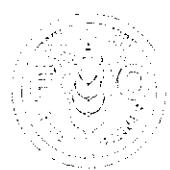


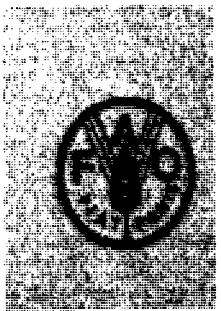
Breeding poplars for disease resistance

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FOOD
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UNITED NATIONS

Breeding poplars for disease resistance



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FOREWORD

Poplars are amongst the oldest contemporary angiosperm genera with over 125 species recorded as fossils and 30 to 40 species existing today. They are dioecious and are more frequently propagated from cuttings than seed, lending themselves to the creation of clones and the cultivation of recognizable and clonally reproducible hybrids. They have long been cultivated in Asia as well as in Europe but their more recent development dates from the 18th century when North American poplars were imported to form hybrids with European species, a trend which is now extending to West and East Asia.

Their utility lies in the frequently rapid growth potential of species, their hybrids and certain clones as well as the wide use to which poplars can be put to provide industrial wood, fodder for animals, shelter, energy and timber for domestic and farm use. At the 17th Session of the FAO International Poplar Commission in October 1984, it was noted that whereas sales of poplar wood were declining in developed countries, they were vigorously increasing in developing countries under the stimulus of local demand.

Poplars, generally dependent on good soils and adequate soil moisture for their best development, are frequently associated with agricultural crops. The expansion of their range to less favourable sites as well as the increase in their resistance to disease and insect attack is a challenge to poplar breeders working with basically fast-growing and well-formed cultivars of the genus.

Imparting wide adaptability coupled with durable disease resistance is an extremely important aspect of this breeding programme. Principles and strategies which can be applied are elements of the modern armoury of technology which can be transferred to developing countries to improve the culture of poplars, alleviate serious deficits in the supply of domestic wood, energy and fodder and pressure on degraded natural vegetation resources essential for the protection of soils and environment.

This paper, prepared under a contract with FAO by Professor B.A. Thielges of the College of Agriculture, University of Kentucky, USA, under the auspices of the FAO International Poplar Commission, was presented as a background paper to the session of the ad hoc Committee on Poplar Breeding during the 17th Session of the IPC at Ottawa, Canada, in October, 1984. The work was partly conducted in the Commonwealth Forestry Institute (U.K.) and included travel in Europe. The help of all contributing national institutions: INRA, Institut National de Recherche Agronomique, Olivet (Orléans), France; SAF, Istituto di Sperimentazione per la Pioppicoltura, Casale Monferrato, Italy; Station de Populiculture, Geraardbergen, Belgium, is gratefully acknowledged.



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Introduction

The genus Populus represents a significant component of the world's potential renewable resources for the 21st Century. Readily-propagated, fast-growing and amenable to plantation culture, poplars have been planted for pulp and wood products in temperate and subtropical regions. They contribute significantly to some national and regional wood markets (Viart 1979a), and also serve as a substantial source of farm income in some countries (Prevosto 1979). It seems quite possible that poplar culture may offer some potential to provide a significant amount of biomass for energy production, especially on a regional level in developing nations (Zsuffa and Morgan 1982). Moreover, there is an admirable record of major gains in productivity through genetic selection and breeding, and improvement in cultural techniques. All of these attributes serve to make poplar an attractive option for planting in both developed and developing nations.

Because of the history, scale, and intensity of research and development programs in Populus there is a relatively large amount of information and experience available that may be applied to new programs in developing nations. Almost six decades have passed since the sustained poplar breeding efforts of Stout, Schreiner and McKee (Stout, *et al.* 1927) and, in the interim, the number of scientists engaged in poplar research and development has increased dramatically. For example, the most recent World Directory of Forest Geneticists and Tree Breeders (Nienstaedt 1978) lists almost 200 persons with some interest or involvement in the genetic improvement of Populus species. To assist in the direction and coordination of this work, the International Poplar Commission of the F.A.O., was established in 1947 and now includes 32 member nations. Three of these countries maintain special institutes devoted to poplar research and development programs for poplars and other "fast-growing species".

The investment in research and development has been justified and major strides have been made to improve the productivity and utilization of poplars. There is a less positive aspect of this 60-year record of accomplishment, however. Species of poplars are now commonly planted outside of their natural ranges and frequently in stressful environments in terms of biological agents as well as physical factors. The genetic base of selection and breeding programs in many countries remains essentially the same as it was at the inception of the program, and often is precariously narrow. At the same time, the genetic variability of populations of indigenous Populus species has been destroyed or significantly eroded, often as a direct consequence of major national genetic improvement programs and agricultural and reforestation practices utilizing introduced species and/or interspecific hybrids.

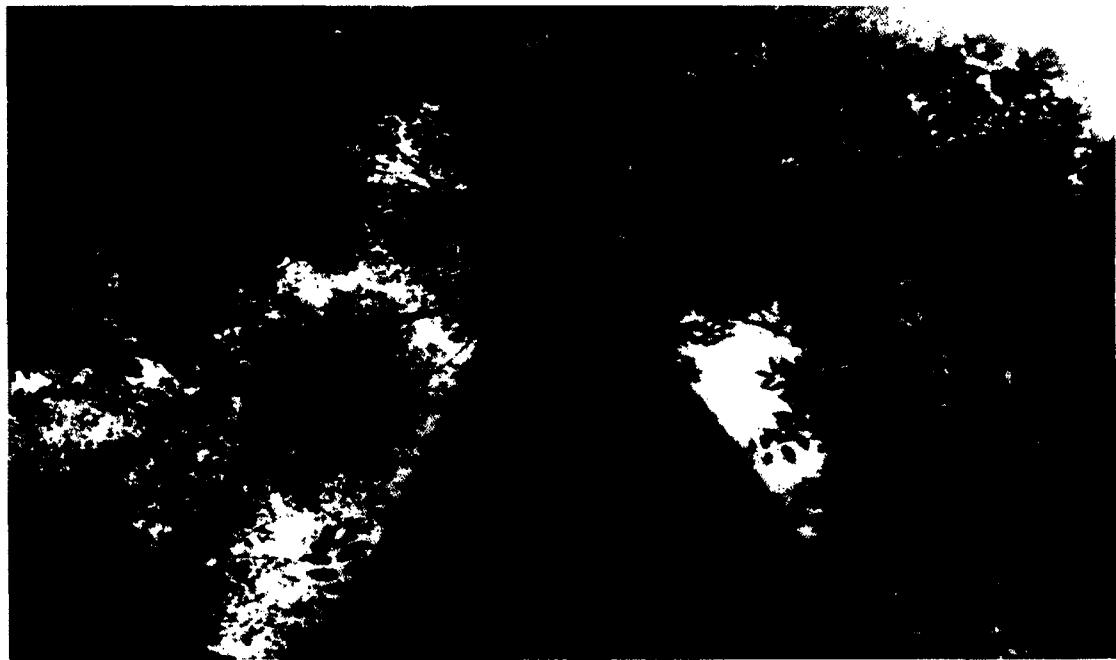
In a critical review of the history and current status of genetic improvement programs in Populus, Mohrdieck (1983) identified these shortcomings and many others. In what is probably the major premise of his paper, he questions the place of the element of time in the context of contemporary poplar breeding strategies. He is justifiably critical of the widespread and almost traditional (at least in Europe and North America) use of selection and direct clonal propagation as a breeding method to obtain immediate but limited short-term gains, and the almost total lack of breeding strategies that encompass longer-term goals and incorporate sexual reproduction to increase genetic variability and maximize potential gains (e.g. recurrent selection).

1. Mixed Poplar hybrid plot, Geraardsbergen, Belgium



Natural stands and/or plantations of Populus should be conserved as source populations for future genetic selections for disease resistance and growth rate.

2. Euramerican hybrid at Geraardsbergen



Selections should concentrate on outstanding phenotypes that not only have good form, rapid growth rate and desirable wood properties but also resistance to diseases that are prevalent

Since obtaining resistance to diseases is such an important aspect of genetic improvement programs in poplar, the question of long-term goals is important. A perennial species that will suffer 10 or more annual attacks by any number of dynamic, highly-variable pathogenic micro-organisms before it is harvested must arrive in the field as the product of a breeding program that has maximized its capacity to endure such a barrage of potential disease. The loss of the ability to withstand disease attack by a plant cultivar is often expressed as a "breaking-down" of its resistance. Obviously though, the genetic resistance system of the plant remains intact and it is the genetic capacity of the pathogen population that has changed to overcome the plant's resistance, usually as a direct response to selection pressures imposed by the widespread employment of one or a few "resistant" host genotypes (i.e. a change in the environment for the pathogen).

Thus, the breeding strategy we seek for poplars is one that will provide resistance that will persist over time. In contemporary parlance, such resistance is referred to as "durable". It has also been called "stable" resistance (and indeed, does imply relative stability) and since it is a property of the host as perceived by the breeder, could also be called "reliable" or "dependable" resistance. However, the term "durable" seems to be most widely used and accepted now (FAO 1983) and will be used herein.

For new programs in developing countries, the concept of durable disease resistance is extremely important; these programs cannot afford the major investment in scientific personnel, facilities and time needed for an alternative defensive or reactive breeding program. Durable disease resistance is a property of the host population, not of the individual genotype or cultivar, and thus its concepts are rooted in population genetics. Since many current poplar breeding programs were conceived and set in motion in an era predating the widespread application of principles of population genetics to tree breeding, it is appropriate to review and evaluate the potentials for durable disease resistance in poplars, in the light of current knowledge. Since new programs in developing countries will need to rely on information and technology from established programs in developed nations, we need to ask if the pre-population genetics philosophies and breeding strategies of poplar improvement programs are appropriate now. More specifically, what strategies are needed to maximize productivity and generate disease-resistant populations on a long-term basis? Are there alternatives to consider?

The objectives of this paper are not to criticize what has been done in relation to disease resistance in poplar, because most of what has been accomplished has been admirable. Rather, the objectives are to review some of the past and current research and development efforts, especially as they pertain to relationships between sustained productivity and durable disease resistance, and to use these as a basis for exploring some alternative ideas and breeding strategies that may be applied in developing nations.

Most of the ideas and concepts regarding disease resistance contained herein are not new to plant breeding and have their origins with the population - based resistance theories of Vanderplant (1963). Many aspects of the strategies presented have been thoroughly explored and promoted by the FAO (Robinson 1977, Buddenhagen and de Ponti 1983). They have been presented, in various aspects, during at least two major convocations on breeding for pest resistance in trees (Borlaug 1972, Browning *et al.* 1982, Segal *et al.* 1982). Not so surprisingly, some elements of these population - based strategies have also been applied to Populus, not only recently (Mohrdieck 1983, Thielges 1982, Weisgerber 1983), but more than a decade ago by Schreiner (1970) who advocated the establishment and maintenance of a broad genetice base in breeding populations, the

utilisation of localized gene pools and testing sites, and the employment of multiclonal varieties in production populations.

Poplars as a World Resource

The genus Populus is one of the oldest contemporary angiosperm genera and is believed to have originated in China and Japan (Khosla and Khurana 1982). Subsequent migration was characterized by widespread introgression which has left a fossil record of over 125 species. Today, the genus is still characterized by a relatively high degree of phylogenetic diversity and contains 30 to 40 species, depending upon one's perception of the taxonomic status of Populus alba L. These species are placed taxonomically into 5 sections - Turanga, Leuce, Aigeiros, Tacamahaca and Leucoides (Rehder 1940, Pourter 1979). Recently, a sixth section, Ciliata, has been proposed to include the Himalayan species P. ciliata Wall. ex Royle (Khosla and Khurana 1982). Populus species are found throughout the temperate and subtropical regions of Asia, Europe, North Africa and North America from about 22° N to 70° N latitude. One species, Populus euphratica Oliv., have an isolated population in equatorial Africa.

Because it is a variable and widely distributed genus, Populus species and hybrids are adaptable to a broad range of sites. This range of adaptability and other features such as relatively fast growth, desirable fiber and wood properties for a variety of products and, for species of some sections, ease of hybridization and vegetative propagation, have contributed to a significant plantation culture of Populus throughout the world. In addition to forest plantations for fuelwood, pulpwood, lumber, veneer and other products, poplar plantings have been employed for windbreaks, stabilization of slopes, river banks and roadbeds, reclamation of stressful sites such as surface - mined lands and former sea beds, and for aesthetic improvement. Nearly 1.5 million hectares of poplar plantations in Europe, Asia, Africa, the Mid-east, North and South America, Australia and New Zealand supplement and estimated 20 million hectares of natural Populus forests, located primarily in North America (Viart 1979b). The area of Populus plantations has been increasing steadily; in 1979, close to 150,000 hectares of new plantations were established world-wide (FAO 1979).

It has been estimated that more than 90% of the poplar cultivation throughout the world is concentrated on species of the section Aigeiros (Pourret 1979). This is primarily due to the ease of hybridization between species of this section (and, to some degree, between Aigeiros and Tacamahaca species), the broad adaptability of these species and hybrids to sites in temperate and subtropical zones, and their ready vegetative propagation by stem cuttings. For about 60 years, the breeding, selection, propagation and plantation cultivation of Aigeiros poplars has evolved to a significant level of activity on an international scale.

In recognition of the importance of the Aigeiros and Tacamahaca poplars and their hybrids in world cultivation and the significance of their potential for greatly increased use in programs of developing nations, the remainder of this paper concentrates on these two sections. For discussions of disease problems and breeding strategies in other sections of the genus, particularly Leuce, the reader is referred to recent reviews and reports by Mohrdiek (1983) and Weisgerber (1982, 1983).

Major species of sections Aigeiros and Tacamahaca in Plantation Culture

Section Aigeiros

Two major species of this section are employed widely in plantation culture both within and outside their natural ranges; Populus deltoides Bartr. which is native to North America, and P. nigra L. of Europe and Asia. These two species are undoubtedly also the most economically important and widely distributed in plantation culture of the genus. In addition to their use as species cultivars, the hybrids P. deltoides x nigra are the famous "Euramerican" hybrid cultivars (Populus x euramericana (Dode) Guinnier) which have been planted, world-wide, for decades.

Populus deltoides Bartr. is commonly known as eastern cottonwood or, simply, cottonwood in the United States and Canada. It has a large natural range which extends from the Atlantic coast to the great plains region (from about 70° to 115° West longitude), from south Texas and the entire coastal plain of the Gulf of Mexico to the Great Lakes Region of Canada and the United States (from about 27°-30° North latitude) in the east, to the Canadian Provinces of Manitoba, Saskatchewan and Alberta (about 52° North latitude) in the west. Two major varieties are recognized (Little 1971); P. deltoides Bartr. var. deltoides of the United States and Canada east of 100° West longitude, and P. deltoides var. occidentalis Rydb. (the "plains cottonwood") which occurs mainly to the north and west of the range of var. deltoides, although there is a significant area of sympatry between about 95-100° West longitude. Cottonwood attains very large dimensions (up to 40m in height at 35 years) especially on deep, well-drained alluvial soils in the southeastern United States. It is also able to survive and grow on a wide variety of less optimal drier and colder sites. It occurs extensively in pure or mixed stands regenerated from seed and is utilized for a number of products including pulpwood, veneer and lumber. Many cultivars of P. deltoides, such as 'Harvard', 'Lux', 'Canadian' and 'Saskatchewan' have been tested and released for commercial planting and are widely - distributed and grown under those names throughout the world.

Populus nigra L. is the major Populus species of Europe, western Asia and North Africa. It covers a range including most of the southern and central areas of Europe from about 30°-55° North latitude and from 15° West to 110° East longitude. Very few extensive natural stands of P. nigra remain, and most of these are in hilly or mountainous regions in the Mediterranean area. P. nigra is also adaptable to a wide range of environmental conditions, including very droughty sites, but it too survives and grows best on the deep, well-drained soils of river valleys. Taxonomically, the species is somewhat complex and some systematists propose a number (three or more) of subspecies. However, Pourter (1979) recognizes three major naturally-occurring varieties; two of them, P. nigra var. caudina Tenore and P. nigra var. neopolitana Tenore in southern Italy and the third, P. nigra var. thevestina Dode is found in the Near East, North Africa and the Balkans. There are many cultivars of P. nigra utilized in commercial culture throughout the world, among them P. nigra cvs. 'Italica' and 'Chile'.

There is another Aigeiros species that is native to the southwestern United States and also occurs in Mexico (Baja California), Populus fremonti S. Wats. Additionally, some taxonomists have accorded species status to geographic varieties of P. deltoides var. occidentalis Rydb., i.e. P. sargentii Dode and P. texana Sarg. (Rehder 1940).

Section Tacamahaca

This section encompasses all of the so-called "balsam poplars" and is one of the largest in the genus, comprising at least 12 recognized species, most of which are native to Asia or North America. Only two of these, however, have been of any significance in plantation culture and in breeding for disease resistance; Populus trichocarpa Torr. and Gray of Western North America and P. maximowiczii Henry of Asia. These species and a few others have been used as parents in crosses within Section Tacamahaca and also with Aigeiros species, primarily P. deltoides.

Populus trichocarpa Torr. and Gray is a fast-growing forest tree of the Pacific Northwest area of Canada and the United States. Its range extends northward along the Pacific coast from California through Oregon, Washington and British Columbia into Alaska (from isolated occurrences at about 32° North Latitude to about 61° North Latitude). It also has a rather extensive inland component to its range eastward through Southern British Columbia, Oregon, Washington, Idaho and Montana. P. trichocarpa is not only the largest poplar in North America but also the largest hardwood species of the Pacific Northwest. On very good sites, it may exceed 40 meters in height at 35 years. No taxonomic subspecies or varieties of P. trichocarpa are formally recognized but there are coastal and inland ecotypes; the inland type can tolerate drier sites and does not grow as rapidly as the coastal type. Several cultivars of P. trichocarpa are grown in Europe, perhaps the best known of which are cvs. 'Fritzi Pauley' and 'Blom'.

Populus maximowiczii Henry is native to Japan, Korea and eastern Siberia. It is a fast-growing tree which may attain large dimensions in natural, mixed forest stands. P. maximowiczii was used extensively in early hybridization programs in the United States (Schreiner and Stout 1934) and was the female parent of a number of widely used hybrid clones including 'Oxford' and 'Androscoggin'.

There are several other Tacamahaca species which may be of value in terms of providing a genetic resource of disease resistance in breeding programmes. Among these is Populus balsamifera L. which occurs transcontinentally in Canada and also in limited areas of the northern United States. This is a fairly large tree, capable of attaining a height of 30 meters or more at age 50 years. Several of the Asian species may be of interest as well, including Populus laurifolia Ledeb. of Siberia and a number of little known species from China, i.e. P. szechuanica Schneid. P. simonii Carr., and P. yunnanensis Dode which may well be hybridized and cultivated on a major scale in that country.

Some major Disease Problems of Populus

As might be expected in an ancient, genetically diverse and widely-distributed genus such as Populus, there has been a co-evolution of numerous parasitic organisms, many of which can be pathogenic. Additionally, the significant expansion of the ranges of Populus species through interspecific hybridization and plantation culture has provided for a greatly extended spectrum of pathogen contacts and challenges and has generated a complex set of host-pathogen interactions.

A list of more than 110 organisms that are pathogenic on Populus was compiled by Berbee (1964) and at least 75 of these pathogens are capable of attacking species of sections Aigeiros or Tacamahaca and/or their hybrids. Many of these diseases are relatively minor in terms of the damage they inflict, or are of limited distribution. Still others, such as Armillaria, Fomes, Nectria and Uncinula are ubiquitous and non-specific to Populus. Many, however, are obligate parasites on Populus and, in theory,

and be governed by genetically controlled interactions with the host plant which have evolved to the point that, in nature, host and pathogen populations are maintained in a state of dynamic balance. In general, even these diseases are not too damaging to native stocks of poplar; however, they have the capacity to cause significant mortality and/or loss of productivity when challenged by homogeneous monoclonal plantations and/or when introduced to an area of poplar culture wherein the new hosts have no native resistance.

It is with these latter diseases that this paper is concerned but it is beyond its scope and purpose to consider any but the most important of them. Fortunately, a review of the literature on the distribution, economic impact and control of Populus diseases provides a means of obtaining a consensus of the most dangerous pathogens, using these criteria:-

- economic importance of losses or potential losses caused by the disease;
- risks to developing nations, either from the pathogen being indigenous to the area or from its introduction from other areas of poplar culture;
- evidence of (or potential for) effective control through genetic selection and breeding against the disease.

