduced pathogen can more easily be controlled when detected at an early stage.

Sammanfattning

Pinus contorta har på senare år fått allt större betydelse inom svenskt skogsbruk. Hittills har 150.000 ha planterats med contortatall, för närvarande ungefär 50 miljoner plantor årligen. Andelen contorta kommer dock att begränsas genom den nya skogsvårdslagen, som föreskriver att "contortatall bör användas framför allt i områden där det är svårt att med inhemska trädslag åstadkomma en tillfredsställande föryngring". Endast 0,2 % av den produktiva skogsmarksarealen får årligen planteras med Pinus contorta i Norrbottens, Västerbottens och Jämtlands län, 0,1 % i övriga landsdelar norr om 60°N br. Varje ägarkategori med en större brukningsenhet än 1.000 ha tillåts plantera högst 50 % contorta årligen. Detta är en begränsning av flera skogsbolags contorta-odling. Vilken är bakgrunden till detta beslut?

Att introducera nya snabbyäxande trädslag har länge intresserat skogsforskare. I Sverige har man gjort försök med ett flertal barrträdsarter. Pinus contorta har visat sig vara den mest produktiva. Contorta-tallen härstammar från västra Nordamerika och har ett mycket stort utbredningsområde i nord-sydlig riktning från norra Kaliforniahalvön (31°N) till mellersta Yukon (64°15'). Arealmässigt sett ligger huvudförekomsten i British Columbia och Yukon. Pinus contorta har en mycket vid ekologisk amplitud, både när det gäller klimatiska och edafiska faktorer. Ingen annan tallart har så stor tolerans för nivåskillnader som Pinus contorta. Den växer ute vid Stilla Havskusten och upp till 3.900 m ö.h. i Sierra Nevada (Kalifornien). Pinus contorta har utvecklat flera väl differentierade geografiska raser eller varieteter. Av dessa är det varieteten latifolia, som är av intresse inom svenskt skogsbruk.

De första försöken i Sverige anlades redan i början av 1900-talet. I Norrland är de äldsta contorta-planteringarna från slutet av 1920-talet. I flera av de äldre försöken var proveniensen okänd. Ofta var den för sydlig och detta resulterade i en hög frekvens stjälpskador, stambrott, gaffelgrenighet och angrepp av svampar och insekter. Proveniensförsök under senare år har visat, att det är nödvändigt att välja frö av betydligt nordligare härstamning än tidigare, för att få ett tillfredsställande föryngringsresultat. Förflyttningsanvisningar för contorta-tall har utarbetats av Hagner & Fahlrot (1974), Remröd (1977) och Skogsstyrelsen (1979).

Under en femårsperiod har en serie Pinus contorta-planteringar i norra Sverige undersökts årligen med avseende på olika typer av skador, framför allt angrepp av parasitsvampar (Karlman 1976, 1979, 1980a, 1980b). Resultat från dessa undersökningar visar att proveniensvalet har avgörande betydelse, när det gäller att undvika allvarligare skadeangrepp av inhemska parasitsvampar. Men inplantering av främmande trädslag i stor skala är alltid förenat med viss risktagning. Skogsbiologerna har erfarenhet att bygga på. Det klassiska exemplet är Weymouth-tallen, Pinus strobus, som i mitten av 1500-talet infördes till Frankrike från Nordamerika, och började odlas i större skala i Tyskland under tidigare delen av 1800-talet, senare också i Frankrike och Österrike. Under 1800-talets mitt angreps plötsligt de europeiska odlingarna av en skadesvamp, som under en 30-årsperiod spred sig över kontinenten med förödande resultat. Weymouth-tallen hade ingen inbyggd resistens mot angrepp av denna parasitsvamp. Dessvärre infördes denna rostsvamp från Europa till USA omkring 1906-1910 och spreds successivt över hela Weymouth-tallens utbredningsområde. Även närbesläktade tallarter utsattes för mycket svåra angrepp. Det finns fler liknande exempel på global spridning av svåra svampsjukdomar. Almsjukan (Ceratocystis ulmi) och kastanjesiukan (Endothia parasitica) hör förutom Cronartium ribicola till de klassiska exemplen. Introduktionen av bl.a. douglasgran (Pseudotsuga menziesii) i Centraleuropa hotades av svåra svampepidemier under 1920talet. Inplantering av detta nordamerikanska trädslag lyckades bättre i Storbritannien, där man för övrigt har lång erfarenhet av exoter. Brittiskt skogsbruk baseras huvudsakligen på införda barrträdsarter. Pinus radiata och arter av släktet Eucalyptus representerar exempel på lyckade inplanteringar av trädexoter. Dessa trädslag har fått stor ekonomisk betydelse på södra halvklotet.

Relativt få svampar har en global utbredning. Levande svampsporer kan dock spridas mellan kontinenter i luftmassorna. Förmodligen är denna sporspridning av liten betydelse. Människan är den främsta orsaken till att svampsjukdomar överförs från en kontinent till en annan, bl.a. genom import och export av timmer, ympris, plantor och i vissa fall frö. Det ökande resandet mellan kontinenter i jetåldern har trots införselrestriktioner ökat risken för global spridning av patogener. Andra faktorer som kan vara fatala för exoter är tillfälligt ogynnsamma väderleksförhållanden och felaktigt val av ståndort. Vidare kan nya svampraser uppstå, mer aggressiva mot det införda trädslaget.

