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POPULATION STRUCTURE, SOMATIC INCOMPATIBILITY, AND SPOROCARP OVERWINTERING in *CHONDROSTEREUM PURPUREUM*

by

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POPULATION STRUCTURE, SOMATIC INCOMPATIBILITY, AND SPOROCARP OVERWINTERING IN *CHONDROSTEREUM PURPUREUM*

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ABSTRACT

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Key words: *Chondrostereum purpureum*, population structure, somatic incompatibility.

An investigation was conducted of the population structure, the somatic incompatibility reaction, and sporocarp overwintering in *Chondrostereum purpureum* (Pers.:Fr.) Pouzar, a proposed mycoherbicide of undesirable hardwood species. *Chondrostereum purpureum* breeding populations of recent cut-over sites in Thunder Bay, Ontario were found to have a high number of individuals possessing different alleles for somatic incompatibility. Up to nine fungal individuals per wood unit (logs, stumps) were found, with the majority of wood units having only one to three individuals. The macroscopic appearance of the somatic incompatibility interaction zone on malt extract agar varied among paired isolates and was occasionally ambiguous. Phenotypic variability of the interaction zone ranged from scant mycelia to massed hyphae between the two colonies. Microscopically the sparse interaction zone had chains of swollen spindle-shaped cells, while the massed interaction zone had distorted hyphae, encoiled hyphae, and hyphal knots. Of overwintered sporocarps collected in the spring of 1998 and 1999, 86% produced viable spores. Basidiospore levels in the spring may be greater than once thought, and thus may pose a threat to winter-damaged trees. This should be considered in the assessment of the epidemiology of *C. purpureum*, and in the assessment of this fungus as a biocontrol agent.

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INTRODUCTION

RESEARCH OBJECTIVES

The main objective of this project was to use the somatic incompatibility reaction as the criterion in determining local population structure of *Chondrostereum purpureum* (Pers.:Fr.) Pouzar [formerly *Stereum purpureum* (Pers.:Fr.) Fr.] (Nakasone 1990) in Thunder Bay, Ontario. Egger (1992) described population structure as "the pattern of distribution of individuals within a species, and their organization into groups that share greater overall genetic similarity" (p. 193). Population studies are useful in discovering the means of fungal dispersal, as the distribution of somatically incompatible individuals in a substrate is a reflection of the mode of colonization (Rayner and Todd 1982a). Worrall (1994) attributes the value of understanding fungal pathogen population structures and colonization means to its usefulness in the establishment of epidemiological models and disease management strategies. *Chondrostereum purpureum* as a cause of silver leaf disease in fruit trees and with its potential role in birch decline, is a serious fungal pest in fruit orchards and forests. Because of its role as the cause of disease in many hardwood species, its endemic nature in forests, and its proposed use as a mycoherbicide, an understanding of the population structure of *C. purpureum* is important.

Harvested areas provide abundant infection opportunities for this fungus, with plenty of dead woody material to quickly amplify the population. It may also act as a wound pathogen, causing dieback and decline in the remaining live trees, which are often wounded in the harvesting process. The population structure of *C. purpureum* includes the incidence of the fungus and the degree of relatedness within the population. The population structure was observed at three levels. At the first level, genetic variability was assessed among isolates found on individual stumps or

slash, in order to make determinations about the prevalence of multiple infections by *C. purpureum* within individual wood units, possibly representing multiple infections in the previously living tree. The occurrence of multiple infections in live trees may result "in a mycotoxin-tolerance threshold being exceeded" (McLaughlin 1991, p. 18). As well, the determination of the population structure within individual wood units may shed more light on the life strategy of *C. purpureum*. Genetic variability was determined by pairing pure culture isolates of *C. purpureum*, and observing for reaction lines indicative of somatic incompatibility between the isolates. The second level was a survey of infected wood units and assessment of relatedness between isolates from different individual trees/stumps/slash to determine incidence and genetic variability over a small area (314 m^2). The incidence and relatedness over the whole clear-cut was the third level. Random pairings of isolates collected from over the study area were used to assess genetic variability.

As the somatic incompatibility reaction had a variable appearance and was occasionally ambiguous, a preliminary study of the microscopic appearance of the interaction zone between paired *C. purpureum* dikaryons was undertaken. This included examination of the somatic incompatibility interaction zone to determine if the manifestation of somatic incompatibility was distinguishable at the microscopic level.

Another objective was to determine the ability of *C. purpureum* sporocarps to successfully overwinter under natural conditions. Currently *C. purpureum* sporocarps are thought to be of significance for only a single season. Observations on overwintering success, as determined by the ability to produce viable spores, may contribute to our understanding of, and establish the possibility of, early spring/summer infection of winter damaged trees by basidiospores.

CHONDROSTEREUM PURPUREUM

The fungus *Chondrostereum purpureum* has been found on all continents except Antarctica (Chamuris 1988). *C. purpureum* is the causal agent of silver leaf disease (Brooks and Moore 1926; Brooks and Storey 1923; Peace 1962) in orchard trees such as apricot, prune, pear, peach, cherry and apple (Adaskaveg and Ogawa 1990), and causes disease in forest trees such as mountain ash, maple, poplar, willow, birch, hawthorne, and shrubs like gooseberry, rose, cotoneaster and nanking cherry (Maruyama and Hiratsuka 1985). The fungus has been occasionally reported on some conifers (Chamuris 1988; Nakasone 1990). The disease may remain limited to only a few branches, or it may lead to the death of affected branches within a year and tree mortality in as little as two or three years (Maruyama and Hiratsuka 1985). Sudden silverleaf outbreaks in orchards lead to decreased fruit production (Chaney *et al.* 1973) and tree mortality causing considerable economic loss.

The sporocarp of *C. purpureum* is characterized by a smooth hymenium, a morphological characteristic that places it in the family Thelephoraceae (French 1991, p. 170)[1]. Originally classified as a species of *Stereum* because of its stereoid sporocarp, Reid (1971) agreed with Pouzar in the placement of this species in the genus *Chondrostereum* because of its monomitic sporocarp, non-amyloid spores, and vesicles in the hymenium. The *C. purpureum* sporocarp has a beige and tomentose pileus, with a hymenial surface that starts out purplish, but later becomes buff

---

[1]French followed Burt's (1920) concept of placing *S. purpureum* in the artificial family Thelephoraceae. Later, the fungus was placed in Pilát's family Stereaceae, a family whose delimitations remain unclear; Chamuris (1988) placed *C. purpureum* in the artificial family Corticiaceae *sensu lato*.

to brown (Cartwright and Findlay 1958; Thomas and Podmore 1953). The sporocarp when attached to a wood substrate may be flat or bracket shaped (Cartwright and Findlay 1958) and is similar in appearance to several *Coriolus* spp.

In live trees fruiting occurs at the base of affected branches or just above the root collar (Maruyama and Hiratsuka 1985). Fruiting may be extensive over any exposed surface of dead woody material (Wall 1997).

New basidiocarps of *C. purpureum* are produced in spring and autumn when it is cool and damp (Wall 1991). Wall (1997) found that the production of sporocarps could be expected to last as little as two years following infection by *C. purpureum*, when they are then displaced by other common saprophytic hymenomycetes (Fritz 1954; Rayner 1978; Rayner 1979; Rayner and Todd 1979; True and MacDonald 1973). Conversely Hintikka (1993) found that new *C. purpureum* basidiocarps were found on stumps five to seven years old, which may have occurred due to resistance such that the tree's mortality was extended and sporocarp production continued.