Using these criteria, the five most damaging or potentially damaging Populus diseases and their causal agents are:-

Melampsora Leaf rust (Melampsora spp.)

- Marssonina antrachnose or leaf spot (Marssonina spp.)
- Xanthomonas canker (Xanthomonas populi Ridé)
- Bothiciella canker (Bothiciella populea Sacc. and Briard)
- Septoria leaf-spot and canker (Septoria musiva Peck)

These diseases, their impacts in plantation culture, and the potentials for selection and breeding for effective resistance to them are briefly summarized, below. Additional general references to the importance, impact, and management of these and other damaging poplar diseases are AFOCEL (1981), Barnéoud et al. (1982), Castellani et al. (1979), Mühl-Larson et al. (1979), Pinon (1984), Siwecki (1976a and b), Thielges and Land (1976a) and Viart (1979b).

Melampsora Leaf Rusts (Melampsora spp.)

Leaf rust, caused by a number of Melampsora species, is probably the most widely-distributed and serious foliar disease of the Aigeiros and Tacamahaca poplars and their hybrids. There are at least 8 Melampsora species capable of infecting these poplars, but most damage in plantation cultures may be attributed to these three species:-

- M. allii-populin Kleb. (Europe, North Africa)
- M. larici-populin Kleb. (Europe, Japan, South America, Australia, New Zealand, South Africa)
- M. medusae Thüm (North America, Southern Europe, Australia, New Zealand).

Other potentially-damaging Melampsora species are indigenous to India, China, Japan and Korea.

The rust fungus attacks poplar leaves in mid-summer. Heavy attacks, early in the season and in conditions of temperature and humidity favourable to the rapid development of the pathogen, are especially damaging. Prolonged severe attacks may cause significant

leaf necrosis leading to premature leaf abscission which can result in complete defoliation of very susceptible hosts. This early defoliation causes a significant reduction in growth and may also predispose the affected trees to secondary problems such as damage from early frosts and increased susceptibility to Dothiciza populea.

The economic impacts of *Melampsora* rusts may be substantial. Widin and Schipper (1981) have estimated that attacks by M. medusae may cause volume growth reduction up to 65% in susceptible poplar clones grown in plantations in the central United States. This pathogen is generally responsible for only a moderate level of mortality in plantations. However, in Australia and New Zealand where both M. medusae and M. larici-populina were introduced, the interaction of populations of these exotic pathogens with those of introduced poplars in clonal plantations, led to replacement of the commercial clones in those two countries in only a few years (Pryor 1976, van Kraayenoord and Wilkinson 1976). Locally selected, rust resistant clones are now planted (Pryor and Willing 1982).

Variations in susceptibility to *Melampsora* leaf rusts has been exploited to select resistant phenotypes for breeding and for direct clonal propagation, especially in Europe. High heritabilities have been calculated for resistance to M. medusae (Jokela 1966, Thielges and Adams 1975) and M. larici-populina (Siwecki 1980). Variable pathotypes of several of the rusts exist and have been reported for M. medusae in the United States (Shain, personal communication) and Australia (Singh and Heather 1982), for M. larici-populina in the Netherlands (van Vloten 1949), Belgium (Steenackers 1982), Australia (Chandrashekhar and Heather 1980, Heather et al. 1980) and New Zealand (Latch and Wilkinson 1980), and to M. allii-populina in Italy (Magnani 1965).

Additional information on the etiology, epidemiology and management of *Melampsora* rusts may be found in Heather and Chandrashekhar (1982), Shain (1976), Siwecki et al. (1982) and Taris (1968).

Marssonina Anthracnose or Leaf spot (Marssonina spp.).

Several Marssonina species are pathogenic on Aigeiros and Tacamahaca poplars and their hybrids but, from an economic standpoint, the two most important species are M. populi (Lib.) P. Magn. and M. brunnea (Ell. and Ev.) P. Magn. The latter species is especially destructive to poplars in plantation culture and is currently the major pest problem in Italy and other parts of Europe. In addition to its wide distribution in Europe and North America, M. brunnea has been reported in New Zealand, India, China, Japan and Korea (AFOCEL 1981).

This pathogen attacks leaves, petioles and succulent stems of susceptible poplars just at the time of bud burst and shoot growth initiation (Pinon and Poissonnier 1975). Brown spots appear on the infected tissue and these enlarge and merge to cause necrosis. Heavy and prolonged attacks may lead to defoliation. Severe infection of petioles and green twigs is a good indication of a high level of susceptibility to M. brunnea (Pinon 1980). As with the *Melampsora* leaf rusts, premature defoliation by Marssonina spp. causes a reduction in volume growth and may increase the host's sensitivity to other pathogens.

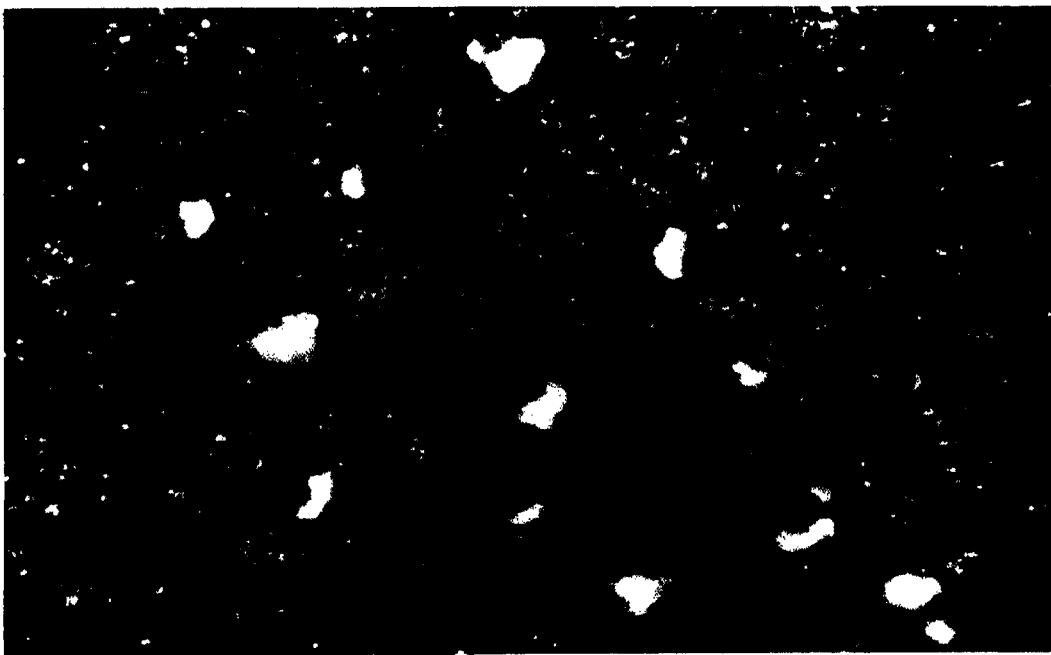
Marssonina brunnea has caused an estimated mean loss of 16% of wood volume annually in production plantations in Italy. Especially susceptible cultivars have suffered a growth loss of up to 60% (Castellani and Cellerino 1969). Similarly, a reduction of almost 60% of woody biomass was caused by M. brunnea attacks in nurseries in France (Pinon and Schvester 1983). Frequent and severe Marssonina attacks may also cause significant mortality (Van der Meiden 1962).

3. Bacterial canker on hybrid poplar near Nantes, France



Bacterial canker of poplars caused by Xanthomonas populi Ridé is a serious problem that has significantly affected poplar culture in northern and central Europe.

4. High magnification photo of Marssonina Leaf spot



Two of the most destructive foliar diseases of Populus are Melampsora Leaf rust and Marssonina Leaf spot (here, M. brunnea Ell. and Ev.). This high-magnification photo illustrates the extent of necrotic leaf tissue.
(Photos courtesy of Dr. Louis Shain, University of Kentucky)

As observed in a number of reviews, variation in susceptibility to M. brunnea is apparent at the species level and below (AFOCEL 1981, Castellani *et al.* 1979, Pinon 1984). Populus trichocarpa is extremely resistant to M. brunnea as are other species of the section Tacamahaca, in general. Populus nigra and P. deltoides generally vary from high levels of resistance to moderate levels susceptibility. Hybrids between P. deltoides and P. nigra (Euramerican hybrids) segregate across the entire spectrum of reactions in Italy, from highly resistant to completely susceptible. Spiers (1983) has observed variable pathotypes of M. brunnea on a variety of clonal species and hybrid hosts in New Zealand.

Additional information on Marssonina species may be obtained from AFOCEL (1981), Cellerino (1976, 1979), Cellerino *et al.* (1979), Pinon (1980 and 1984) and Schipper (1976).

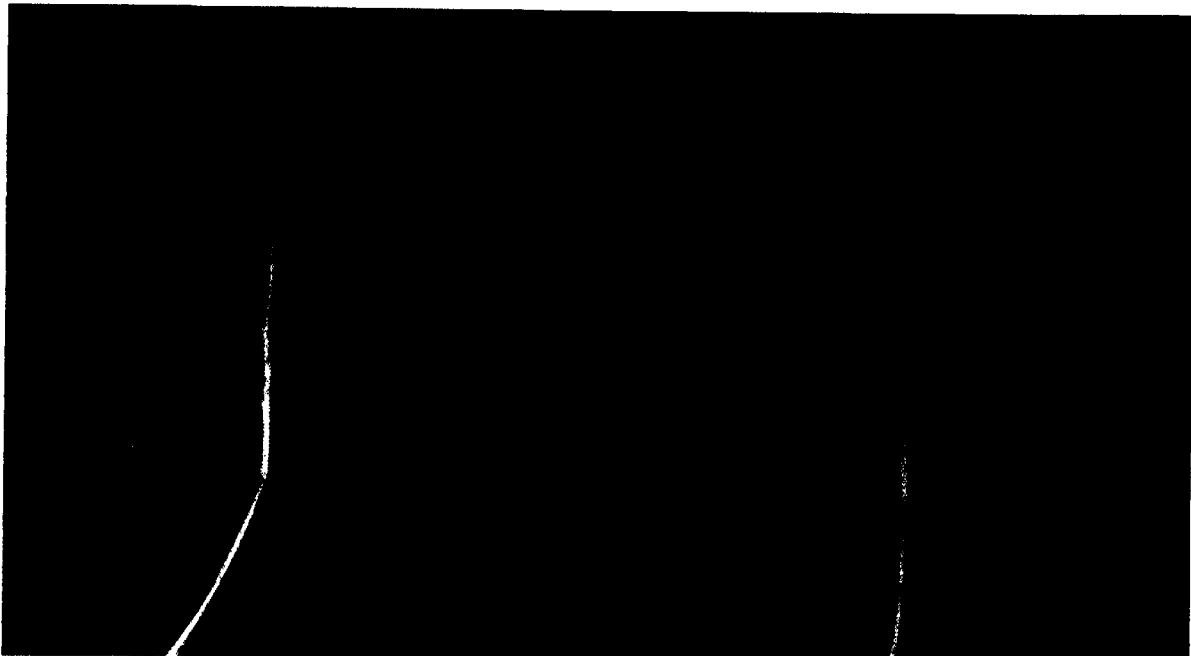
Bacterial Canker (Xanthomonas populi Ride)

This very damaging branch and stem canker has been known in Europe for over 100 years (Kechel 1982) but it was not until 1958 that its causal agent, an immobile, gram-negative, aerobic bacterium was identified (Ridé 1958) as Aplanobacterium populi Ridé. Subsequently, its designation was changed to Aplanobacter populi (Ridé 1963) and, more recently, to Xanthomonas populi Ridé (Ridé and Ridé 1978). This bacterium is highly specific to the Salicaceae and there are two subspecies reported, one of which is the cause of bacterial canker of Populus (X. populi subsp. populi Ridé) and the other the cause of a canker of Salix (X. populi subsp. salicis deKam (de Kam 1978). Subspecies populi is evidently characterized by a number of pathotypes; studies of a large number of geographic strains used to evaluate a series of standard reference clones indicated a pattern of continuous variation in pathogenicity (Ridé and Ridé 1978).

The manifestation and rate of progression of bacterial canker disease symptoms vary among Populus species and cultivars. The disease affects young plantation trees (up to about age 6) and the irregular, erumpent stem cankers which develop 1-3 years after infection of susceptible hosts are extremely damaging. Active cankers induce changes of tree form by stem breakage and subsequent sprouting, and also cause massive degradation of wood, even when they are healed-over. Large cankers or multiple cankers may kill trees by girdling the stem. Because of variability in rates of auto-infection and because external evaluation of small or apparently healed cankers may be misleading, it is difficult to screen trees for resistance to bacterial canker disease. Cankers that appear to be benign often harbor active bacteria internally, thus dictating additional screening of isolates from the cankers (Kechel 1982). Because of the difficulties with inoculation, screening, and evaluating levels of resistance to bacterial canker in the field and in the laboratory, a major international program is now operative to standardize these and other procedures (Ridé 1982).

Bacterial canker in Europe is generally more pathogenetic on Populus deltoides, P. trichocarpa and P. maximowiczii than it is on the native P. nigra (Koster 1971, Steenackers 1972). Field tests of large numbers of clonal cultivars of species and species hybrids have yielded a wide range of variation in susceptibility (Kechel 1983, Ride 1982). Additional information on bacterial canker disease may be obtained from Burdekin (1972), Castellani *et al.* (1979), and Ride (1980).

5. Poplar leaves, one infected one not infected with Melampsora



Genetic differences in susceptibility to diseases are often readily apparent in the field as shown here for Melampsora medusae Thüm.

(Photo courtesy of Dr. Louis Shain, University of Kentucky).

6. Leaf sections infected with Melampsora in an in-vitro test



Genetic variation in disease susceptibility may also be evaluated through in vitro tests as illustrated for Melampsora medusae Thüm. (Photos courtesy of Dr. Louis Shain. University of Kentucky).

Dothiciza Canker (Dothiciza populea Sacc. and Briard)

Dothiciza canker is a wide-spread and very significant disease problem of poplar plantations in Europe. It has been reported on a number of species and hybrid cultivars in North and South America (Berbee 1964) but, at least in North America, Dothiciza canker is of minor importance (Filer 1976).

The pathogen attacks both branches and stems and is initially recognized by the presence of clear; chestnut-coloured spots of various sizes on the bark. As disease progresses, the spots darken to deep brown or black, forming a blister or depression. The cambium and woody tissue beneath these structures become moist, discoloured and, finally, necrotic. As the necrotic areas increase in size, the branch or stem may be girdled and the host tree may be killed.

This disease is often associated with epidemics of others diseases, such as Melampsora leaf rusts or Marssonina leaf spots, and it is capable of causing heavy and wide-spread economic losses. Steenackers (1982) has attributed the high mortality observed in stands of P. euramericana var. robusta in Belgium to severe outbreaks of D. populea following an epidemic of Melampsora leaf rust.

Of the several important disease of Populus discussed herein, Dothiciza canker is probably the one for which there is available the least amount of information on the potential for genetic improvement of resistance. The evaluation of the degree of genetic control of susceptibility to Dothiciza is often difficult and confusing because it is a disease commonly related to physiological intolerance or environmental stresses in the host population. It is often associated with moisture stress, freeze damage, physical injuries or, as mentioned earlier, with attacks by other pathogens. Some pathologists consider improved nursery and plantation cultural practices and chemical control in nurseries and new plantations to be the most efficient and effective ways of managing this disease (Filer 1976, Cellerino and Lapietra 1979).

On the other hand, there have been a number of reports of clonal differences in susceptibility to Dothiciza canker, especially among Euramerican hybrids. For example it was generally considered that the cultivar 'I-214' was much more resistant to Dothiciza canker than the cultivar 'Robusta', especially in northern and central Europe. Recently, however, 'I-214' has been heavily damaged by Dothiciza canker in Germany and Yugoslavia (Marinkovic 1980). Thus, there is a possibility that new, more virulent pathotypes have evolved or have been introduced in those areas. Magnani (1959) hypothesized that there were more virulent pathotypes of Dothiciza populea in northern and central Europe than in southern Europe as an explanation for the originally observed differential susceptibility of 'I-214' and 'Robusta'. Finally, Siwecki (1980) and Herpka (1982) have provided statistical evidence for genetic control of susceptibility to Dothiciza populea by calculating high broad- and narrow-sense heritabilities for canker resistance in progenies of various intra- and interspecific crosses in Populus.

Additional information on Dothiciza stem canker may be obtained from a number of general reviews (AFOCEL 1981, Siwecki 1976a & b).

Septoria Leaf Spot and Canker (*Septoria musiva* Peck)

This fungal pathogen has been very damaging in plantations of hybrid poplars in North and South America. In fact, it has been such a problem that it has effectively prevented the general utilization of Euramerican hybrids in Canada, the United States and Argentina. Because it is especially virulent on these hybrid cultivars, it poses a significant threat to poplar culture world-wide, especially in Europe and Asia where Euramerican hybrids are widely-planted. In contrast to its pathogenic action in hybrid plantations, *S. musiva* is generally limited to a leaf spot disease in native poplar stands in North America (Waterman 1954). However, it may spread from the foliage to branch and stem tissue where it forms small cankers that may serve as infection sites for other canker-producing pathogens such as *Cytospora*, *Dothiciza* or *Fusarium*. Because of these tendencies to predispose the host to other pathogenic organisms, *S. musiva* has been referred to as a "pioneer organism" on *Populus* (Filer 1976).

On hybrid poplars with Aigeiros or Tacamahaca parentage however, the Septoria canker is generally more active and aggressive. On these highly susceptible hosts dark brown bark cankers may form and develop to the extent that the tree's growth is retarded and wood quality is significantly degraded. Several cankers may grow together, effectively girdling the stem and killing the tree. In plantation culture, total biomass of susceptible hybrid clones may be reduced by over 60% in 3 years (McNabb, et al. 1982).

It was observed very early on that there was clonal variation among hybrid poplars in susceptibility to Septoria canker, and that there seemed to be more resistance in *P. deltoides* than in *Tacamahaca* poplars. These observations have been confirmed by more recent studies in Canada (Zalasky et al. 1968) and the United States (Moore et al. 1982) and these later studies have also reported a wider range of clonal variability in resistance. There is a good correlation between heavy Septoria leaf rust infection and susceptibility to Septoria canker; thus, efficient nursery screening for leaf spot will effectively select against Septoria canker (Filer 1975).

Other Potentially Dangerous Diseases

Two other diseases of *Populus* are worth brief consideration because of their potential for world-wide damage to poplar culture. Both of these pathogens are easily transmitted via infected poplar stem cuttings. Hence, there is a great danger that they may be introduced to developing nations in breeding stock obtained from elsewhere in the early development of a breeding program.

The first of these diseases is Poplar Scab (also called "Travelures" in France) caused by *Venturia populina* (Vuill.) Fabr. (conidial form, *Pollacia elegans* Serv.) This disease is characterized by defoliation and dieback or withering of young shoots. It is especially dangerous and damaging because it attacks early in the growing season, hence the name "spring defoliation" in Italy. In the 1930's, this disease caused annual losses in productivity of up to 35% on "Canadian" (northern *P. deltoides*) cultivars in the Po Valley and the search for resistance to *V. populina* was the subject of a successful genetic selection program by Jacometti (Cellerino and Anselmi 1982). As a result of this program, the increased cultivation, in Italy and elsewhere, of hybrids of more southerly selections of *P. deltoides* ("Carolinians") relegated Poplar Scab to a disease of minor importance. *Venturia populina* has, however, remained endemic in Italy, France and elsewhere in Europe in relict stands of "Canadian" poplars in piedmont and mountain areas. More recent selection and breeding for resistance to *Marssonina* has resulted in a reintroduction of genes of northern selections of *P. deltoides* in production cultivars and it

is feared that Venturia may again become a significant pathogen as these new cultivars are more widely distributed and cultivated in great numbers (AFOCEL 1981, Cellerino and Anselmi 1982, Taris 1980).

The other potentially damaging organism is Poplar Mosaic Virus (PMV) which originated in Europe and quickly spread to Japan and North America via the exchange of *Populus* stem cuttings among researchers. The virus causes a classic light green-yellow mosaic or mottling of poplar leaves and petioles. It is especially damaging on 2 to 3-year-old plants in stool beds or nurseries where it causes necrosis and shoot fasciation of infected individuals. Poplar Mosaic Virus is capable of causing serious growth losses in young plantations established with infected cuttings. It seems to be most damaging to *Populus deltoides* selections of southerly origins and to hybrids with that parentage (Anselmi and Cellerino 1982). Efficient bioassays and immunological tests have been developed to detect the presence or absence of PMV in breeder's stocks (Cooper and Edwards 1980) and nursery selection for resistance and the exclusion of infected plant material from propagating beds should be effective in controlling the spread of Poplar Mosaic Virus.