Inom sitt utbredningsområde i västra Kanada är *Pinus contorta* utsatt för angrepp av en mängd parasitsvampar, och det skulle förmodligen få allvarliga följder, om någon av dessa introducerades i Sverige av misstag. Flera av dessa svampar är potentiella skadegörare på *Pinus sylvestris*.

En av de svåraste parasitsvamparna på Pinus contorta i södra och mellersta British Columbia är Atropellis piniphila, som orsakar stamkräfta med kraftigt kådflöde, i likhet med angrepp av Crumenulopsis sororia. Atropellis dödar i regel inte träden, men dessa utsätts för en tillväxtförlust och kvaliteten på stammarna blir sämre.

Endocronartium harknessii är den mest vanliga och den mest destruktiva rostsvampen som angriper Pinus contorta i västra Kanada. Denna rostsvamp sprids från tall till tall och har inte någon annan art som mellanvärd. Svampen orsakar svårartade gallbildningar på grenar av Pinus-arter. Den dödar sällan större träd, men orsakar tillväxtförluster. Infekterade stammar bryts ofta av snö och vind. Unga plantor dödas i regel. Dessvärre är Pinus sylvestris mycket mottaglig. Denna parasitsvamp förekommer ännu så länge enbart i Nordamerika, liksom Atropellis piniphila. Ett potentiellt hot mot både Pinus contorta och Pinus sylvestris i Sverige är Cronartium comptoniae, som värdväxlar mellan två- och trebarriga Pinus-arter och vissa Myricaceae-arter t.ex. Myrica gale. Denna parasitsvamp orsakar stamkräfta basalt på stammen med svåra skador i plantskolor och planteringar, men är inte av större betydelse i naturliga föryngringar eller planteringar äldre än 10 år.

Pinus contorta och Pinus sylvestris angrips också av ett flertal andra rostsvampar t.ex. Colesporium asterum, som värdväxlar mellan tall och arter av släktena Aster och Solidago. Pinus-arter visar olika grad av mottaglighet.

Arter av släktet Comandra utgör alternativa värdväxter för Cronartium comandrae, som orsakar fleråriga sårskador på både Pinus contorta och Pinus sylvestris. Comandra-arter förekommer inte i norra Europa och därför utgör inte denna rostsvamp något överhängande hot mot contortaodlingarna i Sverige.

Cronartium coleosporoides f. coleosporoides värdväxlar mellan Pinus contorta och amerikanska arter av följande släkten: Castilleja, Melampyrum, Pedicularis och Rhinanthus. Dessa värdväxter är mycket frekventa i Skandinavien. De svåraste infektionerna förekommer i plantskolor och i planteringar. Angrepp på äldre träd orsakar tillväxtförluster, men yngre plantor dödas mestadels.

Följande skyttesvampar orsakar tillväxtförluster på Pinus contorta: Davisomycella montana, D. medusa, Lophodermella concolor, L. montivaga och Elytroderma deformans. Ännu har inte någon av dessa parasitsvampar uppmärksammats i norra Europa.

Bland raden av rötsvampar som infekterar *Pinus contorta* i västra Kanada är det *Heterobasidion annosum* och *Armillariella mellea* som åstadkommer de största förlusterna för skogsbruket. Båda dessa patogener förekommer inom hela norra tempererade zonen.

Dvärgmisteln, Arceuthobium americanum, förorsakar svåra tillväxtförluster på Pinus contorta i västra Kanada. Dvärgmisteln är inte någon parasitsvamp utan en flerårig fanerogam vars frön är relativt tunga, varför spridningsförmågan är rätt begränsad. Infektionen kan därför kontrolleras genom skötselåtgärder.

Slutsatser: Mycket talar för en fortsatt satsning på Pinus contorta i norra Sverige, bl.a. höga produktionssiffror, åtminstone temporär resistens mot två inhemska patogener, knäckesjuka (Melampsora pinitorqua) och gråbarrsjuka (Lophodermella sulcigena), en mycket vid ekologisk amplitud och en god förmåga att komma igen efter skadeangrepp. Historien visar dock, att det finns vissa risker, som måste uppmärksammas i samband med inplantering av exoter, även om riskerna för liknande epidemier som de *Pinus strobus* utsattes för har reducerats genom ökade kunskaper om rätt proveniensval. Trots detta finns vissa riskfaktorer att ta hänsyn till:

- En parasit från *Pinus contortas* naturliga utbredningsområde i västra Nordamerika kan av misstag introduceras i Sverige och orsaka omfattande skador på både *Pinus contorta* och *Pinus syl*vestris.
- Pinus contorta kan angripas av någon av Pinus sylvestris parasitsvampar, som den inte har utbildat resistens mot.
- 3) En saprofyt eller en relativt oförarglig parasit från contortatallens utbredningsområde i västra Nordamerika eller i Skandinavien kan bli mycket aggressiv under ändrade ekologiska förhållanden eller på en ny värdväxt.

Att vi till 100 % satsar på en art av samma släkte som vår inhemska tall, utgör förmodligen den största riskfaktorn. Det hade troligtvis varit mindre riskfyllt att istället satsa på arter av andra barrträdssläkten, för att undvika att de inhemska barrträden drabbas av det införda barrträdets patogener. Flertalet av *Pinus contortas* parasitsvampar är potentiella skadegörare på *Pinus sylvestris*.

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