C. purpureum is tetrapolar and heterothallic (Robak 1942), with cultural characteristics as described by Stalpers (1978). Wall *et al.* (1996) found allopatric homokaryon isolates from different regions of Canada were mating compatible, thus *C. purpureum* readily outcrosses and there is little impediment to gene flow among Canadian populations.

C. purpureum is a primary saprophyte that produces a white rot (Adaskaveg and Ogawa 1990) of recently wounded and freshly killed hardwood material (Fritz 1954; Hintikka 1993; Rayner and Boddy 1986). Although it grows rapidly, *C. purpureum* has a slow rate of decay (Rayner and Boddy 1988 p. 269; Rishbeth 1976), which has been suggested to be the result of its ability to use only nutrient reserves of live parenchyma cells (Guinier 1933, cited in Cartwright and Findlay 1958). Luttrell (1974) has characterized *C. purpureum* as having hemibiotrophic behaviour; where tissue dies following infection, thereby conferring to the fungus the advantage of

primary occupation of the food resource at the time of death. In this way *C. purpureum* may pre-empt other saprophytes in the competition for recently-dead wood substrates (Fritz 1954; Luttrell 1974). Spiers and Hopcroft (1988a) postulated that in a similar manner *C. purpureum* might lie as a latent infection that becomes active when host susceptibility increases or compartmentalization is overcome. Wall (1991) found that *C. purpureum* could survive for at least six years in successfully compartmentalized discolored wood, and in this way living trees may act as the reservoir for the fungus, and thereby provide the inoculum for further infection (Spiers and Hopcroft 1988a).

McLaughlin's (1991) observation of the re-emergence of a canker far removed from the point of original infection and cankering, demonstrated that *C. purpureum* could be an aggressive pathogen on birch seedlings. This indication that the fungus could overcome the strongest of the barrier walls, the external wall surrounding the decay (Shigo 1984, cited in McLaughlin 1991), is supported by Wall's (1986) conclusions that *C. purpureum* may invade live cambial tissue and associated sapwood.

C. purpureum may spread by root grafting (Maruyama and Hiratsuka 1985) although wounds infected via airborne basidiospores are usually the route of new infections (Brooks and Moore1926; Brooks and Storey 1923; Grosclaude *et al.* 1973; Maruyama and Hiratsuka 1985). Gadgil and Bawden (1981) found *C. purpureum* in 12.4% of experimental pruning wounds, making it the most frequently isolated of decay-causing fungi in a New Zealand orchard.

There have been several seemingly contradictory studies on seasonal susceptibility to *C. purpureum*, with different researchers finding winter (Stanislawek *et al.* 1987), late winter/early spring (Brooks and Moore 1926), spring/early summer (Beever 1970), mid-summer (Spiers *et al.* 1998; Wall 1991), and late summer (Dumas *et al.* 1997) to be the time of increased tree susceptibility. There appears to be a general consensus that susceptibility peaks at some time in

spring or summer. Wall (1991) described *C. purpureum* as fruiting at times when tree susceptibility is low, noting that with this tendency, and the ability of healthy trees to compartmentalize infection, this fungus, under normal conditions, may be a threat only to trees compromised by stress. Supporting this, de Jong *et al.* (1996) found *C. purpureum* basidiocarps on live trees, were associated only with injuries.

Silvering of the leaves of affected trees is the optical result produced when a polygalacturonase toxin produced by *C. purpureum* (Miyairi *et al.* 1977) causes the palisade mesophyll cells to separate from the epidermis and each other (Peace 1962). Silvering may not occur in all species affected by this fungus (Peace 1962; Spiers and Hopcroft 1987), or even in some epidemic situations where swift mortality may preclude the advent of the silvering symptom (Setliff and Wade 1973). In birch seedlings McLaughlin (1991) found symptoms of *C. purpureum* infection included small, unevenly pigmented, and lackluster leaves, and silvering scarcely noteworthy in large trees.

Darkening and discoloration of affected wood caused by fungal production of laccase (Miyairi *et al.* 1982, cited in Chamuris 1988) and black zone lines may be observed in trees infected with *C. purpureum* (Setliff and Wade 1973). Plugging of the vascular system by wood gums (Williams and Cameron 1956, cited in Chamuris 1988) may be evidence of invasion of the xylem tissue by the fungus (McLaughlin 1991). When a rapid decay course occurs, a characteristic reaction zone may not be present (Pearce *et al.* 1994), which may be due to the ability of *C. purpureum* to "either invade functional xylem rapidly, or propagate xylem dysfunction ahead of the infection front, whilst avoiding, detoxifying or suppressing host defensive responses" (Pearce 1996, p. 227). Thomas and Podmore (1953) characterized early decay by *C. purpureum* in black cottonwood as a pale-brown stain, where wood strength appears unaffected. Advancing

decay results in the fading of the stain as the wood becomes bleached, brittle and light weight (Thomas and Podmore 1953; Spiers and Hopcroft 1988a).

A massive birch dieback phenomenon occurred between 1937 and 1949 in southeastern Canada and northeastern United States (Braathe 1995). Birch dieback characteristics described by Pomerleau (1953a) included "discoloration and wilting of the leaves, smaller and thinner foliage, dying of twigs and branches, which progressively extends from the top to the base of the crown, and finally to the death of the entire tree" (p. 147). Although recent work by Braathe (1995) indicated that spring thaw and subsequent frost at a critical point in bud burst may have led to this phenomenon, symptoms of birch dieback suggest a systemic injury (Balch 1953), not unlike what is observed in *C. purpureum* infected birch. The large scale dieback of birch has long been postulated to be a result of changes in tree water economy due to disruption in normal water conduction (Greenridge 1953); and vascular dysfunction is a leading cause of the symptoms seen in trees infected with *C. purpureum* (McLaughlin 1991; Spiers and Hopcroft 1987). In *C. purpureum* infected trees, the translocation of mycotoxins produce symptoms far from the point of active infection (Cartwright and Findlay 1958). McLaughlin (1991) suggested this as a reason for the failure of the fungus to be isolated in early studies of birch dieback (Hansbrough 1953; Horner 1953; Pomerleau 1953b; Redmond 1953a; 1953b; Stillwell 1955).

More recently some studies have found an association between *C. purpureum* infection and birch with decline symptoms or discolored wood (Allen 1996; McLaughlin 1991; McLaughlin and Setliff 1990; Setliff and McLaughlin 1991; Morawski *et al.* 1958, cited in Allen 1996). Because wood discoloration due to damage or disease is most rapid in birch compared to other hardwoods (Shigo 1965, cited in Allen 1996), wood decay and discoloration in birch is a serious problem that has lead to its decreased value as timber. Because white birch is a common

ornamental tree in many Canadian cities, the importance of dieback and decay in birch is not limited to its decreasing commercial value for the forestry industry.

McLaughlin (1991) postulated that *C. purpureum* may act on infected trees in one of two ways. It may be a primary pathogen with the capability of killing parts or all of a tree quickly, or it may act as a predisposing factor, with decline symptoms a result of mycotoxins and secondary organisms. Factors that influence tree health may be largely based on the success of compartmentalization of infection within the tree, as ineffectual compartmentalization may allow mycotoxin seepage into the sap flow or infection to overcome the compartmentalization walls and to spread (McLaughlin 1991). Vascular disruption caused by the mycelium plugging the xylem (Spiers and Hopcroft 1988a) and compartmentalization of water-conducting tissue (McLaughlin 1991) are believed to disrupt vascular translocation leading to wilting and other decline symptoms.