Disease Severity in Natural Stands and Plantations

Without exception, all of these diseases have the potential to limit significantly the survival and productivity of *Populus* over major areas of its natural and extended range. Also without exception, these diseases have a much more severe impact on plantation culture of poplars than in wild stands. Actually, in regard to the frequency and the severity of disease epidemics over the past 50 years, poplar growing has much more in common with the cultivation of agricultural crops than with classical forest plantation culture. In general, poplar cultivation is characterized by the same "cropping system" employed for annual crops and this amounts to a more-or-less widely planted, uniform monoculture of a single clone.

In plantation culture, the poplar host, which in nature is characterized by heterogeneous populations of outbreeding, heterozygous individuals, is limited to one or a few vegetatively-propagated genotypes. This static, homogeneous population of the poplar host is set in place to challenge one or more potentially damaging pathogen populations which are dynamic and, in nature, very heterogeneous. Obviously, it is only a matter of time until the pathogen population becomes, through selection, genetically adapted to this ubiquitous host genotype, thus efficiently parasitizing the entire host population.

In Europe, this plantation system of host/pathogen confrontation has led to the need for several decades of defensive or reactive breeding (or, more accurately, selection and clonal propagation) to maintain resistance in commercial plantations. In fact, it is probably fair to say that the ease of vegetative propagation has, in the face of cycles of severe disease problems, been the salvation of the commercial growing of black and balsam poplars in Europe. At the same time, it may also be accurate to observe, as did Mohrdiek perversely, inhibited the development of broadly-based genetic improvement programs in *Populus*. This is especially unfortunate in the case of philosophies and strategies regarding disease resistance; faced with a disease emergency, vegetative propagation has served as a handy and, in the short-term, effective solution to the problem. Unfortunately, it has also effectively served to obviate the need to develop long-term breeding strategies with goals of attaining more durable or stable population-based resistance to pathogens.

Contemporary poplar culture epitomizes the transitional trend in forestry away from systems of extensive management of natural stands of mixed species and/or uneven age classes toward systems of intensive culture of monospecific and, usually monoclonal even-aged plantations. Many of the same factors that influenced the rapid development of modern or "mechanized" agriculture a century earlier have contributed to this transition in forestry. These factors include greatly increased demand for wood products, the relative scarcity and increasing cost of land for forest culture in the face of competing usages, the need for increased quality and uniformity of products, and significant developments in mechanical planting, harvesting and processing equipment and systems.

To exploit more fully the potentials for productivity, breeders of agronomic and horticultural crops applied genetic principles to their crop systems and obtained rapid gains in yield and quality. Cultivars that are characterized by their great degree of uniformity in germination, growth rate, plant form and size, time of maturity, shape and size of fruit or head, and chemical content were developed and released to commercial growers. In general, these uniform cultivars were designed to be planted, cultured, harvested and processed over a broad geographic area. Variability due to interactions with the local environment could be amended by nutritional or chemical additives, if necessary. Theoretically, this product and/or yield-oriented homogeneity in the highly artificial crop population or agroecosystem was obtained at the expense of losing the buffering heterogeneity, or homeostasis, that was inherent in wild or landrace populations of these plants.

The resistance to damaging pathogens of many of these genetically homogenous crop cultivars has periodically failed under pressure of a rapidly-evolving microorganism, and this has generated cycles of serious disease epidemics. In response to this, the majority of breeding efforts in agronomy and horticulture over the past several decades have been aimed at restoring the genetic resistance of these cultivars that has "broken-down".

The observed "breakdown" of resistance is, in reality, the predictable outcome of the interaction of a host population of one or a few genotypes and a much more variable and highly mutable pathogen genotype. The former exerts tremendous selection pressure on the latter, which favours the greatly increased frequency, in the pathogen population, of that genotype or genotypes which can overcome the host's resistance mechanisms by evolving to a degree of physiological specialization.

This situation is generally a consequence of breeding strategies that employ selection and breeding techniques that develop and favour the performance of individual genotypes at the expense of population homeostasis. The epidemics are simply artifacts of intensive agriculture caused by employing this limited host genotype too widely and in highly artificial, homogenous populations. In this plantation monoculture, the innate host-pathogen balances of the natural pathosystem have been significantly modified to favour the pathogen. To perpetuate the plantation culture, these balances can only be restored by chemical control and/or continual "defensive" selection and breeding, and then only temporarily.

In Europe and some areas of North America, poplar production systems have been committed for some time to major investments in a plantation culture that has been designed to produce a uniform quality of wood or fiber at a maximum yield per unit of land area. Even though, in many situations, the individual increments of land are relatively small and held in many ownerships, the overall result is that substantially large areas of land are devoted for periods of 10 to 25 years or more to even-aged, generally monoclonal stands representing genetic populations that are infinitely more restricted

than those represented in natural ecosystems. These artificial populations of poplars, the product of human design and strategy, are established in a milieu of relatively unmodified pathogen populations.

Unfortunately, the temporal, spatial and biological environment of the poplar plantation greatly favours the pathogen and the risks are even greater when the poplar host is an exotic or off-range species and/or the plantation is on a poor or marginal site. In truth, a poplar plantation is a much riskier venture, in terms of its potential to suffer damage from pathogens, than its agronomic counterpart. Much of this increased risk is due to differences in the factor of time, in both the absolute and relative sense. A poplar plantation, in contrast to an annual crop, must have the capacity to endure multiple and variable periods of potential infection. Over a harvest cycle of 10 years, extremes of climate, mechanical damage and insect depredation may serve to weaken the host trees and thus increase their susceptibility to infection by pathogens. More importantly, the genetically static poplar host must prevail for 10 years against dynamic pathogen populations that are highly mutable, are characterized by the capacity for both sexual and asexual reproduction in the same generation, and may be seasonally polycyclic. In poplar culture, and in forest plantation management in general, a destructive mid-cycle disease epidemic is more damaging, operationally and economically, than one occurring during the first year after planting.

On a broader scale of time, the pathogen is definitely at an advantage in a situation of defensive or reactive breeding to counter a more virulent pathotype or an introduced pathogen. In this situation, vegetative propagation may only partially offset the definite disadvantage posed by the relatively long life cycle of the poplar host as compared to the pathogen.

Last, but certainly not least, breeding and selection and testing for disease resistance are costly activities not only in terms of time, but in facilities, personnel and funds as well. At the best of times there is a shortage of scientific manpower and funding in relation to the urgency and magnitude of pathogen problems. This tends to favour short-cuts or incomplete studies aimed at providing, within a relatively short time frame, general solutions to disease problems that may be easily and uniformly applied over relatively large and diverse geographic areas.

If significant, long-term progress against pathogens that damage or destroy poplar plantations is to be obtained, breeders must operate with the knowledge that the very creation of a plantation culture form a significantly narrowed genetic base upsets the natural host-pathogen balance, in terms of genetics and epidemiology, in favour of the pathogen. Consequently, the breeder must employ selection, breeding, and propagation techniques that minimize this negative balance. Further, and most importantly, these techniques must be used in a breeding strategy that is aimed not at the improvement of the individual host tree genotype, but at the genetic improvement of the host population with due understanding of the biology of the pathogen.

This is especially important and critical to long-term genetic gains in a genus such as Populus which, being dioecious, is an obligate outbreeder that has maintained itself in the wild, despite predacity by many pathogens and insect pests, by presenting these damaging agents with large, heterogeneous populations composed of heterozygous individuals. Adoption of long-term philosophies and breeding strategies is even more important in those species of poplar that are easily propagated by cuttings, thus providing breeders with a strong temptation to utilize this technique not as merely one means of obtaining gains in a long-term breeding strategy but as the primary or even

sole technique in a program that hinges upon the field selection and direct propagation, on a commercial scale, of limited clonal material (one or a few resistant cultivars). This serves effectively to circumvent the possibilities for genetic improvement offered by sexual recombinations of selected parents and recurrent selection. In other words, one must resist the strong temptation to use vegetative propagation not just as one means to an end of genetic improvement, but as an end in itself.

Populus Breeding Programs and Disease Resistance

A detailed review of the historical development and current status of world-wide programs in Populus breeding is beyond the scope and purpose of this paper. The topic has been addressed previously, however, (Mühle-Larsen *et al.* 1979), and most recently by Mohrdiek (1983). Additionally, a more comprehensive review of earlier efforts in breeding for disease resistance was provided by Schreiner (1963). The primary purposes of the summary treatment of historical aspects of breeding for disease resistance in this discussion are to emphasize the close connection between poplar diseases and the development of genetic improvement programs, the major priority that resistance to diseases has assumed in selection and breeding programs, and the significant impacts of these cause-effect linkages on the development of philosophies and strategies for poplar breeding and management over the past 70 years.

The depredations of a number of diseases have always served to set limits on the economical culture of poplars, not only through their impacts on stand productivity and/or survival, but also because of their abilities to cause significant degradation of wood quality. Even though many of these destructive diseases have always been part of the ecosystem in which pure or mixed stands of poplars naturally grown, they do not often pose a major problem in these situations. One reason, of course, is that the genetic and spatial relationships in natural stands regulate host-pathogen interactions and maintain an effective balance which seldom is shifted to favour the pathogen to a point where a disease "epidemic" is evident (Browning, 1979, Robinson 1979). Also, as Schmidt (1978) observed, the functional diversity of natural forests often masks the damage caused by indigenous pathogens particularly when one does not distinguish between disease incidence and disease loss.

Nevertheless, just as in agricultural crops, disease incidence and impacts are always biologically and economically more severe when forest trees are grown in plantations and this seems to be especially true for the poplars, which are normally grown in monoclonal plantings. This was as true 60 years ago as it is in 1984. The poplar selection and breeding work begun in 1924 by McKee, Stout and Schreiner for the Oxford Paper Company is generally credited with being the first large-scale, industrial production-oriented program for the genetic improvement of forest trees. This work was initiated following a severe epidemic of Melampsora rust which had almost entirely eliminated the Euramerican hybrid (P. deltoides x nigra) clones "Eugenei" and "Regenerata" from the company's nurseries in Maine. These hybrid clones had been imported from Europe where they and many others had been selected from spontaneous (or "natural") hybrids between the native P. nigra L. and P. deltoides Bartr. which had been introduced into Europe in the mid-18th Century. They were of interest to the company because it was found that they grew much faster than the native aspens (P. tremuloides and P. grandidentata) and balsam poplar (P. balsamifera). As the propagation and planting of these Euramerican clones increased, so also did significant disease problems; in addition to Melampsora rust, these imported clones were damaged by Dothiciza and Cytospora cankers. Thus, this earliest major program of poplar improvement that employed actual breeding

was undertaken specifically to produce new hybrid poplars that would be resistant to these diseases and still outgrow the native poplars and the introduced hybrid clones from Europe (Stout and Schreiner 1933).

Even Augustine Henry, the man to whom the first written record of successful *Populus* interspecific hybridization is generally ascribed (Henry 1914), was eminently aware of and concerned with the need for increasing the resistance of poplars to disease. In his 1914 paper Henry, in discussing the increase in "vigour" to be gained by producing F_1 interspecific hybrids, observed that "individuals of great vigour are undoubtedly less liable than weaklings to the attacks of fungi".

Convinced of the gains in growth and disease resistance to be obtained through hybridizing plants Henry, who was Professor of Forestry in the Royal College of Science at Dublin, began actively promoting the interspecific hybridization of forest trees as a major research and development activity, to be undertaken in the best interests of the country (Henry 1910). At about the same time, he and a number of associates at the Kew, Cambridge and Glasnevin Botanical Gardens and at other locations in England and Ireland, began a rather ambitious project of controlled, interspecific crosses in *Populus* and a number of other forest tree genera. In 1912, two hybrid poplar progenies were produced, one of which was the result of a successful cross between *Populus angulata* (*deltoides*) x *trichocarpa*. This progeny grew very rapidly and one seedling attained a height of over 10 feet (3.3m) in 27 months; this seedling was cloned and designated *Populus generosa* Henry (Henry 1914).

I have provided these detailed results of Henry's historical experiments in the genetic improvement of poplars to illustrate that obtaining increased disease resistance was a stated primary objective even in this earliest documented work. Additionally, and somewhat amazingly, Henry forwarded a philosophy for selection and propagation that, even more remarkably, has dominated the genetic improvement activities in the genus *Populus* since 1914 when he observed that "the first-cross (F_1) does not come true from seed; and it would be a great drawback if we were obliged to wait until the newly-made trees bore flowers and fruit. The first-cross, in short, can only be multiplied by vegetative reproduction. This is easy when the trees are readily propagated by cuttings, as in the case of poplars and willows." Later, in the same paper, Henry was of the opinion that "it is evident that when a valuable hybrid has been produced, it can be propagated and put on the market, if necessary, without delay."

Thus, in 1914, Henry essentially provided not only an idea for increasing tree growth rate and disease resistance through hybridization (and rather detailed descriptions of the techniques for doing so, incidentally) but he also formulated a genetic improvement strategy and a production philosophy that have dominated the cultivation of poplars for 70 years with very little, and only recent, modification. This strategy consists of random interspecific hybridization, selection for rapid growth and disease resistance from among the F_1 progeny, direct vegetative propagation of the selections, and their rapid employment in monoclonal production populations.

It is not at all surprising then, that the direct establishment of clonal plantations and line plantings of natural and artificial poplar hybrid clones, together with clones of "Carolinian" and "Canadian" selections of *P. deltoides*, gradually but very effectively displaced the natural stands and plantations of the native *Populus nigra* L. in many countries. Ironically, in the 1930's, many of the clones developed in the Oxford Paper Company program were imported by European countries and these undoubtedly provided

a much greater contribution to the plantation poplar culture of Europe than they ever did to that of North America.

The steady conversion of natural stands and landrace plantations of P. nigra to monoclonal plantations of exotic species and hybrids was accompanied by a concurrent increase in observable mortality, damage and loss of productivity caused by a number of disease organisms. Many of these diseases were indigenous but others, such as Marssonina brunnea, were imported with their exotic host. Often, disease problems became severe within 5 to 10 years following a change to the exotic cultivars. The general reaction to this increase in disease incidence and severity provided the stimulus for the transition of most European programs in poplar research and development from efforts concentrating on simply selecting clones and vegetatively propagating them for commercial release, to those employing directed breeding (at least in terms of producing intra-and interspecific F_1 hybrids from disease resistant parents) and the selection and testing for disease resistance.

Cellerino (1982) has succinctly and graphically chronicled the pattern of parallel evolution of monoclonal poplar culture characterized by a progressively decreasing genetic base which is primarily of exotic origin, and the consecutive cycles of severe epidemics of various diseases in these plantations which, in turn, have occasioned the need for consecutive cycles of reactionary or defensive breeding and selection to alleviate the situation. He describes the situation in Italy between 1915 and 1982, but the cause-and-effect pattern and the timing was much the same throughout central and southern Europe. In terms of pathosystem genetics, European poplar culture disease history is probably the best forestry example analogous to the "boom-and-bust" cycles of disease-limited productivity that have been characteristic of intensively cultured and narrowly-bred agronomic crops. For new programs of Populus culture, particularly those contemplated in developing nations, the Italian-European experience is worthy of close analysis; it illustrates many of the most important concepts to consider when formulating breeding strategies and management policies that have the incorporation of durable disease resistance as a major goal.

As recounted by Cellerino (1982) the Italian poplar culture in 1915 was mainly confined to the upper Po Valley; clones of (northern) P. deltoides x nigra hybrids were planted at wide spacing and those disease problems that existed (Dothiciza, Valsa, Melampsora) were not too acute because the wide spacing in the plantations, and the numbers of different natural hybrid clones that were used effectively slowed the dispersion of diseases. After 1915, there was a major epidemic of Venturia populina which began in Turin and, in 15 years, covered a large area of the country. Between 1915 and 1930 a program of genetic selection against V. populina and the other diseases which were most prevalent on "Canadian" or northern clones of P. deltoides and its hybrids was conducted by Jacometti. As a result of this work, poplar growers made a massive and fairly rapid conversion to growing only the southern or "Carolinian" P. deltoides selections, or hybrids of these. These clones were generally resistant to V. populina and the necrotic bark disease but were, unfortunately, subject to a viral disease which was not immediately observed and diagnosed. As the virus progressed, it was selected against and, in 1928, the clone "I-214" was developed and released. This clone was resistant to most of the diseases prevalent at the time, including the leaf rust caused by Melampsora allii-populi which had developed into a contemporary problem.

From 1940 to 1965 clone "I-214" became the mainstay of commercial plantations and it eventually came to represent about 65% of the entire poplar culture of Italy, by this time primarily because of its high level of resistance to Melampsora rust. In June of

1963, however, an epidemic of Marssonina brunnea was reported in Belgium and the Netherlands. It spread southward to Italy within 3 months and, by 1964, all of the Italian poplar culture, including clone "I-214", was affected. In the area between Casale Monferrato and Venice, it was possible to grow "I-214" only with chemical control of Marssonina, and most of the other commercial clones could not be commercially grown at all. From 1964 to 1980, about 75% of the poplar breeding effort in Italy concentrated on finding resistance to Marssonina.

Fortunately, several fast-growing and Marssonina resistant clones have been developed but, ironically, this work has reintroduced into commercial clones and breeding populations the genes of northern selections of P. deltoides, and there is now a fear that Venturia populina may once more be a problem in Italian poplar culture. Thus, in 60 or 65 years, the disease situation in Italy is poised to come full circle from successive cycles of selection and breeding against Venturia, virus, Melampsora and Marssonina.

To safeguard the commercial poplar culture of Italy against a recurrence of Venturia and possible epidemics of other diseases such as Melampsora medusae and Xanthomonas populi, which do not now occur in Italy but are found in several neighbouring countries, the breeding strategy has been significantly altered. The program now is geared to produce F_1 hybrids from controlled crosses between P. deltoides and P. nigra, utilizing over 250 parents of each species that have been selected for growth rate and resistance to diseases in greatly-expanded provenance and a half-sib progeny tests. Large numbers (100,000 or more) of P. deltoides seedlings were obtained from appropriate climatic areas in the United States in the 1960's, and an intensive program of selection of native P. nigra provenances and families has also been completed. The crossing program is designed so that both general and specific combining abilities of each parent can be determined. These criteria will be used eventually to reduce the breeding population to about 80 parents of each species. A rigorous selection program is employed in the evaluation of F_1 progeny to eliminate poor families from the breeding population. Resistance to diseases is the highest priority in the initial phases of selection, followed by growth rate/yield and wood quality.

It is fair to say, despite some local variation in the specific diseases and in their sequence and timing, that there has been a similar evolution of disease resistance breeding program for poplar in other European countries, as well. Successive waves of epidemics of Venturia, Melampsora, Dothiciza, Marssonina and, in central Europe, Xanthomonas have, in general, set in motion a gradual but general trend of less reliance on breeding strategies that are centered on random mass production and screening of hybrid material of various types and the direct propagation of resistant seedlings as clones to be tested for commercial release. There has been a noticeable shift to strategies employing a systematic, pedigreed base for selection and breeding and more interest in investigating alternatives such as recurrent selection and development of multiclonal lines. These shifts in philosophy are important because they represent the employment of powerful techniques which should significantly increase the genetic base of both the breeding and production populations, thus serving to improve the potential for developing durable disease resistance in Populus.

Genetics, Epidemiology, and Durable Disease Resistance in
Wild Pathosystems

Over the past 20 years, pathologists, geneticists, and breeders have begun to examine the very major differences observed in plant host-pathogen relationships in nature and under cultivation. In general, the former situation is characterized by stability of disease incidence but lower levels of productivity, and the latter by the potential for increased productivity but accompanied by marked instability of disease incidence typified by frequent epidemics limiting productivity and, indeed, threatening the very survival of the plant in a crop system. Out of this process has come a critical examination and reevaluation of past ideas, techniques and strategies regarding disease resistance breeding and the formulation of concepts and methodologies which have contributed to the development of new, alternative strategies for attaining the goal of durable disease resistance in productive populations of cultivated plants.

Most of the material concerned in this discussion is familiar by now although some of it is still controversial. Much of this controversy seems, upon review, to center upon the semantics of some new terminology, which is unfortunate and counterproductive. However, there are also some more legitimate areas of contention which concern these new theories and their applications to crop breeding and management. Introductions to the basic topics of pathosystem genetics and population-based breeding for disease resistance and recent reviews of their application are provided by Browning (1979), Browning *et al.* (1982), Day (1975, 1977), Fry (1982), Nelson (1978) Robinson (1979, 1980, 1981) Simmonds (1979) and Vanderplank (1963, 1968, 1975, 1982).

The concepts and applications of durable, population-based disease resistance are especially appropriate to the breeding of Populus and other forest trees. The inherent capacity of forest ecosystems to "buffer" disease was reviewed by Dinus (1974) and Schmidt (1978), and Thielges (1982) discussed the biological, physical and economic attributes of forest trees and their plantation culture that provide distinct advantages for the attainment of durable disease resistance in production systems as compared to agronomic or horticultural crops. Prior to an examination of the breeding strategies most appropriate to obtain durable disease resistance as an integral feature of the Populus plantation culture in developing nations, a review of some principles of pathosystem genetics and how these affect balanced, population-based resistance in production populations is needed.

Until about 1970, the goal of most programs involved with breeding for resistance to plant diseases was the protection of the individual plant. The host genotype was rearranged by hybridization, backcrossing, selfing or other appropriate techniques to enable it to ward off diseases caused by its interaction with specific virulent pathotypes or "races" of a pathogen. These Mendelian methods were, generally, aimed at obtaining a "good source of resistance" and were applied by screening the host against the virulent pathotype. These "defensive" breeding strategies, based upon tailoring a cultivar to resist a specific pathogen race, were significantly reinforced and encouraged by the gene-for-gene resistance concept (Flor 1956). Despite very significant progress in obtaining resistant cultivars of many crop plants by these methods some major problems soon developed. When confronted with a new and different disease race or pathotype the resistance of many widely-planted cultivars appeared to "break down" and new genes for resistance to this virulent pathotype had to be found and incorporated into the productive cultivar. Thus, many crop systems became characterized by a situation in which each resistant cultivar was selected and bred to the point of "physiological specialization" against a specific pathotype (or a few pathotypes) but it might well be highly susceptible to a spectrum of other virulent pathotypes. These potentially destructive pathotypes might

7. Mixed stand of *P. deltoides*, *P. nigra* and hybrids near Orléans, France



Selections must be adequately field-tested for disease resistance on or near the sites where they will be planted before they are released for production. In this test at the I.N.R.A. Laboratory at Orléans, France, the taller trees are a Melampsora rust-susceptible clone which serve as a source of inoculum for the test trees in the foreground. As the season progresses, the test trees are evaluated for resistance to local rust strains under field conditions.

currently be present only at a very low frequency in the pathogen population, or might potentially arise through mutation and/or recombination and greatly increase in frequency due to strong selection pressure exerted by the "resistant" host population.

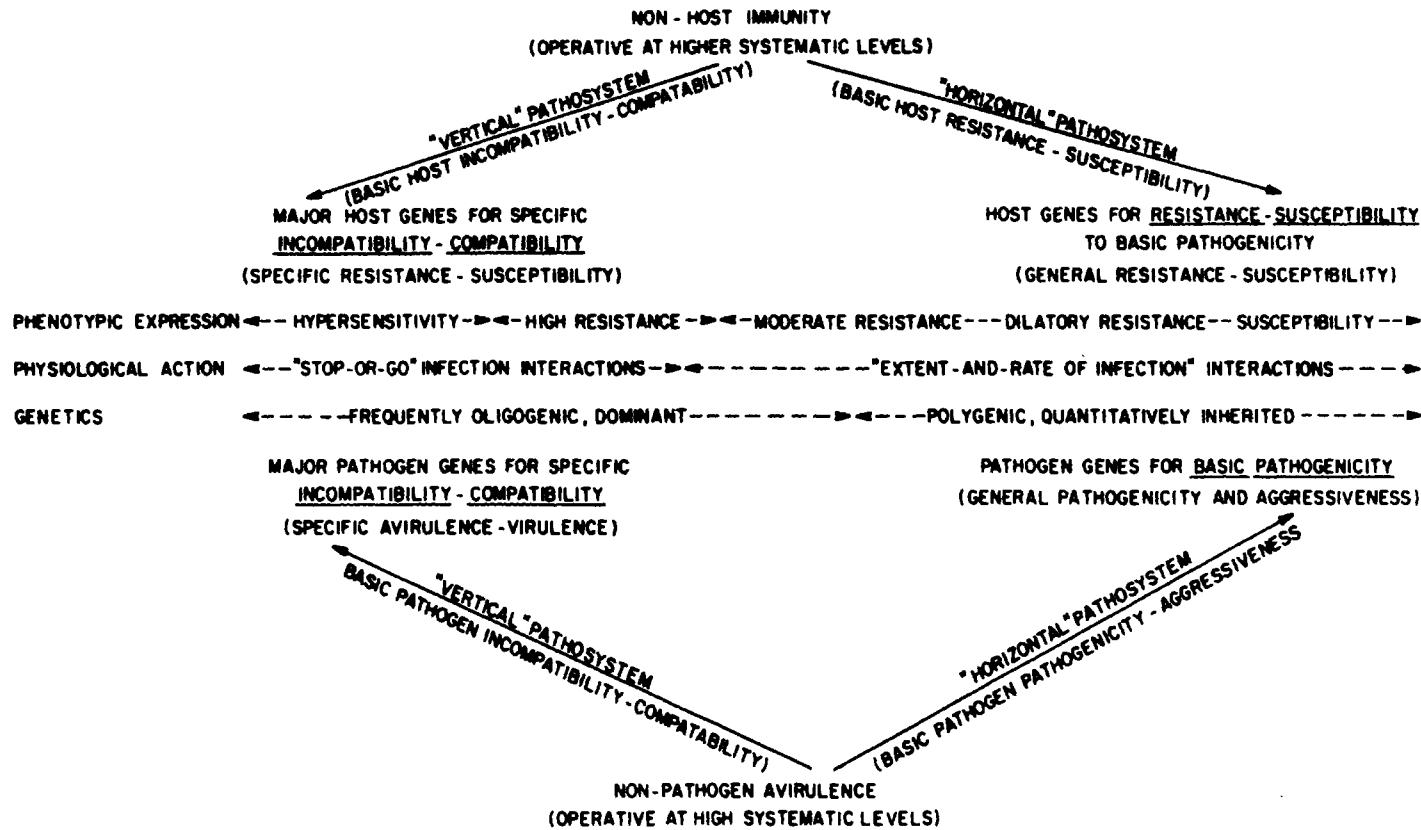
Following the very damaging southern corn leaf blight epidemic of 1970, a special Committee on Genetic Vulnerability in Major Crop Plants was appointed by the National Academy of Sciences of the United States to investigate the extent of genetic uniformity in major crops and the dangers of this to national and world food supplies. Their findings showed that this practice of breeding highly productive, physiologically-specialized cultivars had resulted in an extremely dangerous erosion of the genetic base and no efforts towards conservation in almost every major crop plant in the country. For example, 9 varieties represented 50% of the total 110 million ha planted to wheat, only 6 varieties accounted for 71% of 165 million ha of corn, and 96% of the 1 million acres of peas grown in the country were three cultivars. Unfortunately, this situation is probably not limited to the United States but is typical of the advanced agricultural systems of all developed nations.

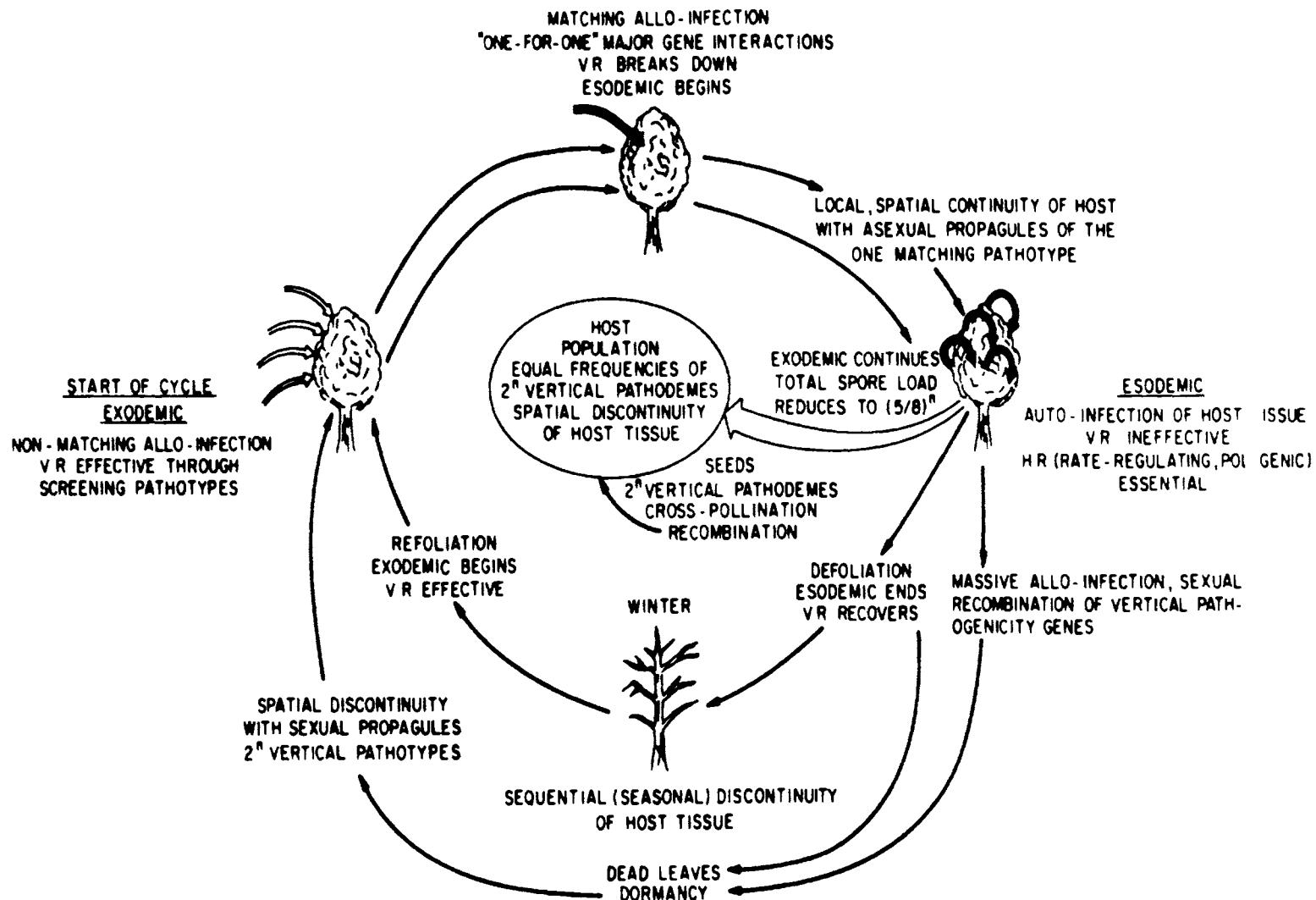
There have been, for some time, departures from the traditional, gene-for-gene, Mendelian genetics-based breeding strategies. The search for alternative strategies was stimulated by Vanderplank (1963, 1968) who placed increased emphasis on the epidemiological aspects of plant disease and the genetic interactions of the host population with those host pathogens. The gene-for-gene/resistance-susceptibility concept was characterized as a differential host-pathogen interaction by Vanderplank which he termed Vertical Resistance (VR). But he also recognized another genetic resistance system that is operative against all pathotypes or virulent strains of a pathogen and which he termed Horizontal Resistance (HR). According to Vanderplank, the function of VR is to buffer the host population during an epidemic by discriminating against different strains or pathotypes in the ambient inoculum, thus delaying the onset and reducing the intensity of the epidemic. On the other hand, HR is not effective against infection at this stage but acts to reduce the rate of disease development on infected tissue. Therefore, HR and not VR, serves as the major genetic protection mechanism of the individual host plant. This is an important differentiation, because it will be seen that one of the major limitations to obtaining durable resistance to diseases has been the improper application of VR in selection and breeding.

The population approach to breeding for disease resistance was explored, in terms of basic genetics and epidemiology, by Browning (1979) and Robinson (1979). Their discussion are summarized herein to illustrate the genetic and physiological systems interacting at the levels of individual genotypes and host-pathogen populations in the pathosystem and to review the dynamics of VR and HR with an example showing how each system is assumed to operate during an epidemic. In the context of this discussion, the host and pathogen populations are considered as a co-evolving subsystem of an ecosystem.

The hypothetical co-evolution of an interacting pathosystem (Browning 1979) is illustrated in Figure 1. The figure has been modified to include some alternative terminology for the VR and HR resistance systems. The two extremes in this evolutionary system are non-host immunity and non-pathogen a-virulence which are characteristic of host-pathogen interactions at higher systematic levels (e.g. Melampsora medusae is pathogenetic on some Populus species but not on Quercus). These extreme situations for host and pathogen are at the top and bottom of the figure, respectively. The co-evolving Vertical and Horizontal pathosystems are illustrated to the left and right of Figure 1. The central portion of the diagram thus represents a continuum of the range of host-pathogen interaction between these two systems in terms of the genetic substrate, the

Figure 1. Hypothesized System for Host-Pathogen Co-Evolution (From Browning, 1979)





physiological action of resistance and the phenotypic expression of disease. The Vertical (or Incompatibility - Compatibility) Pathosystem is therefore characterized, phenotypically, by a differential reaction of the host to the pathogen (infected or non-infected), operates physiologically as a stop-or-go mechanism in terms of development of the parasite on host tissue, and is controlled genetically by single (or few) matching, dominant-recessive genes in host and pathogen. In contrast, the Horizontal Pathosystem (or Basic Resistance - Susceptibility system of the host) is characteristically manifested on infected host phenotypes which may range from moderately resistant to susceptible, due to variable physiological control of the rate of development of infection and, generally, is under quantitative (polygenic, non-Mendelian) genetic control.

The interaction of the Vertical and Horizontal Pathosystems (and, thus, the mechanisms of VR and HR) during an epidemic in a wild pathosystem are summarized in Figure 2. The illustration is very appropriate to this discussion, as it is a description of the attack of a leaf rust (an obligate parasite) on a population of deciduous trees, and it thus serves as a general diagram of the Populus-Melampsora pathosystem. The diagram has been modified slightly from Robinson (1979) and some definitions are necessary to follow the discussion of its sequence of events. Pathodemes are the spectrum or range of host genotypes in the pathosystem, while pathotypes are the pathogen counterparts. The exodemic is the phase of the epidemic characterized by allo-infection (by fungal spores, in this case) from the ambient environment. The esodemic is the phase of the epidemic which depends upon auto-infection of genetically-homogeneous host tissue, and may involve vegetative growth of the pathogen.

Vertical resistance is effective in the exodemic because the range of host pathodemes in the population selectively screens the range of incoming pathotypes (spores). In a heterogeneous, wild host population, some plants will become infected, but most will not. In the infected individuals (those with matching, gene-for-gene allo-infection) VR is therefore overcome and the esodemic phase of the epidemic begins on those infected host trees. At this point, the polygenic HR system becomes all-important, and it acts to regulate the rate of pathogen growth and therefore the extent to which the disease is expressed on the infected individual. Thus, upon infection, the plants displaying HR may appear, phenotypically, to range from relatively resistant (a few, localized lesions) to highly susceptible (severe necrosis and defoliation) while those displaying VR could be placed in only two phenotypic classes; susceptible (including the total range of HR phenotypes, above) or resistant (only those completely free of infection).

In terms of their effects on the attainment of balance in the natural pathosystem, the discontinuities illustrated in Figure 2 are significant. Spatial discontinuity, in this example, is provided by the degree of heterogeneity of VR genes in both the host and pathogen population. Sequential discontinuity is needed to terminate the esodemic (auto-infection) phase and thus allow the VR system to recover. It is provided by the seasonal dormancy of the host; leaf abscission terminates auto-infection and breaks the epidemic. The following spring, the new leaf tissue will be free of parasites, and thus VR is restored and again is effective in screening the incoming allo-infection.

Based upon the sequences and relationships summarized in Figure 2, Robinson (1980) developed the concept of an "evolutionary stable strategy (ESS)" for a pathosystem. The ESS is defined as the "best possible" strategy of inherited behaviour patterns at a specified systems level, arrived at by the competitive elimination of all inferior, inherited strategies", and providing "maximum survival value, economies, resilience, flexibility, homeostasis and, above all stability. It is also an autonomous (i.e., self-

regulating) strategy". Under the concept of an ESS, the VR system obviously requires discontinuity for the maintenance and, therefore, its survival value will be directly related to the degree of discontinuity. Wild populations of Populus and other temperate, deciduous forest tree species are generally characterized by both spatial and sequential discontinuities; therefore, VR could play a relatively major role in the ESS of pathosystems such as Populus - Melampsora and Populus - Marssonina.

In any given host-pathogen system that has co-evolved, there will always be HR, but VR never occurs alone and is always mixed with HR (Vanderplank 1975). It is generally agreed that the VR system has evolved more recently than the ubiquitous HR system and Browning (1979) has postulated that "in a diverse setting, the incompatibility-compatibility system (VR) probably contributes significantly to maintaining homeostasis where both systems occur". Also, Browning's concept of the "protection of indigenousness" through the interactions and "dynamic balance" between VR and HR is remarkably similar to Robinson's evolutionary stable strategy (ESS).

It is now generally believed that the basic function of VR is to protect the host population while the basic action of HR is the protection of the individual host plant. More importantly, it is also generally recognized that VR has been widely misused in the traditional crop breeding programs because it was employed not to "buffer" populations that were created by selection for HR, but to develop physiological specialization in homogeneous cultivars at the cost of the loss of HR in these cultivars and, more abstractly, the loss of VR in the homogeneous population. Much of this damage was done through the practice of rejecting all but the completely "resistant" phenotypes in disease screening and using these in breeding programs.

Thus, as a rule, HR offers the greatest potential for stability and durability of protection and VR, when it is present, serves to confound the process of screening for HR. Finally, it is recognized that VR, when properly regarded and managed, may be used effectively in conjunction with HR to attain relatively durable population-level protection from disease.

Wild Pathosystems, Agroecosystems and Populus Plantations

The concepts discussed above provide some background on the genetic and epidemiological principles underlying the current trend to develop new philosophies and strategies for disease resistance breeding; new approaches based on achieving an acceptable balance between productivity and durable disease resistance by manipulating the genetics of the host population. There is, unfortunately, an almost complete lack of scientific information on the wild pathosystems from which man has selected and developed our modern cultivated crops and, therefore, most of the foregoing discussion was based upon conjecture. If more attention had been paid to the evolution and dynamics of these wild pathosystems in the past, it would surely have reduced the suboptimization now bred into all crop pathosystems. As it now stands, all factual knowledge of plant pathosystems is based upon studies of crop pathosystems. Thus, and even more unfortunately, if the above theories which have been developed for the workings of wild pathosystems are correct, then studies of crop pathosystems have served to generate a good deal of incorrect and misleading information or, in Robinson's (1980) terms, "artifacts of agriculture".

Wild pathosystems are characterized by relative stability and the general absence of widespread violent epidemics. In contrast, most crop pathosystems are notoriously unstable and prone to epidemics. The same degree of contrast, of course, may be found by

comparing natural stands and forests of poplar with monoclonal plantations. In crops a "good source of resistance" is more than likely a single, inadequately tested Vertical pathodeme. When this resistance is overcome by one or more different pathotypes, a new VR is genetically constructed by breeders. During this process, techniques such as back-crossing lead to genetic uniformity, HR genes are lost, and the crop "population" may consist of a single (or very few) VR genotypes. When placed in an environment of climatic fluctuation and exposed to highly mutable, heterogeneous pathogen populations, a homogeneous host population such as this is very susceptible to severe disease attack. The monoclonal poplar plantation provides a sobering analogy.

The optimal situation, probably, is one in which the plantation population would retain, to the greatest possible degree, the positive attributes of the population structure of the wild stand. To be economically acceptable, of course, this would have to be accomplished without a significant loss of productivity. Robinson (1980) has proposed the "crop stable strategy (CSS)" which is based upon population breeding techniques aimed at maximizing HR without significant suboptimization (loss of yield, quality, etc.) Founded upon the principles of the ESS of natural pathosystems, the CSS system is most efficient when it is applied to obtain local maximization of resistance and other economically-important traits and, as such, it requires more intensive testing and screening in the local environments in which the crop system will be established.