Scheepens and Hoogerbrugge (1988, cited in de Jong *et al.* 1990) found that *C. purpureum* had a two-year mortality efficacy rate of 61%, aptly demonstrating the potential of *C. purpureum* as a mycoherbicide of broad-leaved weeds. Winder and Shamoun (1991) note a paradigm shift within forestry with the goal of using biocontrol to decrease competition from weeds rather than to reduce their numbers. Application of *C. purpureum* to stumps has been demonstrated to reduce sprouting or sprout viability in *Acer rubrum* L. (Wall 1990), *Alnus sinuata* (Reg.) Rydb. (Comeau and Harper 1996), *Alnus rubra* Bong. (Prasad 1996), *Populus tremuloides* Michx., *P. grandidentata* Michx. (Dumas *et al.* 1997), *Betula papyrifera* Marsh., and *Prunus pensylvanica* L.f. (Jobidon 1998; Wall 1990). Wall (1994) found that coupling frilling treatment of unwanted *Alnus rubra* with application of *C. purpureum* cultures increased tree mortality, and Prasad (1996) found that this increased foliage mortality. At this time certain *C. purpureum* isolates are being tested for their environmental impact, so that eventually a safe biological control

product can be used for conifer release treatments and for clearing utility rights-of-ways (Jobidon 1998).

POPULATION STUDIES OF FUNGI

There are a variety of methods that may be used in the study of fungal populations and their structure. These techniques involve directly or indirectly assessing genetic variability within the intraspecific genome. Isoenzyme, protein, and virulence studies may determine biochemical pathway commonalities within a population, and DNA analyses enable observation of the variability at specific loci and regions of the genome. The number and distribution of mating-type factors and somatic incompatibility groups may be used to examine genetic variability at loci governing these behaviours.

Sen (1990) states that isoenzymes may be superior to the somatic incompatibility technique, because the degree of genetic relatedness among closely related individuals might be assessed. Although Burdon (1993) has suggested that analysis with isoenzymes may not sufficiently reflect variability within lower population levels for many species. As isoenzyme markers are limited to the coding regions of DNA (Egger 1992; McDermott and McDonald 1993), this reasoning may extend to any measurable characteristic such as virulence (Leung *et al.* 1993; McDermott and McDonald 1993). As well, because they may be subject to environmental, and thus evolutionary influences, characteristics such as virulence and isoenzymes may represent convergent evolutionary pathways rather than actual population structure (Leung *et al.* 1993; McDonald and McDermott 1993). Hence analytical techniques that reflect variation in universal or regional specific characteristics may not be ideal for determination of population structure at regional or local levels.

Restriction DNA analyses "provides for large numbers of markers from coding and non-coding regions of the DNA" (Egger 1992, p. 195), possibly circumventing detection of variation found only in regions of *genic* (coding) DNA which is more highly conserved, thus less variable (Egger 1992; McDonald and McDermott 1993). Greater levels of variation may be found within *intervening* DNA (transcribed DNA excluded following RNA processing), and *intergenic* DNA (sequences which are non-transcribed) (Egger 1992). Thus, general or specific DNA markers appropriate for exposing genetic variation at the desired population hierarchical level are possible (Egger 1992; Tan *et al.* 1994).

Correlation between DNA and somatic incompatibility (SI) analyses of fungal genetic variation vary from poor (Jacobson *et al.* 1993; Vilgalys and Gonzalez 1990), to good (Kohli *et al.* 1992; Marçais *et al.* 1998; Rizzo *et al.* 1995a; Roy *et al.* 1997), and to perfect (Chamuris and Falk 1987; DeScenzo and Harrington 1994; Garbelotto *et al.* 1997; Holmer *et al.* 1994; Kohn *et al.* 1991; Smith *et al.* 1994; Vasiliauskas and Stenlid 1998a; 1998b). Roy *et al.* (1997) observed that although their DNA profiles for *Phlebiopsis gigantea* (Fr.) Jül. isolates corresponded largely with their SI results, the two techniques are based upon "unrelated genetic criteria" (p. 2101). It seems likely that unless the restriction sites, or regions of sequenced DNA are within loci coding for the SI reaction, the correlation between DNA analyses and SI within a population may be coincidental.

Worrall (1997) listed three incompatibility systems in the basidiomycetous fungi. The first system, *intersterility*, is between "biological species"; thus hyphal fusion or mating may not normally occur. The *sexual incompatibility* system is based on genetic similarity where common mating type alleles will prevent mating *e.g.* $A_1B_1xA_1B_2$ or $A_1B_1xA_2B_1$. In cases where the mating type alleles are not in common, mating may occur between two homokaryons to produce a heterokaryon (Worrall 1997); also called a dikaryon in the basidiomycetes (Todd and Rayner

1980). Worrall (1997) explains that the heterokaryon forms the "secondary mycelium" which contains genetically different paired nuclei in each cell, with one from each homokaryon. The third system, *somatic incompatibility*, also called vegetative or heterokaryon incompatibility (Carlile 1987) occurs with genetic dissimilarity (Worrall 1997). When heterokaryons of different genotypes meet, recognition of non-self occurs, and hyphal fusion does not take place. If on the other hand the hyphae recognize each other as "self", anastomosis (hyphal fusion and exchange of cytoplasmic and nuclear contents) occurs and the two individuals will grow together forming one thallus of intermingling hyphae (Worrall 1997).

The "unit mycelium" concept (Todd and Rayner 1978; 1980) allowed intraspecific hyphal fusion between multiple genetically dissimilar dikaryons enabling large fruiting structures otherwise thought impossible (Buller 1931, p. 155-169). Because evidence for this phenomenon in nature is lacking, it has been replaced by the "individualistic mycelium" concept, where somatic incompatibility serves to delimit fungal individuals within an interbreeding population (Rayner 1991a; 1991b; Rayner and Boddy 1988, p. 205; Rayner and Todd 1979; Rayner *et al.* 1984; Todd and Rayner 1978; 1980). SI also acts to secure food resources for the individual (Rayner and Todd 1982b), thus this mechanism is a form of territoriality (Rayner 1991b; Rayner *et al.* 1984). The most significant evolutionary benefit of SI is that it prevents negation of sexually derived genetic variation within populations, which would happen if somatic compatibility were the rule (Lane 1981; Todd and Rayner 1978; 1980; Worrall 1997).

Fusion, or anastomosis, of somatically compatible fungi has its advantages as it produces a chimera, which may be more fit than its individual components due to "a greater store of genetic variability with which to respond to . . . environmental change" (Buss 1982, p. 5339). Anastomosis also benefits both individuals as survivorship may be higher among larger individuals, and may allow the reproductive stage to be reached faster (Buss 1982; Worrall 1997).

Buss (1982) has suggested that in the determination of somatic compatibility, kin selection may result, as in many species the SI loci are linked to fertility loci, thus reducing the costs of somatic fusion.

Anastomosis comes with some practical disadvantages, including *somatic cell parasitism*, where one genome benefits to the detriment of the other in the somatic association (Buss 1982). Even more serious is the phenomenon of *genomic replacement*, in which one dikaryon set completely replaces the other after anastomosis (Ainsworth *et al.* 1990; Carlile 1987; Rayner 1991a; Rayner *et al.* 1984). As well, transmission of mycoviruses and other agents of disease may be facilitated by hyphal fusion (Anagnostakis 1992; Caten 1972; Carlile 1987; Rayner and Todd 1979; Worrall 1997). In Canadian isolates of *C. purpureum* there have been studies on an association between virus-like particles of double stranded RNA and hypovirulence (Shamoun and Valverde 1994; Shamoun *et al.* 1996).

Worrall (1997) defines somatic incompatibility as the failure to produce a stable heterokaryon by anastomosis of two non-self individuals, when contact between self hyphae usually produces a stable heterokaryon. Somatic incompatibility may occur rarely in fungi as *fusion incompatibility*, where fusion fails to take place, or more commonly as *post-fusion incompatibility*, where hyphal fusion and cytoplasmic mixing occurs followed by the characteristic macroscopic SI reaction (Carlile 1987). Heterokaryon self-incompatibility, where strains lack the ability to form a stable heterokaryon (Correll *et al.* 1989; Hyakumachi and Ui 1987; Leslie 1993) is distinguished from somatic incompatibility by resulting from pre-fusion events, which prevent anastomosis from occurring. Correll *et al.* (1989) postulated that self-incompatibility might occur due to a mutation at a single gene that controls the anastomosis function.

The somatic incompatibility reaction on artificial media where two colonies interface has been described as a "line of demarcation" (Schmitz 1925), "line of aversion" (Mounce 1929, cited

in Adams and Roth 1967), "barrage" (Vandendries and Brodie 1933, cited in Adams and Roth 1967), and "line of antagonism" (Worrall 1997). As the actual mechanism of SI is poorly understood, Barrett and Uscuplic (1971) described the SI reaction on agar as the "interaction zone", which is the terminology used in this report. This reaction has been correlated in some species to "zone lines" in infected wood, which may serve to delimit the individual and its substrate territory (Rayner 1991a; Rayner and Boddy 1988, p. 430; Todd and Rayner 1978; 1980; Williams *et al.* 1981); although zone lines were not observable in willow infected with multiple *C. purpureum* basidiospores (Spiers *et al.* 2000). The appearance of the SI interaction zone may vary among fungal species and even among isolates of species (Marçais *et al.* 2000; Rayner and Boddy 1988 p. 205; Worrall 1997). Appearances range from thickened walls of aerial mycelia on one or both sides, sometimes accompanied by pigmentation, to a zone of scant mycelia (Worrall 1997). The pigments are thought to be melanin or melanin-like oxidation products due to the presence of phenoloxidases and peroxidases produced by one or both isolates in the interaction zone (Li 1981). These pigments may provide hyphal cells with physical resistance to lysis by the other isolate (Li 1981). The variation in intensity of negative somatic reactions may be an additive result of many different genetic characters (Marçais *et al.* 2000; Worrall 1997).

The chromosomal sites determining SI are termed vegetative compatibility, *v-c* loci, or heterokaryon compatibility, *h-c* loci (Rayner and Boddy 1988 p. 209), *het* loci (Jacobson *et al.* 1998), or *vic* loci (Leslie 1993). Somatic incompatibility groups (SIGs, also called vegetatively compatible groups VCGs) contain members who are somatically compatible because they have identical alleles at loci that govern this behaviour (Leslie 1993). Somatically compatible isolates are not genetically homogeneous as they may exhibit differing mating alleles (Mallett and Harrison 1988), cultural characteristics (Adams and Roth 1967; Rayner and Turton 1982), isoenzyme patterns (Rodrigues *et al.* 1995), and protein profiles (Lewis and Hansen 1991), and so they might

merely have common alleles at the SI loci. Therefore, it should be emphasized that somatically compatible isolates represent members of somatic incompatibility groups rather than genetically unique individuals.

For many researchers the inference that somatic incompatibility may be used to differentiate genotypes is common practice (Leslie 1993; Shaw and Roth 1976; Todd and Rayner 1980), and has been used as the sole criterion in many studies of fungal populations (Anagnostakis 1992; Barrett and Uscuplic 1971; Dahlberg and Stenlid 1990; Fries 1987; Holmer and Stenlid 1991; Kile 1986; Thompson and Rayner 1982; Williams *et al.* 1981). The usefulness of somatic incompatibility in population studies is that "such identifications can be important in determining the number of genetically distinct individuals within a population" (Leslie 1993, p.141), although it is "not useful in determining the degree of relatedness if the two isolates are not identical" (Leslie 1993, p.136). Rayner and Todd (1979) concur that antagonism occurs on the basis of fungal genetic difference without regard for degree of relatedness, yet there is considerable evidence that the SI reaction decreases in intensity with increased relatedness (Adams and Roth 1967; Adams *et al.* 1981; Anagnostakis 1984; Childs 1937, cited in Rayner and Todd 1979; Coates *et al.* 1981; Hansen *et al.* 1993a; Kay and Vilgalys 1992; Kile 1983; Leslie 1993; May 1988; Rayner and Todd 1979; 1982a; Rayner and Turton 1982; Rayner *et al.* 1984; Stenlid 1985; Todd and Rayner 1978; 1980; Worrall 1997), and mating allele similarity (Adams and Roth 1967; Wilson 1991).

In fungal population studies, isolates are transitive when their compatibility is in concordance *e.g.* isolate A is compatible with isolate B, B is compatible with isolate C, and A and C are compatible (Murphy and Miller 1993). A concern in using SI as a determinant of genetic identity appears when a lack of transitiveness is encountered (Jacobson *et al.* 1993), where a definite pattern of compatibility or incompatibility cannot be established. Marçais *et al.* (2000) postulated that SI discrepancies might be the result of difficulty in distinguishing weak

incompatibility from compatibility. It has been suggested that differences at only a few SI loci can lead to these ambiguous somatic incompatibility reactions which may confound interpretation of SI results (Anagnostakis 1984; Malik 1996, cited in Worrall 1997).

Mallett and Harrison (1988) with *Marasmius oreades* (Bolt.:Fr.) Fr. and Stenlid (1985) with *Heterobasidion annosum* (Fr.) Bref. found all pairings between siblings were somatically incompatible. Kay and Vilgalys (1992) found that 90% of *Pleurotus ostreatus* (Jacq.:Fr.) Kummer pairings between full sib heterokaryons and their parent were somatically incompatible. In similar experiments by Murphy and Miller (1993) 98% of *Collybia subnuda* (Ellis:Pk.) Gilliam and 15% of *Marasmiellus praeacutus* (Ellis) Halling sib heterokaryon and parent pairings were incompatible. Thus it seems that the ability to distinguish among related individuals using the somatic incompatibility reaction varies from one fungal species to another. Hence when SI is the sole criterion in population studies, genotypic densities are likely to be underestimated (Adams and Roth 1969; Murphy and Miller 1993).

Leung *et al.* (1993) stated that the somatic incompatibility character is not sufficiently polymorphic to be used as a tool in investigating genetic variability, yet for many fungal species SI is thought to be a polygenic and multiallelic characteristic (Anagnostakis 1987; Rayner 1991a; Rayner and Boddy 1988, p. 209; Rayner *et al.* 1984; Smith *et al.* 1994; Worrall 1997). *Neurospora crassa* Shear & B.O. Dodge with at least ten known genes for somatic incompatibility (Mylak 1976) has been calculated to have 1024 possible SI genotypes (Carlile 1987), and *Podospora anserina* (Rabenh.) Niessl calculated to have 7680 (Anagnostakis 1987) making the SI characteristic for these species extremely polymorphic. Unlike these and other ascomycete species, Marçais *et al.* (2000) has indicated that somatic incompatibility in basidiomycetes is not well-understood. In the basidiomycetes SI is believed to be under the control of fewer (one to four

genes), hence the differentiation among individuals based on somatic incompatibility is expected to be lower (Marçais *et al.* 2000).