This concept of localized, on-site-testing and screening has been advocated by a number of authors as a priority component when planning or establishing breeding programs in developing nations (Buddenhagen 1981 and 1983, Buddenhagen and de Ponti 1983, Simmonds 1983, Robinson, 1980 and 1981). Basically, what is proposed is the localized screening of susceptible (non-vertically resistant) host genotypes against the spectrum of indigenous pathotypes, and recurrent selection. The strategy includes simultaneous screening for all desirable characters and, to minimize the confounding effects of VR if present, the screening is conducted during the esodemic, i.e. on infected host plants. The resultant host population would thus be highly heterogeneous in terms of HR genes. This would impart a population-level homeostasis or buffering against genetic changes in the pathogen population and/or environmental variation, which would contribute to a stable, productive and relatively epidemic-free crop system. Moreover, the creation and maintenance of breeding and production populations of the host that were heterogeneous collections of heterozygotes would provide insurance that the level of productivity and resistance could be maintained or improved in the future.

Vertical resistance, which may play a key role in the ESS of some pathosystems, may be employed to advantage in a crop breeding strategy as well, although there is some controversy regarding the extent to which VR should be employed. The effectiveness of VR when employed as diverse, multiline mixtures of oat isolines to impart a "population-level" resistance to crown rust (Puccinia coronata) was demonstrated by Politkowski and Browning (1978). Moreover, to protect this population to an acceptable level, only 8-10 isolines, each carrying different major VR genes effective against different rust pathotypes, were needed.

Still, a more efficient long-term disease-resistance breeding strategy would probably be one that maximized genetic heterogeneity for HR through recurrent selection under conditions of localized screening and, where possible and appropriate, superimposed a multiline or multiclonal mixture of appropriate VR genotypes into this already diverse host population. A crop pathosystem with this genetic structure for the host population might then be expected to function in a manner similar to the wild pathosystem; maximum protection and homeostasis would be provided by the uniformly high level of HR bred into

the population to reduce the rate of autoinfection during the endemic and this would be reinforced, at the population level, by VR genotypes effectively screening the inoculum to reduce the number of allo-infections in the exendemic.

"Engineering" a structural pathosystem such as this may be difficult or even impossible in many agronomic crops. In a large number of grain, vegetable and fruit crops past breeding practices have placed priority on uniformity in traits such as time of germination and growth to maturity, size, quality and many others which serve to adapt the crop to the economies of mechanical planting, harvesting and processing and to the market (consumer) demands for taste, texture and/or appearance. In terms of the economics of yield and quality, it may prove counterproductive to try to return to a system based upon heterogeneity in the cultivation of these crops.

The same standards for uniformity imposed by the economics of mechanization and marketing serve also to limit the utility of so-called "multi-line cropping systems" in providing durable disease resistance. The "multi-lines" generally cannot be planted in the random cultivar mixtures that would maximize the population-protecting attributes of their combined VR genes because uniformity of germination and date of maturity are so crucial to their management. Instead, they are planted as pure stands of isolines (a "mosaic") selected to provide staggered maturation dates to facilitate mechanical harvesting in sequence. A multi-line cropping system of this type employing four isolines (each a different VR cultivar) would therefore represent a theoretical annual risk of 25 to 100% losses, depending upon variations in climate, the pathogen population and the unique set of complex host-pathogen-environment interactions inherent in every growing season. Under contemporary agricultural practices in developed countries, of course, a great deal of this potential loss to disease is prevented or countered by intensive application of fungicides; there is a chemical back-up system in place that provides a "fail-safe" to an inadequate, non-durable genetic resistance system.

It is highly doubtful that the periodic application of pesticides to even the most intensively-cultured, high return, short rotation forestry plantations would generally be operationally or economically feasible or ecologically acceptable. These significant restrictions dictate that the very highest priority must be given to breeding for durable disease resistance in these artificially-regenerated tree populations.

Paradoxically, the present discrepancy existing between agronomic crops and forest tree plantation culture in the extent of sophistication and the application of disease resistance breeding programs may provide the latter with some distinct advantages in regard to a population-based approach to breeding for durable disease resistance. Historically, the current status of tree breeding programs and, more importantly, the ecological status of wild populations of forest trees, are most conducive to more quickly exploiting the opportunities for genetic gain offered by these strategies.

Past breeding practices for many agronomic and horticultural crops have been aimed, for decades, at producing uniformly-productive commercial cultivars. This practice has very significantly narrowed the genetic base in the production, breeding and, most critically, the source (wild) populations of these crops. In some cases, such as rice, maize and wheat, these uniform crop cultivars bear little genetic resemblance to their

wild progenitors. In these crops and crop systems, there is little knowledge of, and virtually no continuity with, the wild pathosystem. This situation has been recognized, at last, as one posing a significant threat to the continued cultivation of these crops and now major regional, national and even international germplasm centers of "banks" have been established to conserve and/or replenish the heterogeneity of many crop populations.

Tree breeding programs, by contrast, are relatively recent and, with only a few exceptions, have not yet exerted such tremendous selection pressure on wild populations. As a result, tree populations in most locales still represent a wealth of wild-type genetic diversity. Although intensive genetic selection programmes for some native Populus species in Europe, have undoubtedly restricted the genetic base available for further breeding and, introductions of exotic species, and hybridization and extensive substitution of plantations for natural forests have eliminated many wild populations of species such as P. nigra, the genetic diversity available is still relatively large.

An additional factor facilitating the employment of population-based disease resistance breeding strategies for forest trees is that almost all of the commercially important species are outbreeders and, therefore, virtually all current breeding strategies for yield improvement in these species are designed to exploit additive genetic variation through recurrent selection. Most unfortunately, Populus has evolved as an exception to this observation. Although it is, with rare exceptions (see Muhle Larson 1970), a dioecious genus and, therefore, an obligate outbreeder, most genetic improvement programs in Populus have almost completely neglected the great opportunities for recombination and gain offered by the recurrent selection approach and have concentrated entirely on direct vegetative propagation of selections.

Thus, in forest tree species, the continuity between the crop pathosystem and the wild pathosystem is generally excellent and may be supplemented by a wealth of information derived from research in ecology, pathology and silviculture in natural ecosystems. Moreover, in many commercial forest tree species and genera, including Populus, genetic diversity has been sampled, collected and catalogued in provenance and progeny tests and, to a lesser degree, in arboreta. These provide a further, complementary means of genetic conservation and a "wild-type" genepool for selection and breeding. In fact, some provenance and progeny tests have provided a means of first-generation screening of local pathotypes.

The requirements for genetic uniformity in cultural systems and for products are not as critical for plantation-grown forest trees as they have become for agricultural crops. This provides an additional significant advantage to trees in terms of applying population-based breeding strategies. This should remain so even under the most rigorous of management intensities and sophistication of planting, harvesting and processing equipment and systems now in use or proposed for the future. If climatic or market conditions preclude the timely harvest of a tree crop at age 10, it will still be relatively sound and merchantable at ages 11 or 12; thus, there is no need for a uniform time of maturity analogous to that needed, or perceived to be needed, in agriculture. In terms of uniformity in bole size to facilitate mechanical harvesting, it is doubtful that any state-of-the-art mobile tree shears and related processing equipment would be thwarted when confronted with a stem diameter range of 16 to 22 cm in a "uniform" plantation. While it is acknowledged that uniformity in wood properties is more critical to manufacturing, most systems can operate efficiently over a relatively wide range of wood grain patterns, specific gravities, fiber lengths and other traits.

The overall effect of this lower demand for strict uniformity in tree crops than in agricultural crops thus provides additional advantages and a greater degree of flexibility in employing disease resistance breeding strategies using population genetics techniques. For example, in a genus such as Populus a strategy using multiclinal varieties containing a few clones with VR among a broader array of those with HR might be employed to gain the additional advantages VR affords to protecting the population. Large numbers of clones could be used in the production plantations and, with some prior thought and advance planning, these could be bred so that they were able to be completely randomized in a plantation. Thus, population homeostasis and durability of resistance could be optimized in a tree plantation by structuring it both genetically and physically to more closely approximate a natural pathosystem.

Of course, despite these advantages there are still the innate disadvantages common to tree breeding to contend with; relatively long harvest cycles, the large size of the host and the limitations this causes in the design and implementation of appropriate laboratory, greenhouse and field tests, slow sexual maturity, and inconsistencies of juvenile - mature correlations, to name but a few of the major ones. When breeding for resistance to a pathogen with a polycyclic reproductive capacity, highly mutable and adaptive genomes, and a tendency for violent and unpredictable responses to climatic variation, these disadvantages seem considerably magnified.

Nevertheless, there are certain distinct advantages associated with forest trees that make the employment of population - based disease resistance breeding strategies very attractive especially in a genus such as Populus. The remainder of this paper is devoted to a consideration of the factors influencing the choice of breeding strategies and the application of these to the culture of Populus in developing nations.

Breeding Strategies and Adaptability to Change

A breeding strategy should be defined clearly; it may be appropriate and helpful to attempt to do so by introducing the concept of scope and scale. This can be done by contrasting a breeding strategy with a breeding tactic. The latter is a much more objective and narrowly-directed method or technique involving the mechanics of the breeding work. On the other hand, the breeding strategy is generally perceived to be a long-term entity (although it may be subdivided into a succession of phases of shorter duration) with more-or-less specific goals. Moreover, the breeding strategy may be conceived under a particular philosophy which may embody economic and social considerations as well as purely biological ones. Thus, the breeding strategy should be concerned with much more than the simple time and space mechanics of a breeding technique and may, in fact, incorporate two or more breeding techniques (or some modifications of them) in its various phases of development.

The maintenance of a flexible breeding strategy is of utmost importance to a breeding programme in which disease resistance is an important component because the interactions of host, pathogen and environment are so complex and so subject to imbalances and significant changes over both the short and long term. This is especially true when dealing with a perennial host such as poplar which will have to endure 10 or more years of such events as widely varying climatic extremes, changes in virulence of the primary pathogen population or populations, increases in the damage caused by minor pests and, perhaps, the introductions of new pathogens and pests. For these reasons it is important to regard selection and breeding for resistance to diseases as but one aspect of a major programme for the genetic improvement of poplar populations for plantation culture. It is now generally agreed that breeding strategies should be conceived, conducted and evaluated in terms of their short- and long-term effects upon populations of the host

and the pathogens and the changed gene frequencies in these populations, with the long-term goal of attaining an acceptable balance between levels of productivity and levels and duration of disease resistance. Once this balance is arrived at, it must be maintained in the ecosystem by a broadly-based population breeding technique that is sensitive to the complex interactions between the host, the pathogens and the environment which may act to upset this balance by increasing disease frequency or intensity, thus threatening sustained host productivity.

Therefore, the breeding strategy must be one that takes into account the effects that changing host and pathogen gene frequencies have, not simply as measured by host productivity at some point in time, but also in regard to the long-term balances in that particular pathosystem, and even at the higher levels of the ecosystem of which the pathosystem is but one small component. This level of planning and activity introduces a significant opportunity to employ, in the breeding strategy, a component of "preventive" breeding (Buddenhangen and de Ponti 1983). This preventive component is of major significance to a population-based strategy because it allows for appropriate selection and breeding techniques to be aimed not only at obtaining durable resistance to damaging pathogens that can be targeted at the inception of the programme, but also at preventing those minor pathogens present in the system from attaining damaging levels in the more homogeneous plantation culture and, most importantly, reducing the ever-present danger that new parasites introduced into the plantation ecosystem will become important. This preventive philosophy for a breeding strategy is, in terms of its approach to more durable levels of disease resistance, a major departure from the traditional "reactive" strategies of agriculture which are based upon patching-in resistances to diseases as they develop (as new pathogen introductions or as more virulent pathotypes of indigenous diseases) in the genomes of one or a few productive cultivars. These reactive strategies (which, it might be argued, are no strategies at all but only techniques to obtain relatively short-term cosmetic repair) have, unfortunately but understandably, epitomized the philosophy of poplar breeding for the past 60 years.

The need to devise a long-term and flexible breeding strategy for poplar culture is especially critical in developing nations. This is because, in almost all new programmes, advice is initially sought from "expert" consultants from developed countries who are generally interested in quickly attaining significantly increased yields, usually in the first generation. Furthermore, these advisers are also generally familiar with and biased towards the employment of systems which are characterized by the intensive culture of homogeneous, dense stands. In poplar culture, as well as that of other fast-growing trees such as pines and eucalypts, this almost invariably leads to the introduction of one or very few clones, hybrids, geographic varieties or families that the adviser is familiar with and can obtain easily. This significantly narrowed and relatively untested genetic base is propagated (vegetatively, in the case of Aigeiros and Tacamahaca poplars) and more-or-less widely distributed for commercial planting in homogeneous, close-spaced plantations. These single or few host genotypes exert tremendous selection pressure on indigenous or introduced pathogens, effectively serving to initiate the evolution and increase in frequency of rarer, more virulent pathotypes. At the same time, the dense monoculture may modify the microclimate significantly, again favoring the development of large pathogen populations and an unnaturally heavy spore load. Both of these situations interact to cause a marked increase in the potential for damaging epidemics to develop.

The same situations are characteristic of agronomic and horticultural crop breeding efforts in developing countries, of course. The risks inherent in the introduction of new "developed" breeding and cultural systems of this type, characterized by a much-narrowed genetic base, homogeneous dense stands, and very heavy nutrient demands was reviewed by Simmonds (1979). In some instances, these introductions and the biological and

socio-economic modifications that they have caused have been fairly beneficial to the developing nation. In many other cases, however, they have had major negative effects, especially in terms of disease problems which have ranged from mildly disruptive and costly to ecologically and economically disastrous.

Often, the new introduction, be it a variety or clone developed from an indigenous or an exotic species, is planted in an area where it is not resistant to the local pathogens or where new species of pathogens are able to cause disease. The new introduction may likely also be under stress from other factors such as high or low temperatures, water deficits, insect depredation or nutrient imbalance or toxicity. Often, too, interactions of introduced host and/or pathogens with a new and different environment will favour the development of the pathogen population to epidemic proportions. An example of this range of variation in responses for introduced poplar culture is provided by contrasting the experiences with the introduction of the Euramerican hybrid clone 'I-214' in Argentina and Australia. The biological aspects of these situations will be explored in more detail later but, basically, this clone was selected and imported to these countries on the basis of its high productivity and disease resistance in Europe. Clone 'I-214' was introduced to Argentina in the late 1930s. It has been widely planted and has been relatively productive and disease free for over 40 years (Alonzo 1976). In the 1950s and 1960s it was released for planting in Australia and New Zealand where it was severely damaged by the leaf rusts caused by Melampsora medusae and M. larici populina which, in 2 or 3 years, virtually eliminated the clone I-214 from the poplar culture of those two countries.

The important point is that there is often a risk attached to introducing clones into a new ecosystem simply because they have been developed elsewhere for use under systems of intensive culture. Even when they survive the introduction and are found to be moderately successful in increasing productivity, they may generate problems. In many examples of introductions of agronomic crops into developing countries in the tropics, the problems that were generated have been significant and complex. The situation centers around the replacement of a heterogeneous mixture of the locally-adapted landraces which were lower-yielding but somewhat pest resistant, by dense, homogeneous stands of high-yielding varieties bred in Europe, North America or other, more developed tropical countries. In all cases, even those where productivity was increased, there were marked increases in the use of fertilizers and pesticides (Buddenhagen and de Ponti 1983).

Thus, in conceiving a breeding strategy for productivity and durable disease resistance in developing countries, it is appropriate and important to consider carefully the level of technology change that the poplar culture in those countries can bear. A strategy employing homogeneous, dense plantations of a fast-growing but nutrient-demanding clone may provide exceptional initial gains over the first one or two short rotations, but may terminate in the complete collapse of the poplar culture in that country as the inherent fertility of the planting sites is depleted. Likewise, homogeneous plantations of a high-yielding clone selected and developed in Europe for veneer log qualities but only moderately resistant to a number of diseases may not be the best strategy in a poplar culture aimed primarily at producing local construction timber and fuelwood. Here, as in other developed regions, a mixture of 10 or 15 locally-developed and tested clones, perhaps representing less potential productivity but offering more stable disease resistance and, thus, a greater probability of sustained productivity may be much more appropriate. Finally, and of great importance from the standpoint of disease resistance breeding, there is likely to be a relative shortage of trained scientific personnel available to the breeding programme, not only at its inception, but also as it develops and problems begin to appear. A poplar culture served by a breeding programme that is limited in funds, time and scientific manpower is pre-doomed to almost certain failure if it is founded

upon a strategy characterized by a narrowing genetic base and homogeneous production populations requiring continual defensive or reactive breeding and selection to restore resistance.

In light of the above discussion and the history of disease epidemics and defensive breeding cycles in Europe and elsewhere, a breeding strategy for poplar plantation culture in developing nations must certainly include a major component for maintaining a level of durable disease resistance. Moreover, such a strategy must be flexible, economical and, above all, not overly-sophisticated to the point where it becomes impossible to implement and manage. It must also, of course, be acceptable to the growers and end-users.

It may then be asked what is the best way to devise an efficient breeding strategy that will attain these objectives? The answer to this question will vary considerably due to factors such as the location and climate of the developing nation, the products to be produced, the characteristics of the growers, the limitations to scientific resources and, of course, the numbers and types of major indigenous or "introducable" poplar pathogens. Still, there are some basic elements that are of more or less universal application and importance to planning and implementing a successful breeding strategy that can be considered briefly and in general. While these elements are discussed herein more or less specifically in the context of their importance to a breeding strategy for Populus in developing countries, many of them are equally and directly applicable to the development of poplar breeding strategies in developed nations and to tree breeding strategies with a major disease resistance component, in general.

These basic elements, perhaps not in the order in which they should be considered when devising a breeding strategy, are:

- the setting of realistic objectives for the genetic improvement programme, based upon considerations of the opportunities and constraints inherent in the socio-economic environment as well as in the pathosystem in which the poplar culture is to be established;
- the consideration of alternative breeding techniques that may be used or combined in the strategy;
- the identification and maintenance of a large and heterogeneous source population and the development of methods to exploit it to obtain a continual movement of diverse, heterozygous parents into and out of the breeding population;
- the development of suitable priorities and effective methods for screening and identifying outstanding parental combinations and efficiently selecting these;
- the provision of maximum flexibility in the breeding strategy through modifying, adapting and/or combining standard breeding techniques or developing new ones to meet changing biological, economic and social conditions.

These common elements are briefly discussed below; however, the following assumptions are pertinent to their consideration in the context of their place in a breeding strategy aimed at balancing productivity and durable disease resistance in poplar plantation cultures of developing nations.

1. The basic priority in the breeding strategy is the improvement of the rate of biomass produced per unit of land.

2. Resistance to pathogens is considered as only one component of yield and is therefore only one of several traits to be considered in screening and selection.
3. Resistance to pathogens is inherited quantitatively (Horizontal Resistance) and, like yield, is responsive to those breeding techniques designed to exploit additive genetic variance.
4. The resistance breeding effort is directed at providing durable, long-term suppression of the potentials for epidemics by generating populations that maintain a balanced host-pathotype interaction in a relatively localized ecosystem.
5. Given the uncertainties of the occurrence and pathogenicity of indigenous and introduced pathogens and the complex environmental interactions, breeding techniques and systems must be chosen and applied to support a dynamic long-term breeding strategy which includes conservation of the genetic variability of the source population.

Opportunities, Constraints and Breeding Programme Objectives

Some major factors that should be considered when contemplating a breeding strategy that has a major component for breeding durable disease resistance in forest tree plantations were reviewed by Thielges (1982). These factors can be considered basically as biological, socio-economical and institutional, and all of them influence the development of a breeding strategy because they present an array of opportunities and constraints that significantly influence objectives.

Biological Factors

Of primary importance are the biological characteristics of the host and the pathogen and their interactions with each other and the environment of the pathosystem. Obviously, the more one knows about the genetics and physiology of the host and the pathogen and the ecological factors that influence epidemics, the more easily and efficiently one may develop an effective breeding strategy and the more rapidly the genetic gains should accrue as the breeding programme is implemented. It is especially pertinent to new programmes in developing nations, however, to realize that a great amount of genetic improvement may be obtained with a good basic knowledge of biological principles and that the perceived need to accumulate great amounts of information before any genetic progress can be made is, in itself, a major obstruction to the development of a breeding programme. Buddenhagen (1983) observed that "a wish to understand plant biochemistry, physiological control of resistance, and the underlying genetics is laudable. To believe, however, that this understanding is essential before substantial breeding progress can be made is not true and it may engender a self-defeatist attitude that will inhibit progress". Simmonds (1979) was even more candid when he expressed the opinions that "the physiological bases of adaptation are not well understood but this is no impediment to its exploitation because the breeder recognizes it well enough for practical purposes when he sees it" and, later, "better understanding (of disease resistance mechanisms) would be good to have but, fortunately, the plant breeder does not need to understand resistance in order to use it". The rather remarkable progress that has been made over the past 50 years in selecting and propagating poplar clones that are resistant to a number of diseases for which little or nothing is known of physiological resistance mechanisms or their modes of inheritance is evidence of the truth of these statements. It is also obvious that even greater gains will be possible when the mechanisms and genetic control of resistance to poplar diseases are further elucidated.

In terms of generally favourable biological characteristics, tree species that are fast growing and therefore suitable for short rotation plantation culture are very good candidates for the inclusion of durable disease resistance as one trait in a breeding strategy aimed at the improvement of yield and/or quality. This would include Populus, of course, and also other genera such as Eucalyptus, Pinus and Platanus. Other favourable traits of the host species include the existence of large and heterogeneous natural populations, ease of artificial crossing and the elimination or minimization of inbreeding through dioecism or self-incompatibility mechanisms, and the ability to be propagated vegetatively.

The pathogen that is reducing yield or quality and its interactions with the host must also be considered here. When multiple pathogens and/or insect pests are a consideration, it is best to assign the highest priority to breeding for resistance to the obligate parasites. Breeding against these has the greatest probability for success, especially in those situations where host and pathogen have coevolved. In these circumstances, mutual selection pressures have resulted in the evolution of genetically-controlled defense systems in the host which operate effectively against the well-developed parasitism of the pathogen. This of course is the origin of HR and these principles are the basis for the evolutionary stable strategy (ESS) and the crop stable strategy (CSS) theories developed by Robinson (1979, 1980).

Genetic programmes are not as effective against facultative parasites such as the wood rots and some root rots, where factors in the immediate environment such as poor site conditions or mechanical damage are operative on a relatively temporary basis to predispose the host to these parasites. Since they do not interact with living host tissue over evolutionary time, there is no opportunity for selection pressures to develop complementary genetic systems for host resistance and pathogen virulence. The problems caused by facultative parasites in poplar plantations are probably best avoided or remedied on a cultural basis through proper site selection, supplemental nutrition, improved water relations and chemical control. From a genetics standpoint, the best strategy against facultative parasites is to maintain a broad genetic base in breeding populations and maintain heterogeneity in production populations to maximize the effect of any levels of natural resistance or avoidance that may be present.

Introduced pathogens present special problems. Because of the absence of coevolved selection pressures over evolutionary time, the introduced pathogen is generally presented with a genetically "defenseless" and uniformly susceptible host. There is some evidence that, over time, crops such as maize and potatoes have evolved HR in response to selection by introduced pathogens (Vanderplank 1968) but, with poplars and other tree crops, this would be a fairly long process. Probably, the best genetic strategy against introduced diseases is to not repeat past mistakes (as in the Dutch elm disease and chestnut blight epidemics) by searching for a "good source of resistance" (escapes, presumably with VR) and immediately to begin to select the least susceptible trees from the diseased populations, vegetatively propagating these diseased trees if necessary, and to breed for HR.

It is important to consider (and to incorporate in the breeding strategy) that environmental variability may produce differential interactions and that, in a highly variable and mutable pathogen, these may be extremely complex and of great magnitude to the point where genetic screening and selection procedures are significantly confounded. Paradoxically, a major abuse of differential environmental interactions often arises from the results of wide testing. Usually, this is done to attempts to breed for resistance that will be employed over too broad an area, e.g. "regional" resistance when the region covers a large area of land and may include a multitude of highly variable sites and even different climatic conditions. The tendency in such situations is to favour VR over HR.

The solution to the problem is to make breeding a more localized activity and to screen and select for disease resistance on or near the sites where the improved trees will be planted. This is an important concept which will be considered in more detail in a subsequent section.

Socio-economical Factors

Some of the socio-economic factors that should be considered when devising a breeding strategy for a developing country have already been discussed but one or two of them probably bear repeating here under the concept of their influence on the objectives and the breeding methods employed. It was earlier assumed that the major objective of a breeding strategy for poplar culture would be sustained yield improvement, of which durable disease resistance is a very important component, especially in a new programme for a developing nation. It is recognized of course, that yield improvement may be manifested in a variety of ways, e.g. a simple increase in total woody biomass for utilization as chips for pulp or for firewood, in contrast to a concentration of wood fibre in the main stem to improve the utilization of the tree for veneer or timber. Obviously then, utilization will have an important influence on objectives as well as specific breeding and propagation methods that may be applied to attain these objectives.

The breeding strategy must be conceived with a clear understanding of the final product or products and also the yield or quality factors that affect their utilization. This has a major influence upon deciding what traits will be selected for and on the objective setting of priorities or weighting of these traits in a combined selection index. Basically, it is dependent upon common-sense judgements. For example, in a short-rotation plantation system aimed at maximizing the weight of wood or wood fibre produced per hectare for energy or pulping, selection against deforming branch or stem canker diseases that cause a loss of apical dominance is not important if it does not affect gross yield and should not be included in the selection criteria. If, on the other hand, the end product was to be veneer or sawlogs, then these same traits would assume very high priority. The same reasoning applies to other traits as well; there is no need to select for bole straightness or branch angle when the plantation is to be harvested at age 10 and chipped.

The subject of selection criteria is more significant than it seems at first glance, especially as it relates to small new programmes in developing countries. There are numerous reports in the literature of tree breeding programmes with all-inclusive selection criteria aimed at producing a general-purpose "super tree". This tendency is particularly true of public research agencies where there is no product-oriented management strategy and/or grower input to influence the directions of the programme or the breeding strategy. No programme can long afford this level of inefficiency and dilution of effort, least of all new programmes in less-developed nations.

Institutional Factors

Institutional considerations are a final factor providing opportunities and constraints to influence breeding strategy objectives. While budgets, personnel, equipment and facilities are all important items in this category, management strategy is certainly the most critical item. Probably the greatest potential for implementing an effective breeding strategy for sustained yield and durable disease resistance exists in those organizations where there is an internal or in-house research branch coordinating their work with the short- and long-term management and production goals of the organization. Such situations may be found in the larger industrial forestry firms and in those public

(national, state or provincial) agencies where research capabilities are concentrated upon relatively localized artificial regeneration programmes. The latter situation may be characteristic of forestry and/or rural development programmes in some developing countries.

In summary, most agencies providing scientific support for poplar culture in developing nations will have to operate under major restrictions influencing the scope, direction and rate of development of their genetic improvement programmes. Given limited trained scientific personnel, budgets, facilities and knowledge of the genetics and epidemiology of the complex host-pathogen-environment interactions that characterize the pathosystem, breeding strategies may be best directed to controlling obligate parasites that cause disease problems in poplar plantations that are bred for short-rotation plantation culture in localized specified areas.

Alternative Breeding Methods for *Populus*

When breeding methods are related to types of crop populations, only four basic methods are generally considered. These are: 1) inbred pure lines, 2) open-pollinated populations, 3) hybrids, and 4) clones (Simmonds 1979). Which one or more of these four basic methods can be effectively employed in the breeding strategy for a particular tree or crop depends, primarily, upon the mating system, life cycle and effective means of propagation of the plant. Thus, the inbred pure line is an effective crop population breeding method for inbreeding, seed-propagated annual plants; open-pollinated population breeding methods are best-suited to outbreeding, seed-propagated annual, biennial or perennial plants; hybrid breeding methods are effective for outbreeding, seed-propagated annual or biennial plants; and, finally, clonal methods are best used for outbreeding, vegetatively-propagated, perennial plants. Backcrossing, which is considered a major method of crop improvement by some, is here considered as a special-purpose subtechnique that may be used to provide another dimension to these four major breeding methods, all of which are activities performed within the breeding population.

Populus is basically a dioecious genus and, therefore, poplars are obligate outbreeders. Thus, on the basis of reproductive biology, the only major breeding method that cannot be used in a Populus breeding strategy is inbreeding. Further criteria must be employed to evaluate the appropriateness of the three other methods for inclusion in Populus breeding strategies aimed at producing populations of productive, disease resistant trees for planting in developing countries.

Identifying, Exploiting and Maintaining Heterogeneity in the Source Population

This aspect of the discussion of the breeding strategy is primarily concerned with the genetic base of the breeding programme, particularly that of the initial or base population which serves to provide appropriate parents for inclusion in the breeding population. In poplars, as in most other forest trees, the base population may also provide an additional advantage to the breeding programme by serving as a genetic reserve to augment the more temporal and transient breeding population. The existence of such a reserve is of critical importance because it not only provides a mechanism for maintaining a broad genetic base at any particular phase of a breeding programme, but it also adds an important dimension of time to the programme. This "wild type" strategic reserve or even a suitable collection of heterogeneous cultivars, is sadly lacking for most important agronomic and horticultural crops and this represents a threat not only to the cultivation of these plants but to continued long-term progress in their genetic improvement.

The emphasis on maintaining a broad genetic base in a "strategic reserve" population is a relatively new element in agronomic crop breeding strategies. The findings and recommendations of the Committee on Genetic Vulnerability of Major Crops (Horsfall, et al. 1972) were discussed earlier in relation to their emphasis on the use of HR to obtain durable disease resistance and their recommendations to investigate alternative breeding strategies that would avoid the critical narrowing of the genetic base to the point found in the breeding and production population of virtually all contemporary major crop plants. The Committee also made very strong recommendations concerning the need for expansion of crop gene pools and the creation of germ plasm banks or centres. These recommendations have been implemented to a large degree but for many crop plants there will be great difficulty and much time involved in creating a very significant expansion of the gene pool. The question of whether or not some provision for the long-term maintenance of a broad genetic base can be built into a breeding strategy a priori has now been raised, in hindsight, for many crop plants. The answer is yes, and while it may have been realized too late for most cultivated crops, there is still adequate time and latitude to build such an element into breeding strategies for most forest tree species (Libby 1973).

Establishing a broad genetic base for a breeding programme and maintaining it through time seems to depend upon two key elements. The first is the timely preservation of the "wild type" gene pool and the maintenance of a direct biological linkage between this population and the breeding population. Simply stated, this means that there are no reproductive obstacles to employing wild type plants directly as parents in the breeding population. The second important element is the employment, whenever possible, of that breeding technique or combination of techniques that will provide for a maximum amount of genetic recombination among unrelated heterozygous parents.

The first of these elements is probably not possible, or today even desirable, for most food crops. The modern crop cultivars bear little biological resemblance to their wild progenitors and, even if breeding with an element of the wild-type population was genetically feasible, the loss in productivity and/or quality would probably be totally unacceptable. On the other hand, breeding programmes for Populus and other tree genera have not, with very few exceptions, progressed to the point where native gene pools have been significantly depleted and/or where the commercially utilized tree "cultivar" differs greatly, if at all from the wild type. One of these exceptions, unfortunately, is Populus nigra L. in southern and central Europe, but even in this species the narrowing of the genetic base and the biological departure from the wild type does not even begin to approach the severity of that found in most food crops.

In general, then, it is fair to say that the natural stands of Populus species still represent a wealth of genetic variation. It is therefore important that these stands be conserved in adequate numbers and in representative distributions. As discussed earlier, provenance and progeny tests also fulfill the role of a genetic reserve. If genetic variation is not maintained, poplar breeders may soon find themselves in the unfortunate situation of most crop breeders in having to "reconstruct" a genetic reserve from commercial cultivars, their own breeding populations and an input of whatever "unrelated" material they can obtain from other breeding programmes.

The second element, that of maximizing and maintaining both heterozygosity and heterogeneity through the proper choice and application of a breeding technique or techniques, is one that poplar breeders will have to address objectively and with an open mind. There is a need for critical analysis of past and present philosophies and programmes and an opportunity for some innovative research to explore a host of alternatives to current practices. Fortunately, there is also the past experience of breeding

programmes with other plants to look at to provide a historical perspective. Invariably, whenever the negative aspects of these crop breeding programmes are reviewed in light of their effects on inbreeding, construction of the genetic base and constraints to breeding progress, the evidence always comes to bear on the breeding techniques employed.

Thus, when identifying those crops with dangerously narrow genetic bases (which may also serve to identify those with dangerous disease problems, as well) authors compile lists of plants such as potatoes, rubber, coffee, grapes, sugarcane, barley and soybeans. The first five in this list are clonal crops and the latter are inbred lines. This inverse relationship between genetic heterogeneity and risks of disease loss has been known for some time but it was the Committee on Genetic Vulnerability of Major Crops which was responsible for communicating the true degree of danger this represents to modern agriculture. In general, the risk of disease loss due to breeding technique employed, is in the order Clonal > inbreed lines > hybrid > open-pollinated populations (including synthetic varieties).

The selection of appropriate breeding techniques that will avoid or minimize these problems in Populus breeding strategies for developing nations is the subject of a subsequent section. It is most appropriate to introduce it at this point, however, because the breeding technique that is employed at the inception of a new programme has such a significant effect on the genetic base. Historically, a programme based solely on developing clonal or inbred lines is capable of very rapid erosion of the genetic base and should be avoided, where possible, in favour of other techniques or modified to combine elements of other techniques that will serve to promote and maintain heterogeneity.

In a new breeding programme, it is best to use locally-adapted parents when possible, especially at the start of the programme. These locally-adapted trees, whether they be representative of provenances, families or individuals with good general or specific combining ability, will make the most immediate contribution to overall progeny performance. Local selections also offer the greatest potential for maintaining long-term genetic gains. Individuals selected as parents on the basis of a specific desirable trait (such as disease or insect resistance or wood properties) with or without regard for local adaptation, are a second category of potential parent material. These may be individuals, families or even other species in the case of Populus, and they usually enter the breeding programme at a later stage of its development, after well-adapted and productive breeding stocks have been established.

Since locally-adapted parents are so important for obtaining early genetic gain and maintaining it, it follows that heterogeneous source populations of Populus must be maintained at a local level. This is especially important in a breeding strategy that is aimed at durable resistance to poplar pathogens such as Melampsora, Marssonina, Xanthomonas and Dothiciza that must be managed by breeding for HR.

Thus, in developing nations with indigenous commercial poplar species early aspects of the productivity-durable disease resistance breeding programme must include evaluation of these native resources through initial selections in wild stands as well as provenance and progeny testing, as appropriate. Indigenous species and their localized "ecotypes" can be assumed to have developed adequate levels of HR to local diseases through their co-evaluation with indigenous pathogens. Under these circumstances, it is important to ensure that wild stands of these native commercial species are maintained to serve as a heterogeneous reserve for future exploitation. By the same token, local populations of indigenous non-commercial Populus species, if present, should also be sampled and conserved. These reserve stands of lesser species may prove to be extremely valuable in the

future, serving as sources of parents for interspecific crosses to obtain genetic gain in such traits as resistance to diseases, insects or other agents of environmental stress.

In those developing nations where there are no indigenous Populus species, diverse germplasm from foreign sources, even the intensively-cultured Euramerican hybrids, is potentially of more value than it is where native poplars exist. However, in these situations it is of utmost importance to establish a very broad genetic base of this exotic material in situ before the actual poplar breeding and selection begins. Once breeding does begin, this genetic base (which in the case of an exotic species is only a small sample, under the best of conditions) will quickly narrow. To ensure that the initial base is large enough and appropriate to the strategy and the programme the breeder should 1) select these exotic materials personally, 2) concentrate these collections in areas with similar climates, soils and topography, 3) collect large amounts of open-pollinated seed for on-site provenance and progeny tests back home, and 4) include disease resistance in the earliest screenings of all exotic material, placing major emphasis on testing for HR.

The breeder should not place heavy or total reliance on the easy importation and establishment of one or a few commercial Populus clones developed elsewhere by other breeders. There is a tendency for these to be inadequately tested locally, and then vegetatively propagated for planting over large areas. The use of these clones, if they are used at all, should be limited to the initial phases of the new programme and every effort must be made to resist the temptation to limit the pre-breeding testing and selection phase to only these few clones that were developed elsewhere. If the use of inter-specific hybrids is a part of the breeding strategy, this should be handled by locally establishing and testing broadly-based populations of each parental species followed by on-site hybridization and testing. These progenies, produced from exotic but locally-adapted parents, can then be compared properly with commercial hybrid clones available from elsewhere. These initial aspects of new Populus breeding programmes with an emphasis on local adaptation, testing and the establishment and maintenance of a broad genetic base, have been part of the recommendations for new programmes in India (Viart 1982) and China (Weisgerber, personal communication).

In summary, a conservative strategy should be adopted for poplar breeding programmes in developing nations. Major emphasis should be placed on identifying and preserving or creating a broad genetic base for initial parental selections and on maintaining this base through the conservation of indigenous wild stands or some appropriate means of regenerating provenance and progeny tests of both indigenous and exotic species. This heterogeneity of the source population should be emphasized and maintained at the local level. The breeding strategy must be aimed at maintaining this heterogeneity at all levels and it must employ those breeding techniques that promote a maximum of genetic recombinations.

Identifying and Exploiting Outstanding Parental Combinations

In a breeding strategy conceived to combine durable disease resistance with productivity, it must be remembered that more than one disease will probably be selected against, that resistance to diseases is only a few of many important traits to consider and that there is an inverse and exponential relationship between the efficiency of selection and the number of characters that are selected for. This is important, firstly, because the breeder must strike a balance between yield and disease resistance ... a poor yielding but highly disease resistant poplar population would be as valueless, economically, as one with an inherent potential for high yield but a high susceptibility to several major diseases prevalent at the local level. Secondly, in the genus Populus, the breeder will generally have to cope with more than one disease, depending upon the location of the

project. These two considerations mean that there must be a careful ranking of the traits to be selected for and a realistic evaluation of the levels of disease resistance that are sufficient or adequate. Above all, the breeder must resist the temptation to use the selection criteria as a means of identifying and vegetatively propagating the perfect poplar; first, because the status of perfection is never attained in breeding and, second, because this "perfect" poplar will more than likely have been selected on the basis of its VR to one or more diseases and thus the clone will represent only a fleeting, impermanent level of perfection. An example of this was the widespread commercial planting of clones 'Angulata' and 'G3' in Australia and the subsequent losses incurred when they proved highly susceptible to *Melampsora* leaf rust (Eldridge *et al.* 1973).

When contemplating a selection scheme, therefore, it should be remembered that disease resistance, even though it may be an extremely important character for a breeding programme at a given place and time, is only one of many that must be considered. Also, as graphically demonstrated by Simmonds (1979), the economic worth of disease resistance is rarely, if ever, linearly related to expression and it is often easy to get to the point of selecting for more resistance than is practicable or even necessary. He noted that: 1) some level of resistance to a number of diseases is usually necessary because a "minor" pathogen may assume major proportions in time, 2) high levels of resistance, approaching immunity, are desirable if they are not obtained at the expense of other traits, 3) experience shows that even moderate levels of resistance, deployed wisely, are sufficient and, 4) resistance breeding *per se* is a mistaken strategy and should always be undertaken simultaneously with productivity and other economic traits.

It is therefore important to develop a system for ranking traits and a workable method by which to combine their selection. In practice, the breeder will employ an intuitive simultaneous selection procedure but it generally takes one of two forms. The first is independent culling levels, wherein each character is selected independently, based upon some standard. The second form is index selection which, in effect, employs an equation that selects simultaneously but not independently; this equation "weights" the relative importance of each trait, and a high level of superiority in one or two may compensate for mediocrity in several others when evaluated on a relative scale (Simmons 1979).

It is not within the scope of this paper to review the principles and methodology of genetic selection, but there are two or three more points that must be kept in mind. The first of these is to be aware of the potentials for correlations between traits, both positive and negative. Multiple selection serves to reduce the intensity of selection for any individual trait and this reduction is more pronounced if there are negative correlations. An example of a positive correlation of disease resistance and productivity is available for *Populus*; selection for resistance to *Melampsora* rust serves to delay defoliation of the tree and effectively extend its growing season, thus contributing to increased annual increment and stem volume. It must also be remembered that the number of plants needed for an efficient selection programme increases with both the rate of selections and the number of traits selected, and that these should both be kept as low as possible. This is especially critical for breeding programmes in *Populus* and other forest tree genera because there is such a commitment of time and space for testing. Finally, the efficiency of selection must be maximized and this is most easily done by minimizing the environmental variance in experimental plots through a variety of different methods (Buddenhagen 1983, Buddenhagen and de Ponti 1983, Simmonds 1979).