According to Anagnostakis (1992) the wide use of somatic incompatibility in estimating fungal population diversity is because like intergenic DNA, SI "is alleged to be under no selection pressure" (p. 183). Although the mechanism by which SI genes effect the SI reaction is largely unknown, the genes are likely to be under some kind of selection pressure. Fincham *et al.* (1979, p. 195) postulated that a density dependent mechanism controls the population of somatic compatibility alleles, promoting a polymorphic population of alleles, as the maintenance of somatic incompatibility prevents situations where one nuclear genotype exploits another (Hartl *et al.* 1975).

Because the natural population structure of many fungal species is maintained by somatic incompatibility (Rayner and Todd 1979), somatically incompatible colonies "behave as individuals and thus may represent the primary units of selection" (Kay and Vilgalys 1992, p.178). Hence the natural function of SI allows it to reflect variability within populations to a degree that depends upon the species. Although SI is poorly understood, and its ability to distinguish between related isolates for many species is poor or unknown, the somatic incompatibility reaction is generally accepted as a means of detecting genetic variation within fungal populations.

POPULATION STUDIES OF *C. PURPUREUM*

Biochemical testing and DNA analyses have been used to develop our current understanding of the population structure of *Chondrostereum purpureum*. The global *C. purpureum* population is discontinuous in some biochemical and DNA patterns as a result of geographic separation. Shamoun *et al.* (1995) determined little variation in sensitivity to cycloheximide among isolates from Canada, Europe and New Zealand, although Canadian isolates

differed in their reaction to L-Dopa. Shamoun *et al.* (1995) interpreted these findings as low intraspecific variability in the biochemical pathways of *C. purpureum,* indicating that these pathways may be homogenous over the global or continental scale. Ramsfield *et al.* (1998) found isolates from British Columbia, Switzerland and Finland exhibited uniformity in their restriction fragment length polymorphism (RFLP) patterns suggesting that variation in *C. purpureum* mitochondrial DNA is low. Shamoun *et al.* (1991a) found little variation among restriction patterns of the internal transcribed spacer region of the ribosomal DNA repeat, among isolates from Canada and Europe; however the New Zealand isolate showed a unique pattern.

Research by Ramsfield *et al.* (1996a; 1996b; 1997) of the RFLPs of the highly conserved large non-transcribed spacer in ribosomal DNA indicated that there were three nuclear types in *C. purpureum*. Type I is found in all regions studied (New Zealand, Europe and North America), while type II was found only in North America, and type III found only in Europe and New Zealand. They believe that geographic isolation has allowed the formation of distinct nuclear types. From their study it was concluded that gene flow across North America occurs, as there was an almost equal distribution of type I and type II in the central portion of the continent, while type I predominated in the eastern part of the continent and type II in the western part (Ramsfield *et al.* 1996a; 1996b; 1997).

Initial isoenzyme analyses of *C. purpureum* isolates indicated that biochemical variation might be sufficient to characterize isolates (Shamoun *et al.* 1991b). Yet in further studies it was found that the characteristics protein content, enzymatic activity, isoenzyme patterns (Shamoun and Wall 1996), virulence, and growth temperature (Ekramoddoullah *et al.* 1993) were similar among *C. purpureum* isolates from New Brunswick, Vancouver Island, and south-eastern British Columbia. Based on these specific markers, there appears to be little distinctness among Canadian populations of *C. purpureum*. Similarly Gosselin *et al.* found, with the random amplified

polymorphic DNA (RAPD) technique, that there was little significant genetic differentiation between ecoregions of Quebec (1995) and ecozones of Canada (1999). Yet a high degree of genetic variation at the local level has been found at the sub-population level within Canada (Gosselin *et al.* 1995; 1999) and New Zealand (Spiers *et al.* 2000), as the use of RAPD markers enabled differentiation between isolates. Biochemical (Shamoun and Wall 1996) and RAPD analyses (Gosselin *et al.* 1995; 1999; Spiers 2000) have indicated that variation among isolates of *C. purpureum* does not correlate with geographic origin or demonstrate host specialization. In Canada Gosselin *et al.* (1999) concluded that the local variation within geographic subpopulations of *C. purpureum* occurred on a fine scale, with this variability evenly distributed across the country.

As *C. purpureum* spore dissemination is usually local because the spores are not likely resilient enough for dispersal over long distances (Grosclaude 1969, cited in Wall 1997), Ekramoddoullah *et al.* (1993) hypothesized that transport of forest products and nursery stock have contributed to the homogenization of variability among Canadian subpopulations of *C. purpureum*. Because of the genetically homogeneous nature of the Canadian population, and the outcrossing ability putting little restriction on gene flow within the national population (Wall *et al.* 1996), consensus thus far is that the use of *C. purpureum* as a mycoherbicide is not a threat to genetic variation within local *C. purpureum* populations.

Population studies that determine the spatial distribution of fungal isolates may provide evidence of life strategy and mode of colonization of the fungal species. Wind disseminated spores often result in a mosaic of individuals occupying the same wood substrate (Rayner and Boddy 1986; Rayner *et al.* 1984; Williams *et al.* 1981); for example Coates and Rayner (1985) found an average of 7.1 somatically incompatible *C. purpureum* isolates in 0.28 cm^3 of wood substrate. Alternately, sole occupation of the wood resource may indicate an asexual means of colonization

(Anderson *et al.* 1979; Carruthers and Rayner 1979; Rayner and Todd 1982a), or a latent infection previously compartmentalized and only come to the fore as a result of lowered tree defenses (Rayner and Boddy 1986; Rayner *et al.* 1984). Rayner and Boddy (1986) characterize *ruderal* life strategies with fleeting occupation of the resource where rapid assimilation of nutrients allows a hasty reproductive stage to be reached. A form of the *stress-tolerant* life strategy is persistence of the fungus in healthy sapwood until conditions become favourable for latent infection. Coates (1984, cited in Rayner and Boddy 1986) found that *C. purpureum* grew swiftly on cut beech, with isolates from the same log being somatically compatible thus appearing to be the result of latent infection (Rayner and Boddy 1986). Thus it seems that *C. purpureum* may combine ruderal and stress tolerant life strategies, as it is capable of causing ruderal and latent infections, both culminating in early reproduction and replacement by other species.

MICROSCOPIC CHARACTERISTICS OF SOMATIC INCOMPATIBILITY

Rayner and Todd (1982b) found with autoradiographic studies involving rubidium-86, that active translocation of cytoplasmic contents occurs following hyphal fusion between compatible isolates of *Coriolus versicolor* (L.:Fr.) Quél., and that this did not happen between incompatible isolates. Rizzo *et al.* (1995b) observed in *Phellinus gilvus* (Schw.) Pat. that self-paired hyphae intermingled and freely anastomosed, while in non-self pairings, hyphae demonstrated initial anastomosis and subsequent hyphal lysis, which produced a sparse zone observable at both the micro and macroscopic level. Following anastomosis "incompatible combinations initiate a sequence of events that ultimately ends in death of the fusion cell" (Jacobson *et al.* 1998, p. 45). These "senescence pathways" (Rayner and Todd 1979) of programmed cell death may be similar to apoptosis found in animal and plant cells (Jacobson *et al.* 1998), with systems involving

proteases and phenoloxidase initiating hyphal cell death (Rayner and Boddy 1988, p. 209; Rayner and Coates 1987; Rayner *et al.* 1984). Rayner (1991a) noted that interhyphal interactions occurred on a spectrum with "responses from non-contact, to contact interference, to encoiling and penetration giving physiological access, to true fusion giving physiological and genetic access which can be restricted by rejection and septal maintenance or blockage" (p. 55). Although the range of reactions observed might be a function of the polygenic and multiallelic character of somatic incompatibility, Jacobson *et al.* (1998) suggested cell death was the result regardless of the pathway initiated by individual somatic incompatibility genes.

A "nuclear replacement reaction" has been observed in hyphal fusion of *C. versicolor*, where a dikaryon set of the donor hyphae replaces by conjugate division, the disintegrated nuclear set of the recipient hyphae (Aylmore and Todd 1984; Todd and Aylmore 1985). In non-self fusions this phenomenon was seen for up to four days without any change; thus they speculated a delayed SI reaction might have occurred subsequent to their observations. Nuclear replacement may not be involved in SI at all, as the phenomenon was observed equally in self and non-self fusions. The nuclear replacement reaction has also been observed in *C. purpureum* (Ainsworth and Rayner 1989).

Spindle-shaped cells have been observed in the interaction zones of non-self pairings of *C. versicolor*, *Bjerkandera adusta* (Fr.) Kar. (Rayner and Todd 1982b), and *Phlebia radiata* Fr. (Boddy and Rayner 1983), while adjacent hyphal cells may become vacuolated (Aylmore and Todd 1984) and die leaving hyphal "ghosts" (Todd and Rayner 1980). Todd and Rayner (1980) postulated that spindle cells formed because uncontrolled lysis within the cells softened the cell walls, and turgor pressure caused the cells to swell and distort the softening cell walls. Although in later studies Aylmore and Todd (1984) speculated that spindle cells arose from hyphal fusion between somatically incompatible hyphae but had no association with lytic activity. Aylmore and

Todd (1984) suspected that the septa between spindle cells were plugged, and in this way they functioned to separate the fusion cells from the rest of the mycelium (Todd and Rayner 1978). Rayner and Todd (1979) postulated that spindle cells "although sparse, nevertheless efficiently close off the immediate area from the rest of the mycelial system and act effectively as a trap for hyphal tips" (p. 374).

Vacuolation of non-self fusion cells has been reported in *H. annosum* (Hansen *et al.* 1993b) and *Phanerochaete velutina* (DC.:Pets.) Parmasto (Aylmore and Todd 1986). Adams *et al.* (1981) observed cells that became granular "and often disappear leaving hyphal 'ghosts' " (p. 511), while further back they observed hyphae "swell into vesicles, forming chains of interconnected chlamydospore-like cells which eventually proliferate to form the pseudosclerotial antagonistic zone" (p. 511). Barrett and Uscuplic (1971) also observed abnormally short hyphal cells, chlamydospore formation, and darkened cells with cellular disruption in the interaction zone of *Polyporus schweinitzii* Fr. Aylmore and Todd (1986) concluded that the SI reaction is, at least initially, an orderly process of autophagic vacuolation.

Knots of hyphae were observed in the SI interaction zone of *M. oreades* (Mallett and Harrison 1988) and *P. schweinitzii* (Barrett and Uscuplic 1971). Coiling reactions were seen occasionally between self and non-self hyphae of *Stereum hirsutum* (Willd.:Fr.) S.F.G. (Ainsworth and Rayner 1989) and *H. annosum* (Hansen *et al.* 1993b), and in di-mon pairings of *Schizophyllum commune* Fr. (Nguyen and Niederpruem 1984); hence this reaction may not necessarily be a somatic incompatibility reaction. Hyphal coiling has most frequently been observed as an interspecific reaction (Boddy and Rayner 1983; Ikediugwu and Webster 1970; Macre 1967; Rayner and Webber 1984). Macre (1967) observed the winding of hyphae around opposing hyphae forming hyphal knots and cellular deterioration at the contact point between

species of *Hirschiporus*. Hyphal coiling may be a form of mycoparasitism (Rayner and Boddy 1988, p. 219) or part of a replacement reaction (Rayner and Webber 1984).

Hyphal swellings as well as excessive branching have been observed in the interaction zone between incompatible isolates of *Ganoderma* spp. (Adaskaveg and Gilbertson 1987) and *Peniophora rufa* (Fr.:Fr.) Boidon (Chamuris and Falk 1987). Mallett (1989) found that somatically incompatible isolates of *Armillaria* spp. surrounded themselves with a pseudosclerotial plate (PSP) composed of "bladderlike cells". Although the PSPs serve to prevent contact between the isolates, they observed sparse hyphae with bulbous swellings, within the inter-PSP region.

Little hyphal interaction observed between non-self hyphae of *Echinodontium tinctorium* Ellis & Everh. (Wilson 1991), and *H. annosum* (Hansen *et al.* 1993b), indicating that diffusible substances might also mediate the somatic incompatibility response.

The various morphologies of interaction zones observed in different species might indicate that mechanisms for the SI phenomenon are not universal, with the somatic incompatibility reaction differing among fungal species.

OVERWINTERING CAPABILITY OF *C. PURPUREUM* SPOROCARPS

The sporocarp of *C. purpureum* has a wide range of morphologies that are dependent upon humidity and other environmental factors. With high relative humidity and moisture content the basidiocarps are flexible and leathery, and under desiccating conditions they are rigid and brittle. Spiers and Hopcroft (1988b) found that *C. purpureum* sporocarps could survive to water contents as low as 22%, with the cytoplasm becoming condensed and vacuolated. The thin walls of the basidia allow rapid rehydration such that spore production and release follow several hours later (Spiers and Hopcroft 1988b).

C. purpureum sporocarps are long thought to be annual structures, viable for only one growing season and thereafter displaced by other decay fungi (Wall 1997). Wall (1991) observed that *C. purpureum* sporocarps were sloughed off during the dry or winter period, while de Jong (1988, cited in de Jong *et al.* 1990) found that they die following moderate frost. These studies indicate that overwintered sporocarps are not sources of basidiospores in the spring.

Mazur (1960) described how freezing damage to cells might occur in one of two ways. Slow cooling leading to dehydration and extracellular freezing may cause an increased solute concentration, precipitation of solutes, cell shrinkage, and plasmolysis, which may result in irreversible protein denaturation. Rapid cooling may lead to intracellular ice forming in the cytoplasm, which invariably leads to damage of the cellular membrane systems. Hence damage to the cell, due to dehydration and formation of intracellular ice, may occur on a continuum depending upon "cooling velocity and permeability of the cell to water" (Mazur 1960, p. 444). Deverall (1965) suggests that the repeating cycle of freezing and thawing of fungal cells is detrimental to their survival in the wild. However Mazur (1968) ascribes the common survival of fungi *in situ* to the "rarity of intracellular freezing" (p. 383), due to the low cooling velocities found in nature.

MATERIALS AND METHODS

SITE HISTORY

The main site used in this study is adjacent to the north side of the Cascades Conservation Area (CCA), located north of the city of Thunder Bay, Ontario (Figures 1 and 2). This approximately forty acres of land, is owned privately by Vic Laurin Sr., and was harvested in the winter of 1995/96 by Hiles-Laurin Contracting Limited. Prior to harvesting, the tree composition was roughly 90% poplar and 10% birch with a small amount of miscellaneous conifers. Following harvesting of most of the poplar on site in the winter of 1995/96, some of the residual birch was harvested or cut down and left in the winter of 1997/98. The method of harvesting was feller-buncher and skidder.