Of course, the efficiency of selection is also dependent upon the effects of genotype environment interactions (GEI). These interactions should be recognized through testing, and used to advantage in the breeding strategy, if possible. The breeding

strategy for a developing country should focus heavily on local adaptation and the development of pathosystem balance, so GEI is especially relevant in this context. The emphasis in the breeding programme in the developing nation should be on localized testing and selection on or near the site where the poplars will be commercially grown. This, in effect, amounts to utilizing any positive GEI that is present and thus selection for survival and productivity in the area in which the plantation culture will be established will automatically select for tolerance to stress, including diseases, in that environment (Buddenhagen 1983). Barnes (1984) reviewed GEI in the context of its effect on genetic gains for fast-growing forest tree species and discussed a system of breeding that employs localized and somewhat unrelated gene pools which may offer a significant potential for maintaining heterogeneity and exploiting local adaptation in new poplar breeding programmes in developing nations. As far as field testing is concerned, testing a large number of genotypes under controlled conditions will adequately sample the relatively consistent stress imposed by a local environment and, thus, disease resistance and tolerance to environmental stress are automatically components of field selection for productivity in that environment. The procedure is simple but also biologically sound, effective and would be attractive to new programmes that will have to test a large amount of diverse indigenous and/or exotic germplasm.

Since a major goal of the general poplar breeding strategy that is being developed herein is the attainment of durable disease resistance, it is obvious that the emphasis must be placed on selecting for HR to all of the diseases that serve to limit productivity, or have the potential to do so, in the area. Since polygenic control of HR is assumed, this is compatible with selection and breeding for yield, which is also quantitatively inherited. As previously discussed, all co-evolved host-pathogen systems will have an inherent level of HR and, theoretically, early and proper selection and breeding for resistance to an introduced disease should provide for a "construction" of HR (Simmonds 1983, Wastie 1973). Also, because of the long life cycles of trees and the many years they must resist disease in the field, there is universal agreement that a breeding strategy for trees and other perennials that is based upon VR would be courting disaster (Robinson 1971, Day 1975, Simmonds 1983). This is especially true of the genus Populus which has such a wide spectrum of major disease problems.

It is quite probable that, in Populus, VR exists against many diseases. As discussed in the earlier review of important poplar diseases, variation in pathotypes has been reported for all of the important Melampsora leaf rusts, Marssonina brunnea, Xanthomonas populi and, possibly, Dothiciza populea. This will make the screening for HR more difficult and it may dictate that host genotypes screened in either artificial inoculation tests or in the field and evaluated as completely resistant be excluded from the breeding population. Simmonds (1979) suggests that if a specific pathotype is used in screening for VR, then those plants that are totally resistant to it are useless. This is true in terms of their uselessness for the breeding population, but Populus selections with VR may be cloned and put in reserve for future development, as clones, in production populations. This feature of the breeding strategy will be treated in more detail later.

The appropriate methods of screening for HR in the presence of VR, have been presented in a number of plant pathology and plant breeding texts and reviews, including those by Browning (1979), Buddenhagen and de Ponti (1983), Robinson (1979), Simmonds (1979) and Vanderplank (1975).

Returning finally to breeding techniques, the best and most conservative breeding strategy for a new programme of poplar improvement in a developing country will be one which employs breeding techniques that capitalize on the heterozygosity and obligate outbreeding that are characteristic of the genus. This means that techniques that provide

for a maximum of genetic recombination (within, as well as between species) should be favoured. A clonal breeding programme per se is to be discouraged; it is generally only optimally effective in those plants which have an impairment to sexual reproduction. The proper applications of vegetative propagation in Populus are in the testing phases, in seed orchards and in the multiplication of genotypes for the production populations.

The key to a successful long-term breeding strategy is the assemblage and maintenance of a dynamic breeding population made up of good parents that can be exploited in as great a range and number of crosses as the breeding programme can handle. These good parents should be chosen through an adequate programme of progeny testing with an emphasis on localized testing. The progeny tests should be used to determine the levels of general combining ability (GCA) of the parents as well as to identify those rare, superior specific parental combinations (GCA plus SCA) that could be employed to great advantage in Populus seed orchards capitalizing on the dioecism of the genus. The importance of dioecism in aspen breeding was emphasized by Mohrdiek (1983) and he also was rightly critical of the lack of progeny testing and pedigree breeding programmes in Populus, as well as the apparent reluctance of breeders to look beyond the first cycle of selection.

A continual turnover of parental material is also necessary if the breeding programme is to be kept viable. New parents can be selected from the natural stands or provenance tests of the source populations, generated by the breeding programme, or obtained from other breeders' stocks or from commercial populations. It would also be interesting to experiment with exchanges of parents between the local gene pools developed under the multi-population breeding concept discussed by Barnes (1984), which could provide a major advantage to this type of programme for a developing country as it would require little additional investment in sophistication. Under this system, however, the need to maintain adequate and accurate records of pedigree and parentage in the breeding programme becomes critical.

To summarize, the breeding strategy should include a realistic and effective system of parental selection. The number of traits to be included in the programme and the method chosen to weight these are very important. In general, the number of traits should be kept as low as possible and highest priority should be assigned to productivity (yield) or to traits most directly influencing yield. On-site selection for yield may be a most effective means of selection for resistance to diseases and to environmental stress, especially in the earliest phases of the breeding programme. In the selection and screening procedures, all efforts should be concentrated on HR. Breeding techniques that maximize genetic recombination and heterogeneity should be emphasized, and vegetative propagation should be used only for testing and for multiplying the production population. In localized progeny tests, parents should be selected for both general and specific combining ability. Conservation of genetic variation must always be given maximum priority.

Flexible and Adaptive Breeding Strategies

In a new programme for a developing country, probably the greatest advantage for the conception of a viable breeding strategy for Populus would be to adopt the philosophy that the strategy was only tentative. Then, as the programme progressed, the strategy could be modified and adapted to make advantage of new opportunities or to explore new directions, or simply to address more effectively constraints on the programme as they arise, be they biological, like a new disease, or economic, like a reduction in the budget for the breeding programme. Properly conceived and managed, a flexible breeding strategy could also manage to spin-off a good deal of useful applied research, as well as functioning efficiently to produce improved stocks for commercial plantations.

An innovative and flexible attitude toward the breeding techniques employed in the strategy is essential. There has been a trend in plant breeding to increase the use of those methods which promote and maintain heterogeneity. A large and diverse breeding population has obvious advantages when the programme incorporates screening for HR in progeny tests. In discussing the relative advantages of alternative breeding techniques, Simmonds (1979) notes that there may be major advantages gained by combining two or more techniques to provide additional flexibility in new programmes as they develop. One of his examples combines the clonal breeding technique with one aimed at producing open-pollinated progenies and/or synthetic varieties. The object is to combine the best features of each of these techniques into a flexible breeding strategy. This system, which includes progeny testing, is outlined in Figure 3. One of its advantages is that it allows several options for the deployment of resistance in the production population through the use of clones, multiclonal varieties, synthetic varieties or even open-pollinated progenies. Interestingly, Simmonds sees as a major advantage of a strategy employing this combined breeding technique the opportunity to investigate whether or not a clonal breeding method would offer any advantages over the use of interpopulation crosses in a number of species normally propagated by seed. In Populus, of course, the situation is reversed; employing this combined strategy would provide the opportunity to explore a whole new spectrum of options to the classic system of random crossings, direct propagation of selections from clonal tests and their deployment in monoclonal production plantations!

Finally, one of the most powerful options available for maximizing the efficiency and flexibility of a disease resistance breeding strategy is in the deployment of the resistant plants. In poplars, a number of options can be considered. These include uniform, monoclonal selections (the current practice), multi-clonal varieties or synthetic varieties created by vegetatively propagating the seedlings in the upper end of progeny tests or even, as Mohrdiek (1983) suggested, seedling propagation of superior families. As he observed, these options have been available to breeders all along, but were forgotten in the poplar breeders' "continuing search for the perfect clone".

In reality, probably very few other tree genera offer the potentials for effective genetic improvement through the various options combining sexual and asexual propagation that Populus does. The ease of vegetative propagation of Aigeiros and Tacamahaca poplars not only allows the breeder to take advantage of non-additive as well as additive genetic variation, but also affords an opportunity to "construct" production populations of diverse levels of heterogeneity, as required. Dioecism provides a mechanism for taking direct advantage of good specific combining abilities in two clone seed orchards.

It is very important that new programmes in developing countries take full advantage of these options and not simply follow the lead of the programmes that have prevailed in the developed countries. These earlier programmes were established in the era preceding population genetics. The indisputable fact is that, in general, they have managed to produce some rather significant improvements in disease resistance and yield. Hence, there has been a considerable long-term investment in this proven "system" and quite a resistance to explore newer breeding strategies or even breeding techniques that should, in the long run, allow much higher gains to be realised and maintained.

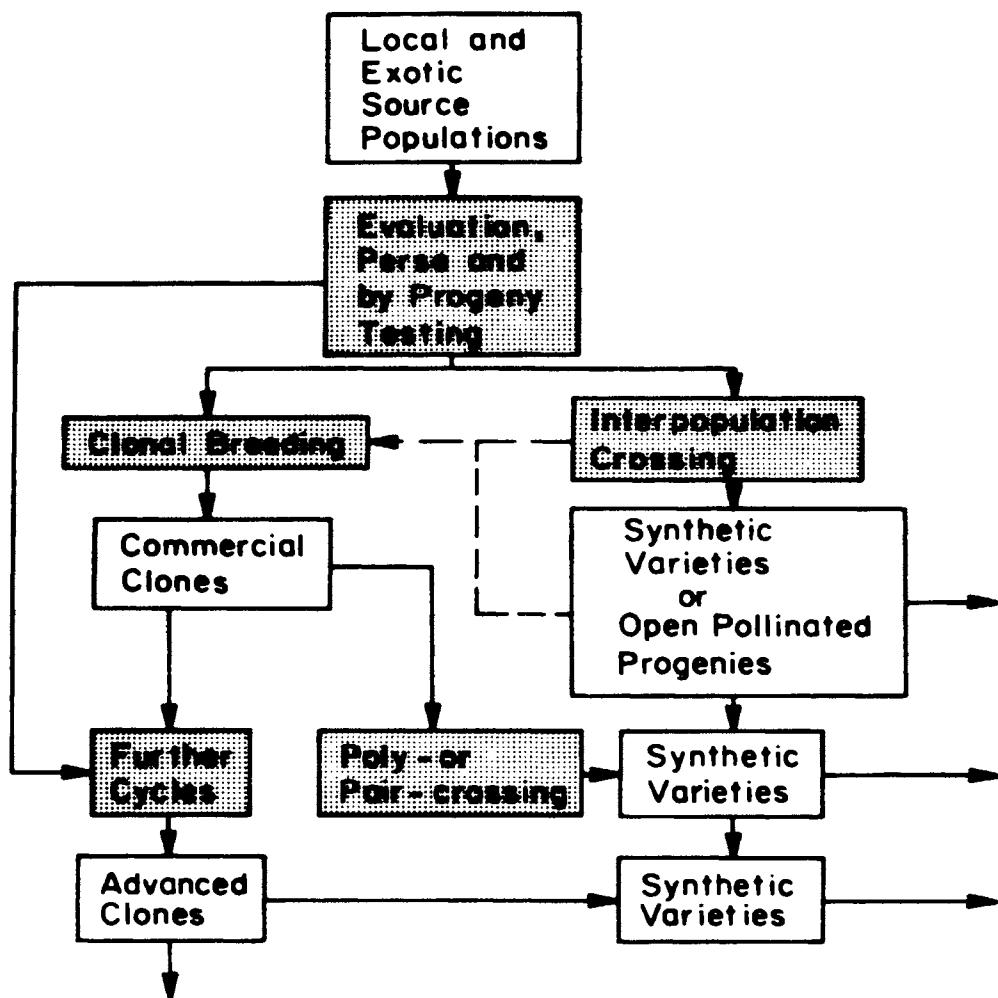


Figure 3. Clonal and Synthetic Varieties Employed as Complementary Breeding Methods for Perennial Outbreeders (Adapted from Simmonds 1979).

FIGURE 3

CLO and SYN as Complementary Breeding Methods in Perennial Outbreeders (from Simmonds, 1979)

The final portion of this paper deals with an alternative breeding strategy for Populus that combines breeding techniques and utilizes multiclonal varieties, as mixtures, in the production population. There has been a great deal of controversy over the use of clones per se, the optimal number of them to employ, the effects of clonal mixtures on productivity and disease resistance, and a number of other considerations. It is not within the scope of this paper to explore the finer points of this controversy, and several recent and comprehensive discussions are available (Burdon 1982, Heybroek 1982, Kleinschmit 1984, Libby 1982). Suffice it to say that the use of clones decreases the heterogeneity of the production population and thus increases the risks of economic damage from diseases and other pests of poplars. If the decision to employ clones in the production phases of the breeding strategy has been made, however, the more unrelated clones that are deployed, the lower these risks become providing that they all have a uniformly high level of HR and have been tested and selected to be grown in a mixture.

This latter point is extremely important as there seems to be a major problem when considering clonal mixtures for Populus plantations; much more of a problem than there is for other tree species. In Picea abies for example, groups of 30 or more clones are tested and selected locally on the basis of their composite performance, and these mixtures are then planted locally, with great success (Kleinschmit, 1984). On the contrary, poplar breeders and growers will invariably report that clonal mixtures of even two or three clones are a great disaster because of major variability in growth rate, and disease incidence and dominance (competition) problems. In my opinion most of these observations are the natural and expected result of selecting, whether systematically or randomly, a group of clones of diverse parentage ranging from two or more pure species to interspecific hybrids, backcrosses and "double" crosses, many of which were developed at other, distant locations and are characterized by a wide range of variability in annual growth patterns and levels of resistance to a number of diverse diseases, and growing all of these together in the same environment. These clones are all such different biological entities that this is somewhat analogous to placing a mixed herd of horses, goats, cows, sheep, bison and camels into the same pasture and expecting them to thrive equally well in the same climate, degree of crowding, diet, and watering schedule! Current research in this area, aimed at developing groups or "sets" of clones selected for similar seasonal growth patterns, levels of disease resistance and wood properties is progressing (Steenackers and Van Slycken 1982, Weisgerber 1982, 1983) and offers an enormous opportunity for both basic and applied research.

A fair summary statement is that, to meet new challenges as the programme develops, a breeding strategy for Populus should be flexible and innovative in terms of goals, breeding methods and deployment of improved populations.

A Breeding Strategy for Populus deltoides

In a review of criteria that should be considered before the inception of an intensive breeding programme for disease resistance in forest trees, Thielges (1982) suggested that Populus deltoides Bartr. was an example of a species that met all of these criteria, which include:

1. Rapid growth rate;
2. Adaptability to single-species plantation culture;
3. A large and environmentally diverse natural range and a high degree of genetic variation;
4. Adaptability to a wide range of sites, including suboptimal ones;

5. Early reproductive maturity (age 8-12 years), production of reliable annual seed crops, ease of "forcing" male and female flowers for controlled pollinations;
6. Dioecism, which provides for the exploitation of specific combining ability and interspecific hybridization in seed orchards;
7. Ease of vegetative propagation by stem cuttings which provides for the exploitation of non-additive genetic variation as well as mass multiplication of resistant, productive genotypes;
8. A wide variety of pest problems that interfere with yield optimization, including a number of diseases that are obligate parasites.

It can thus be seen that the development of a successful breeding strategy for this species will place a great deal of emphasis on heterogeneity, sexual as well as asexual reproduction, and appropriate methods and levels of screening for resistance.

The breeding strategy summarized in Figure 4 is a modification of one that was developed initially as an example of a study that would provide resistance against Melampsora medusae leaf rust (Thielges and Land 1976b), but it can be applied generally to other diseases or combinations of diseases. Also, the general strategy would be effective for species other than P. deltoides and the principles applied would be the same as those illustrated. The general breeding strategy summarized in Figure 4 has two major goals:

1. To maximize high yield and Horizontal Resistance to one or more major disease problems and, of lower priority, to identify and clone any Vertical Resistance genotypes that may be encountered;
2. To begin releasing genetically improved planting stock as quickly as possible after adequate testing.

In this general strategy, the source, breeding and production populations have been functionally separated to facilitate the maintenance of a broad genetic base while also generating a variety of improved material for production. The production population in this example consists of multiclonal lines produced in cutting orchards (stool beds), but the strategy could be modified to produce open-pollinated seed from seed orchards, if necessary. Again, this system must be effective when localized testing is employed on sites representative of major climatic regions and significant planting types.

The potential for greater selection intensities for advanced generation breeding and a mechanism for minimizing inbreeding are provided by establishing and maintaining a broad genetic base in the breeding population. Greater numbers and more heterogeneity also contribute to the possibilities of obtaining a higher level of HR. Thus, it is especially important to insure that the genetic base in a species that is exotic is as broad as possible at the inception of the programme and that it is maintained at this level or increased as the programme develops. Again, the best method of doing this in a new programme for a developing country is through provenance testing prior to the actual start of the breeding programme. The best-adapted trees in the provenance test (individuals, families or entire provenances) can then be selected as parents for the first generation of breeding, and maintained in the provenance test (now part of the local source population) throughout the progeny and clonal testing phases.

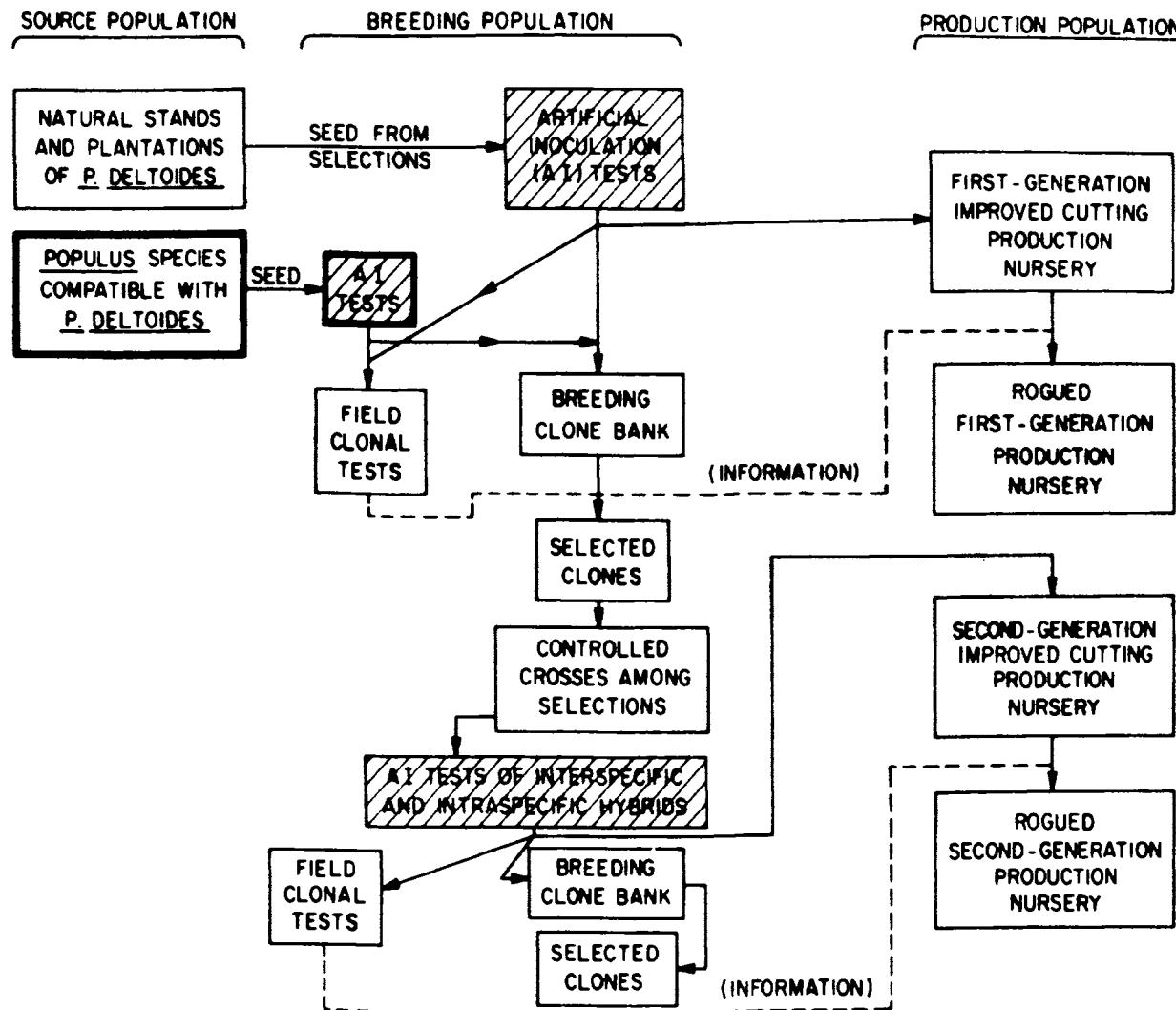


FIGURE 4 - Flow Chart Outlining General Disease-Resistant Breeding Strategy Utilizing Sexual and Asexual Propagation in Breeding Phases. Production Populations are Multiclonal Lines (from Thielges and Land, 1976).