Study areas Mills Block D (MBD) and Williams Block D (WBD) are both 5 ha. cut blocks located on land overseen by the Lakehead Region Conservation Authority (Figure 1). They had a similar species composition as the CCA, and were harvested of their poplar and birch in the winter of 1997/98 by cut and skid method. These settings, following partial cutting of mixed wood stands, with residual live hardwoods and abundant slash and stumps, ideally supports the dual yet integrated ecological roles of *C. purpureum*. Woody debris and stumps provide ample food resources on which the fungus can act saprophytically, and remaining live trees, which are often wounded in the harvesting process, may become infected.

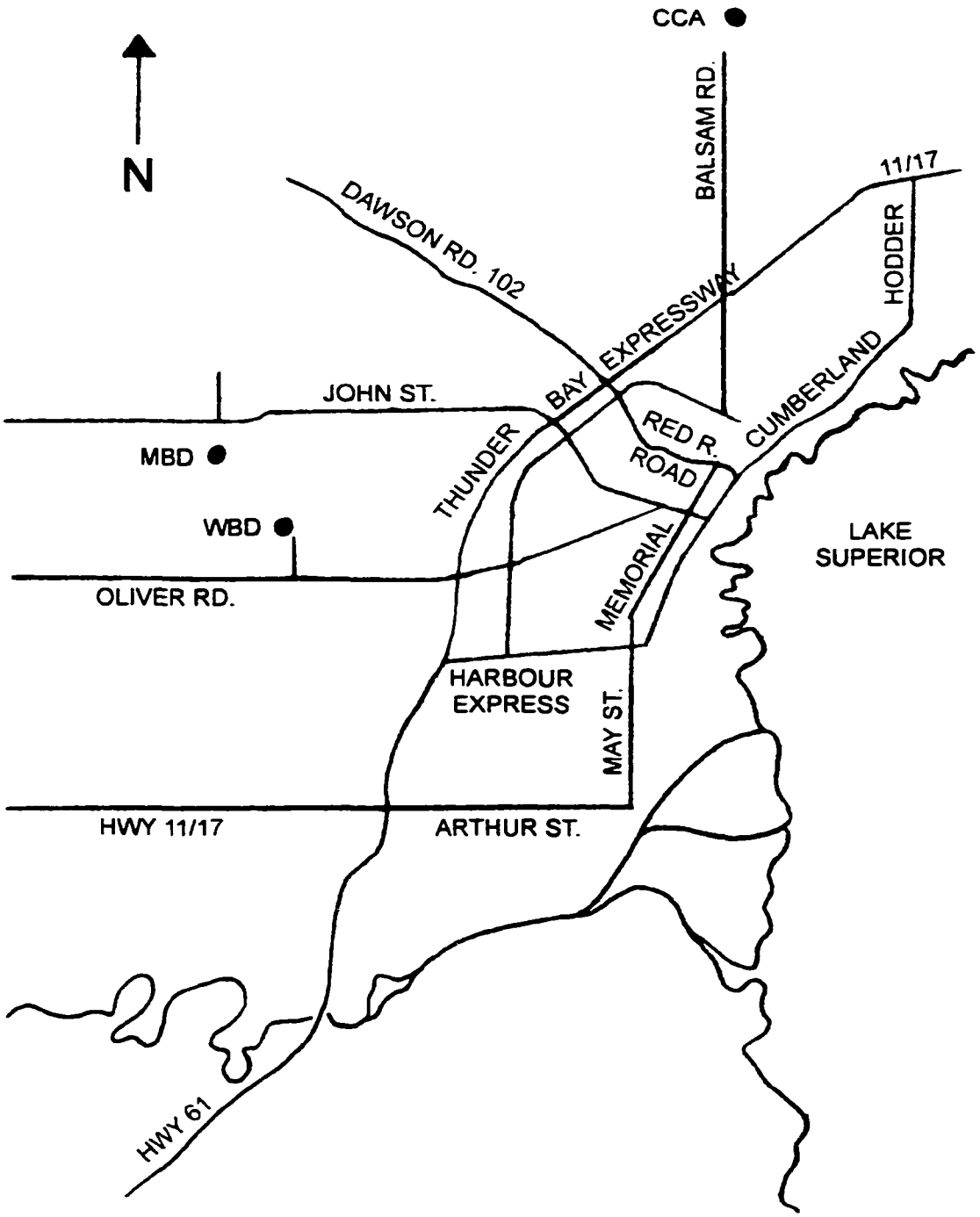

Figure 1. Map of Thunder Bay (Guide Printing and Publishing 1993) indicating the locations of study sites Cascades Conservation Area (CCA), Mills Block D (MBD), and Williams Block D (WBD).

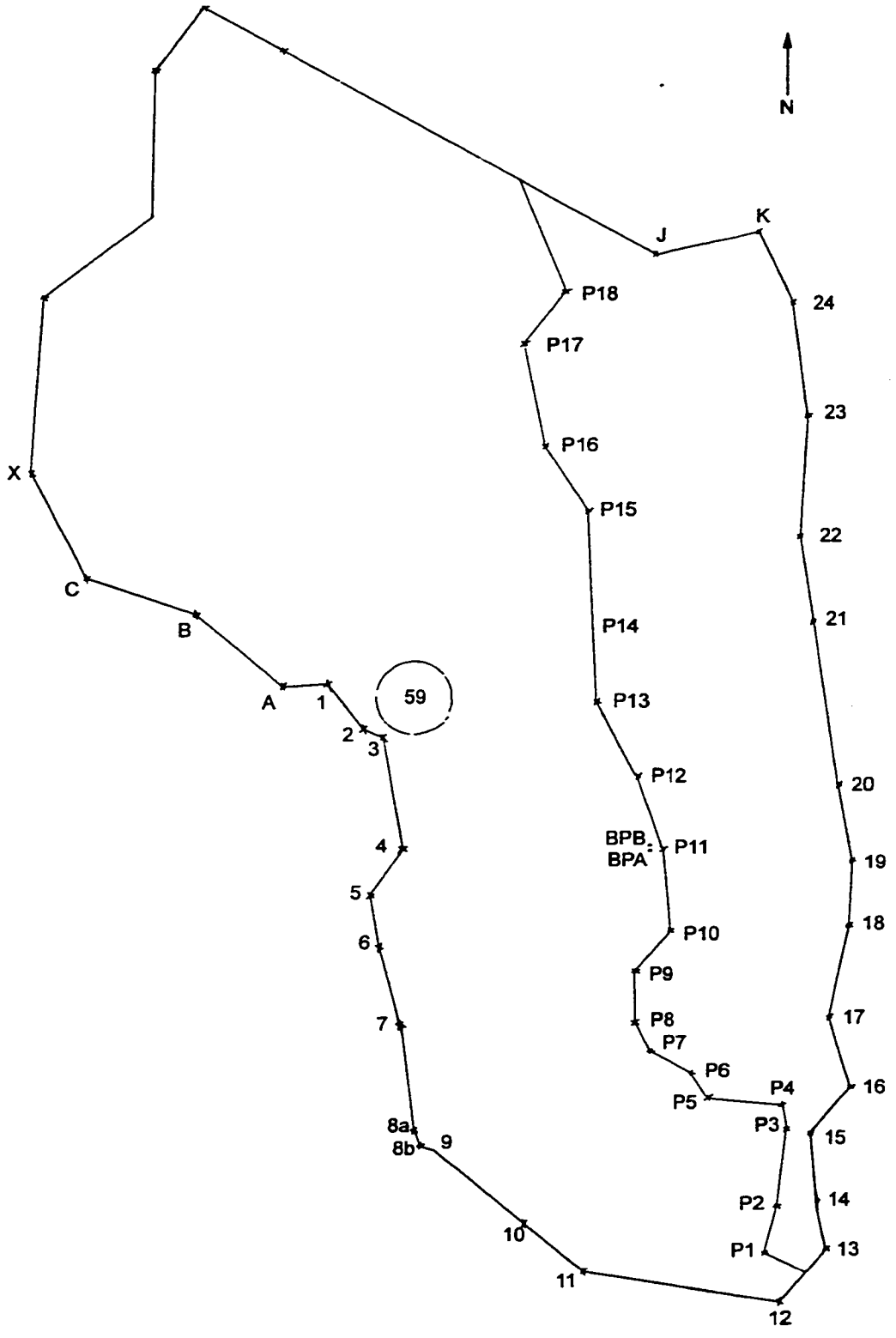

Figure 2. Map of the Cascades Conservation Area (CCA) study site indicating the locations of the path and perimeter benchmarks, Plot 59, Birch Pile A (BPA) and Birch Pile B (BPB).