The strategy outlined in the example also provides the option for exploiting interspecific hybridization. This greatly expands the possibilities for obtaining major genetic gains as the programme develops, especially for resistance to some diseases. The use of interspecific hybridization within and between species of sections Aigeiros and Tacamahaca in Europe was reviewed in an earlier section of this paper. As applied in the strategy illustrated in Figure 4, the introduction of an optional programme with other species is carried out as a separate and parallel activity to the main (*P. deltoides*, in this example) breeding programme. Interspecific hybridization is initiated in later phases of the programme only after thorough testing of the parent species for adaptability and resistance to diseases. The interspecific hybrids are intended to serve as a potential for supplementing the *P. deltoides* gene pool and the hybrids are thoroughly tested with this other material. By keeping the interspecific hybridization programme separate from the main breeding effort it provides maximum flexibility in regard to the adoption or deletion of interspecific hybrids at appropriate stages in the evolution of the breeding programme. Having these options and flexibilities is especially important to a new programme in a developing nation where personnel and funding may be extremely limited and where there is no previous experience with poplar culture upon which to base a breeding strategy.

Also optional in the sample strategy are the artificial inoculation (AI) testing procedures (cross-hatched boxes in the diagram). This method of testing is combined with on-site (local) field resistance testing and it provides a means of mass screening large numbers of seedling progenies in a nursery or glasshouse. It thereby reduces the amount of land needed for resistance testing and greatly increases the efficiency of the field testing that is done; if properly applied, at AI screening will ensure that only the most resistant individuals or families are field-tested. Thus, it would be advantageous for a new programme to utilize an effective screening for disease resistance where possible. It would be an added expense at the beginning of the programme and may cause some delay in start-up while the method is developed but, in the long run, it would save much time and money by reducing the number of large and time consuming field tests.

Whether or not artificial inoculation is used in the initial screenings for disease resistance, the final parental selections are obtained by localized or on-site progeny-testing or testing previously screened clones on or near the areas designated for the production plantations. In both AI testing and field tests, families and individuals are evaluated, if possible, for both VR (non-infection during the exodemic) and HR (rate of disease progression on infected trees during the exodemic). Families or individuals with adequate HR are cloned and incorporated into the breeding population (which may also be constituted as a "clone bank") to serve as parents for the next generation. They can be utilized through open-pollination and mass selection in subsequent generations and/or in more complex crossing schemes where they will be progeny tested for specific as well as general combining ability.

Individuals or families exhibiting VR to one or more pathogens in the artificial inoculation tests and/or the field resistance testing should not be included in the breeding population. These VR selections should be cloned and retained for further testing, especially for their possibilities of being used in multiclinal varieties. Simmonds (1979) reviewed 5 major ways in which VR may be deployed to attain a degree of stability or durability; temporal, geographical or spatial development or use in a constructed multiline or mixture. Because poplars are perennial, none of these five methods should be employed to obtain anything other than short-term or "stop-gap" levels of durability of resistance. Even at that, only the spatial and multiline or mixture deployments are at all feasible. The spatial deployment concept is similar to the "mosaic" pattern reviewed by Heybroek (1982) and the use of multilines was reviewed by Browning and Frey (1981) and by Wolfe et al. (1981). The use of mixtures of clones with

diverse and complementary VR genotypes would be much more effective than the other two deployments and might provide a less risky temporary means of attaining a degree of host-pathogen balance in plantations in the earliest stages of a poplar breeding programme. However, it is probably much safer and more efficient to use these VR genotypes later, to supplement satisfactory levels of HR that have been attained through the breeding programme (Thielges 1982).

The use of both sexual reproduction and vegetative propagation are vital to the attainment of short-term and long-term genetic gains under this example of a poplar breeding strategy. Sexual reproduction is used to obtain new genetic recombinations, to evaluate parents on the basis of their general and specific combining abilities and to replenish the gene pool in the breeding population. Intraspecific hybridization among the initial local (or locally-adapted) selections will maintain maximum levels of heterogeneity for advanced generation selection and breeding and can be supplemented in this regard by wide-crossing and interspecific hybridization, if desired. Again, if interspecific hybridization is employed, it is managed as a separate and parallel activity of breeding, screening and selection, and hybrid genotypes are not incorporated into the production population until adequately field-tested for general environmental adaptability, productivity, and levels of disease resistance. Asexual propagation by the rooting of stem cuttings facilitates field testing as well as mass propagation of selected families or individuals for the production population. It also provides great advantages for the design and establishment of seed orchards. Finally, it serves as a means of exploiting non-additive genetic gains based upon broad sense heritabilities.

Applying this breeding strategy to obtain resistance to M. medusae leaf rust, Thielges and Land (1976b) found that major genetic gains could be expected during the first two generations of breeding. The gains were high because the heritability of resistance to Melampsora rust is high and also because vegetative propagation was used to exploit broad sense heritabilities. It is here that the breeder must resist the temptation to rely solely upon vegetative propagation. Since multiple trait selection will be employed in the Populus breeding strategy, clonal propagation of those selections in which the genes for high productivity and the resistance to a number of diseases are adequately "packaged" will be very attractive to the breeder looking for quick results. Direct propagation of this genotype would preclude the possible dilution or dispersal of additive genes through recombination during sexual reproduction, and it also would serve to capture non-additive genetic variation, if present. In this situation it will be very important for the breeder to place progress in the proper time perspective; the fortuitous combination may be cloned and preserved in a clonal bank or even deployed in the contemporary production population as a short-term measure but it must be remembered that long-term gains will continue to accrue only through the maintenance of a viable programme creating and screening new genetic recombinations in the breeding population. If this phase of the programme is abandoned or curtailed due to over-reliance on an apparently satisfactory level of resistance and productivity contained in one or a few clones, it will be extremely difficult, if not impossible, to reconstitute a heterogeneous and productive breeding population to respond to the emergency created when that narrowly-based resistance is overcome, as it surely will be. Again, this aspect of the breeding strategy is critical to a new programme in a developing nation where it may be virtually impossible to reconstruct a poplar breeding programme were it to be abandoned in favour of mass-propagating "resistant" clones.

Gains in Productivity from a Strategy Employing
Population-based Resistance to Diseases - An Example of a Clonal Mixture

To illustrate some of the principles previously discussed and to indicate the potential for gains in volume of wood produced per hectare that can be obtained in the first generation, it is useful to review briefly the results of an experiment incorporating selection for growth rate and disease resistance into a breeding and/or production population that is a multiclonal mixture. This example is directly applicable to the first generation selections that would be made from provenance or open-pollinated progeny tests established to support a new poplar breeding programme in a developing nation, as recommended under the breeding strategy which has been conceived and discussed herein. This example should serve to illustrate that very adequate initial gains are possible in a poplar breeding programme and are not necessarily obtained at the cost of risky monoclonal plantations and a severely eroded genetic base which precludes genetic gain in future generations.

The Populus deltoides Bartr. plantation discussed below was established in 1967 by cloning the seedling progenies of open-pollinated female trees that had been selected for a provenance test of a major portion of the natural range of the species. The study was replicated on a number of sites in several states in the north-central region of the U.S.A. The plantation from which these data were obtained was located at the Ohio Agricultural Research and Development Center in Wooster, Ohio. Prior to the establishment of the plantation the several open-pollinated seedling families of each provenance were outplanted in a nursery for a year and then each seedling was cloned by taking stem cuttings.

The original seedling population for the Ohio planting contained a number of progenies of more southerly origins. These were not cold-hardy in the Wooster nursery and were eliminated during the winters of 1965-66 and 1966-67. Thus, the surviving 76 families (228 clones) in the 1967 plantation represent a population that had been exposed to natural selection for climatic adaptability. As a result of this pre-planting climatic screening, mortality and injuries caused by early or late frosts and cold winter temperatures were minimal in the test population. This factor greatly improved the efficiency of the subsequent screening for disease incidence and growth variables.

Using a combined selection index for height and diameter growth rate, tree form, and resistance to Melampsora rust and a Fusarium stem canker, the 17 best families were selected from the 76 open-pollinated progenies in the population. From these, the best 20 clones were selected for vegetative propagation and further testing at other sites (Thielges and Leben 1971). The procedure for field screening for Melampsora rust resistance was based upon a quantitative index of extent and rate of infection (Horizontal Resistance), and the degree of genetic variation and heritability of resistance in the population were reported by Thielges and Adams (1975).

Data from two of the three replications (blocks) of the original plantation are presented in Table 1 to compare the growth and yield (m³/ha) at (near-harvest) age 10 of the unselected population, the selected families, and the best clones within these families. The unadjusted volume for the unselected population compares favourable with the volumes reported for similar-aged pure, fully-stocked natural stands of P. deltoides (Williamson 1913), reflecting the maintenance of general climatic adaptability in the population. Yields based upon selected family and clonal means illustrate the degree of increased productivity possible through selection and vegetative propagation, and also indicate a good correlation between performance at selection age 2 and age 10. When volumes are adjusted for mortality, the additional benefits of including disease resistance in the selection criteria are reflected by increased yields per hectare. In this example,

8. Cell culture of Prunus and Populus in the INRA Laboratory at Orléans



Rapidly developing techniques of tissue- or cell-culturing are providing significant improvements for laboratory testing for disease resistance as illustrated by these Prunus and Populus plantlets at the INRA Laboratory in Orléans, France.

9. Mixed stand of poplar hybrids in Belgium



Additional research must be done to determine the effects of combination of clonal mixtures, spacings and cultural treatments on the incidence, rate of spread and severity of infection of various diseases in poplar plantations.

mortality was probably due mainly to Fusarium infection which leads to severe breakage of trees with stem cankers. The insignificant differences in mortality based on family and clonal selection reflect the method of screening for this trait; families were eliminated if even one tree was suspect. Thus, Fusarium resistance was screened on the basis of Vertical Resistance (i.e., infected or non-infected) and served as an "all-or-none" trait to eliminate or include whole families.

TABLE 1. - Comparison of P. deltoides Growth Data at Selection Age 2 and Age 10, Expressed as \bar{x} 's of Population, Family and Clone.

Trait	\bar{x} Age 2			\bar{x} Age 10		
	Population	Family	Clonal	Population	Family	Clonal
Total Height (m)	2.75	3.24	3.46	13.53	14.74	15.67
Diameter (cm)	3.18	3.76	4.11	13.44	14.83	16.79
Tree Volume (m^3)	--	--	--	0.092	0.128	0.186
Stand Volume (m^3/ha) at 2.75 x 2.75 m spacing	--	--	--	122.3	169.8	247.7
Stand Volume, as above, adjusted for mortality (%)	--	--	--	105.2	152.3	222.9
	--	--	--	(14.0)	(10.3)	(10.0)

From Thielges (1982)

Table 2 compares the differences between unselected population means, selected family means and selected clonal means for height and diameter growth and volume yields in terms of selection differentials. For mortality-adjusted volume yields, family selection resulted in a differential of 45% over the unselected population mean while selection on the basis of the best clones within the selected families produced a yield differential of 112% (the SD between family and clonal selection is 46% for volume yield). The data in Table 2 also indicate the maintenance of selection differentials for diameter and height growth rates from selection age 2 through age 10, especially between the means of the unselected population and the clonal selections, again indicating of strong juvenile-mature correlations. Obviously, very substantial gains in yield were produced by propagating the best clones from the selected families and, even with a 20 clone "multiline" to ensure a broad base of Melampsora rust resistance and some Vertical Resistance to Fusarium, selection for growth rate was not diluted and significant volume gains were realized. Simultaneous selection for diameter growth rate and Melampsora rust resistance are compatible because resistance prolongs leaf retention further into the growing season and thus contributes to annual increment.

TABLE 2. - P. deltoides Selection Differentials Compared at Selection Age 2 and at Age 10

Differential ^{1/}	Age 2		Age 10		Volume ^{2/} (m ³ /ha)
	Height (m)	Diameter (cm)	Height (m)	Diameter (cm)	
SD _{fp}	0.49 (18%)	0.58 (18%)	1.21 (9%)	1.39 (10%)	47.4 (45%)
SD _{cp}	0.71 (26%)	0.93 (29%)	2.14 (16%)	3.35 (25%)	125.4 (112%)
SD _{cf}	0.22 (7%)	0.35 (9%)	0.93 (6%)	1.96 (13%)	70.6 (46%)

1/ Where SD_{fp} = selected family \bar{x} - population \bar{x} differential

SD_{cp} = selected clonal \bar{x} - population \bar{x} differential

SD_{cf} = selected clonal \bar{x} - family \bar{x} differential

2/ Stand Volumes (m³/ha) adjusted for mortality at age 10.

TABLE 3. - Comparisons of Age 10 P. deltoides Yields Through Altering Selection Index (at Age 2).

Selection Criteria (Age 2)	Unadjusted Volume (m ³ /ha) ^{1/}		Mortality/Adjusted Volume (m ³ /ha) ^{1/}	
	Family Selection	Clonal Selection	Family Selection	Clonal Selection
5-Trait Index (Standard) ^{2/}	169.8 (100%)	247.7 (100%)	152.3 (100%)	222.9 (100%)
Delete "Fusarium"	170.8 (100%)	240.5 (97%)	145.2 (95%)	199.6 (90%)
Delete "Form"	188.6 (111%)	280.8 (113%)	172.0 (113%)	252.7 (113%)

1/ Percentages indicate departures from "Standard" 5-trait index yields.

2/ Traits selected for at age 2 were: height growth rate, diameter growth rate, Melampsora rust resistance, Fusarium stem canker resistance, tree form (bole straightness and freedom from forking and heavy branches). The combined index was unweighted.

From Thielges (1982)

Table 3 illustrates the importance of early identifying and selecting components of volume yield that relate to harvest yield and to management (product-oriented) objectives when multiple-trait selection is practiced. The inclusion of screening for Fusarium in this study, for example, might have been rejected as being imprecise or overly conservative since incipient or suspected cankers at selection age 2 may have excluded some productive and resistant clones in the rejected families. If "Fusarium" had been deleted from the selection criteria at age 2, there would have been no effect on gross or unadjusted volume per hectare at age 10 with either family or clonal selection (Table 3). However, when age 10 yield is adjusted for mortality, there is a significant loss due to the inclusion of Fusarium-susceptible material. This loss is especially significant under clonal selection where an increase of mortality from 10% in the "standard" selection clonal population to 17% in the population not screened for Fusarium results in a 10% decrease in net yield (m³/ha).

Mistakes in the other direction are also easily made. For example, selection for "form" might have been eliminated if the population in this study was selected to produce maximum pulpable fibre yield per hectare at age 10. Inclusion of form in the "standard" five-trait index could reject, at selection age 2, some fast-growing, disease resistant families and clones. The data from the Ohio study in Table 3 indicate that this was indeed the case; if "form" was deleted at age 2, there would be a significant increase in volume at age 10. Moreover, since the index still screens for Fusarium and Melampsora rust resistance, these gains in yield persist when adjusted for loss due to mortality.

The retrospective manipulation of the data presented above and, in fact, all of the information generated from the Ohio study are not represented herein as conclusive evidence of a successful strategy for selecting and breeding fast-growing, disease resistant P. deltoides in a commercial system. Obviously, volume yield extrapolated on the basis of means of the selected families and clones grown in the 6-tree plots of the test plantation might not be realized in a commercial planting of uniformly fast-growing clones wherein competition would be significantly increased. Also, more replications (but on the same or similar sites) are needed to test the validity of the data. Finally, there remains much to be learned about the mode of inheritance and host-pathogen interactions involved in the Populus-Melampsora pathosystem.

Nevertheless, employing these data to illustrate some of the concepts involved in breeding for disease resistance and yield on a population basis, and the advantages of combining sexual reproduction and vegetative propagation to obtain and maintain an environmentally-balanced or buffered host population, allows for some relative comparisons of alternatives. It seems reasonable to expect that poplar plantations can be structured, genetically and spatially, to maximize yield and provide stable resistance to pathogens by exploiting both Horizontal and Vertical resistance (where the latter exists). In some species, such as Populus deltoides, ease of vegetative propagation provides the potential for relatively rapid progress.

Summary and Conclusions

Because of their adaptability to a wide range of sites and their rapid growth rate, poplars, especially the species of Sections Aigeiros and Tacamahaca, represent a significant source of timber, veneer, fibre and fuelwood for developing nations. Despite these factors and the ease of their vegetative propagation, the successful plantation culture of many poplar species has been hindered by a number of potentially serious pathogens that may cause mortality and/or significant reductions in productivity. In some cases, monoclonal poplar culture has experienced the same epidemic-prone "boom-and-bust" cycle of agronomic crops such as wheat and corn (maize).

Fortunately, poplars and other plantation-grown forest trees in general offer opportunities for selection and breeding aimed at obtaining a population-based level of durable disease resistance without a significant reduction in productivity or quality.

Durable disease resistance is a relative concept but, as used herein, it refers to an adequate level of protection against diseases which will persist over time -- certainly throughout the necessary harvest cycle -- and which obviates or reduces the need for frequent investment in defensive or reactive breeding to restore resistance following epidemics. In terms of epidemiology and pathosystem genetics, durable disease resistance can be best obtained via a breeding strategy that employs selection and breeding techniques aimed at maximizing Horizontal Resistance (HR).

In terms of the several significant diseases limiting the widespread and economical cultivation of black and balsam poplars, experience has shown that the homogeneity represented by monoclonal poplar culture has contributed to genetic imbalances between host and pathogen populations and that these imbalances have sometimes led to severe epidemics. Historically, over-reliance on the selection and direct vegetative propagation of disease-free individuals in monoclonal production populations, as opposed to utilizing long-term breeding strategies employing recurrent selection or some other means of maintaining genetic variability, has served to greatly narrow the genetic base in breeding and production populations. In some species, such as Populus nigra, the indigenous source populations have suffered as well. Thus, each cycle of reactive selection and breeding to restore resistance has been increasingly difficult.

To be efficient, a poplar breeding strategy must be a long-term plan with specific goals, but it should also be flexible and adaptable to change. The strategy also needs to be appropriate to the socio-economical as well as the biological environment in which it will be employed. In developing nations, for example, trained personnel, funds and other resources may be limited and it is therefore important that the breeding strategy not be too sophisticated or expensive.

A conservative strategy is suggested for poplar breeding programmes in developing nations. Major emphasis must be placed upon identifying or creating a broad genetic base for initial parental selections and on maintaining this base through conservation of indigenous wild stands or by some appropriate means of regenerating provenance and progeny tests of both indigenous and exotic species. Heterogeneity in the source population should be emphasized and maintained at the local level, and growth evaluations and screening for HR should be accomplished through local, on-site testing. The breeding strategy must be aimed at maximizing genetic variability at all levels, and those breeding techniques that promote maximum genetic recombination should be employed. The proper applications of vegetative propagation in this poplar breeding strategy are limited to testing, seed orchard establishment and the multiplication of genotypes for production populations.

In the long-term breeding strategy presented herein as an example of one that would combine productivity with durable disease resistance, the source, breeding and production populations were kept functionally separate to promote and maintain adequate genetic variability. Selection and testing for production and disease resistance were done concurrently, and on-site (local) field testing was emphasized. The production populations were multiclonal lines and, based upon an experimental clonal plantation, gains in productivity of over 100% at age 10 were calculated on the basis of a 20-clone mixture in which the clones had been selected for growth rate, form and disease resistance.

It is true that much of the discussion in this paper has related to theories and concepts that have not yet been adequately tested. However, this merely serves to add an additional dimension of opportunities in research and development, as well as in the direct application of these concepts in production populations to improve disease resistance and increase productivity. Basic research in pathosystem genetics and epidemiology is needed as well as more practical studies on the effects of various clonal mixtures or mosaics on disease incidence and extent and rate of spread in plantations. Still more research will be needed to develop appropriate mixtures of clones and determine the spacings that will maximize productivity.

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