POPULATION STUDY OF *C. PURPUREUM*

In October and November 1997, basidiocarps of *C. purpureum* were randomly collected from around the perimeter and central path in a survey of the whole CCA study area. Sporocarps were given an identifying number (Appendix I) based on the order in which they were found while in the vicinity of the nearest benchmark on the map of the CCA study area (Figure 2). A whole or piece of the sporocarp was collected from each distinct grouping of sporocarps on slash and stumps. In the laboratory the sporocarps were rehydrated for 4-24 hours in a humidor of moist paper towel in a glass petri dish. They were then stuck to the underside of plastic petri dish lids with petroleum jelly, from which they cast spores onto 1% malt extract agar (MEA) overnight. For each sample an approximately 5x5 mm area of agar, with spores from the edge of the spore print, was transferred to another MEA plate. In a dark 24°C incubator the spores were allowed to grow into a multi-spore heterokaryotic culture. These individual cultures were used to conduct compatibility tests between 29 (20% of 144) randomly chosen isolates paired in all combinations (406 pairings). To pair all of the 144 CCA isolates in all combinations would have required 10,296 pairings. Round mycelial plugs (5 mm diameter) of multi-spore cultures were placed 1-3 cm apart and observed over one to two months for somatic compatibility. Where the paired isolates grew into a single colony, the isolates were recorded as somatically compatible (+). Where this did not occur, but an interaction zone demarcating the growth of the two isolates appeared, the isolates were determined to be somatically incompatible (-) (Figure 3). Random self-pairings were used as positive controls. There was repetition of pairings when results were inconsistent or ambiguous.

In October 1997, Plot 59 was intensively harvested of any *C. purpureum* sporocarps, with each collection given an identifying number (Appendix I) based on the order in which the

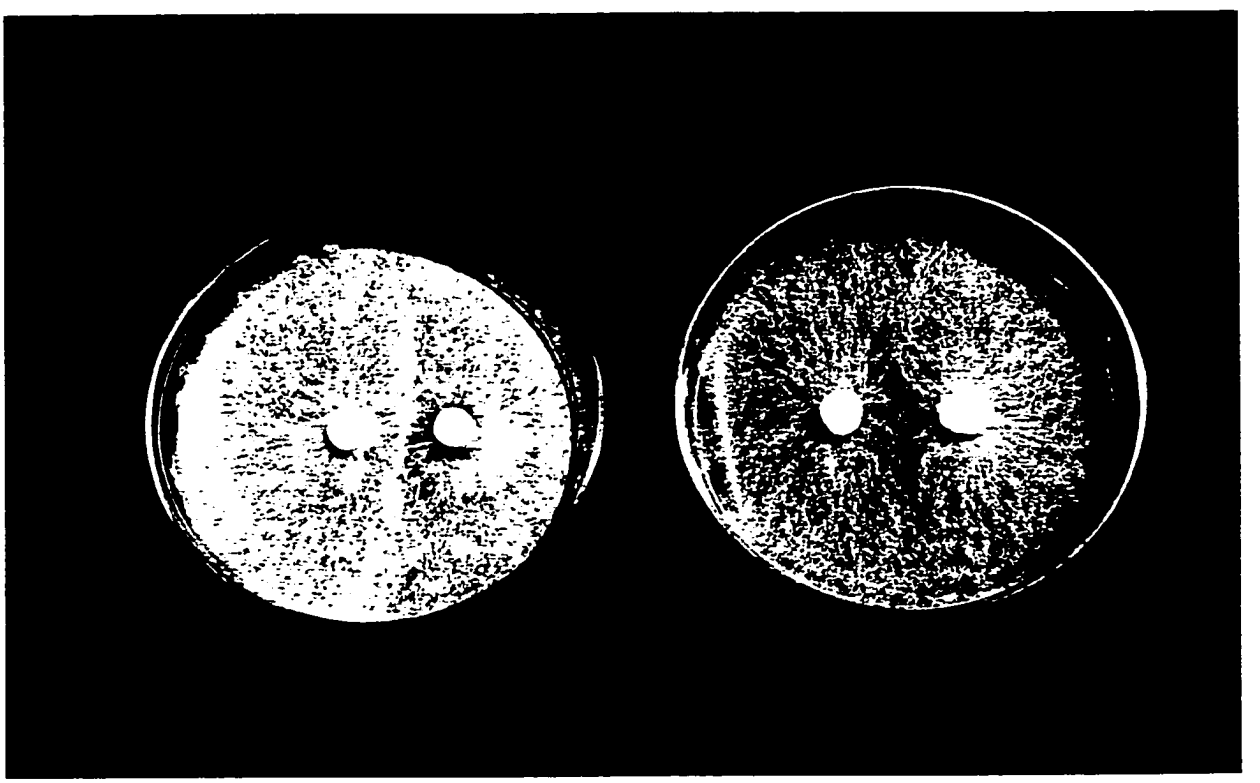

Figure 3. Two-week-old pairings between *C. purpureum* isolates demonstrating somatic incompatibility (left) and somatic compatibility (right).

wood substrate was observed (Figure 7 in the Results section). Laboratory treatment was the same as for the CCA sporocarps except that compatibility testing was conducted among all 20 isolates in all possible combinations (190 pairings). In the fall of 1998, sporocarps were collected from a transect traversing each study area MBD and WBD (Figure 4), and given numbers according to the order in which they were found (Appendix I). The six MBD and eight WBD isolates were paired among themselves in all combinations (15 and 28 pairings respectively).

In the fall of 1998 sporocarps were intensively surveyed and collected from two piles of birch logs, found in the CCA study area that were cut in winter 1997/98 (Figure 5). Logs in Birch Pile A (BPA) and Birch Pile B (BPB) were given either BPA or BPB designations, and then numbered according to the order in which they were observed. The south facing end of the log was designated A, and the north face B, and the side of the log was given the designation S. Sporocarp isolates were given an identifying number with the birch pile, log number, A, B, or S indicating exposure, and a number indicating the order in which it was found clockwise from the top of the face; or if on the side from north to south (Appendix II). Laboratory treatment was as above, except isolates collected from the same log were paired among themselves in all combinations (401 pairings). Of the 191 isolates collected from the birch piles, MBD, and WBD, 36 (19% of 191) randomly chosen isolates were paired in all combinations (630 pairings). The exclusion of MBD isolates was random.

Dikaryon multi-spore stock cultures from each fruiting body have been saved in 1% MEA slant tubes, and are stored at 4°C in the Lakehead University Forest Pathology Laboratory. As well, the sporocarps themselves are stored in paper bags at room temperature in the same location. Some of the fruiting bodies collected in the fall of 1997 were hot air dried while the rest were dried at room temperature.

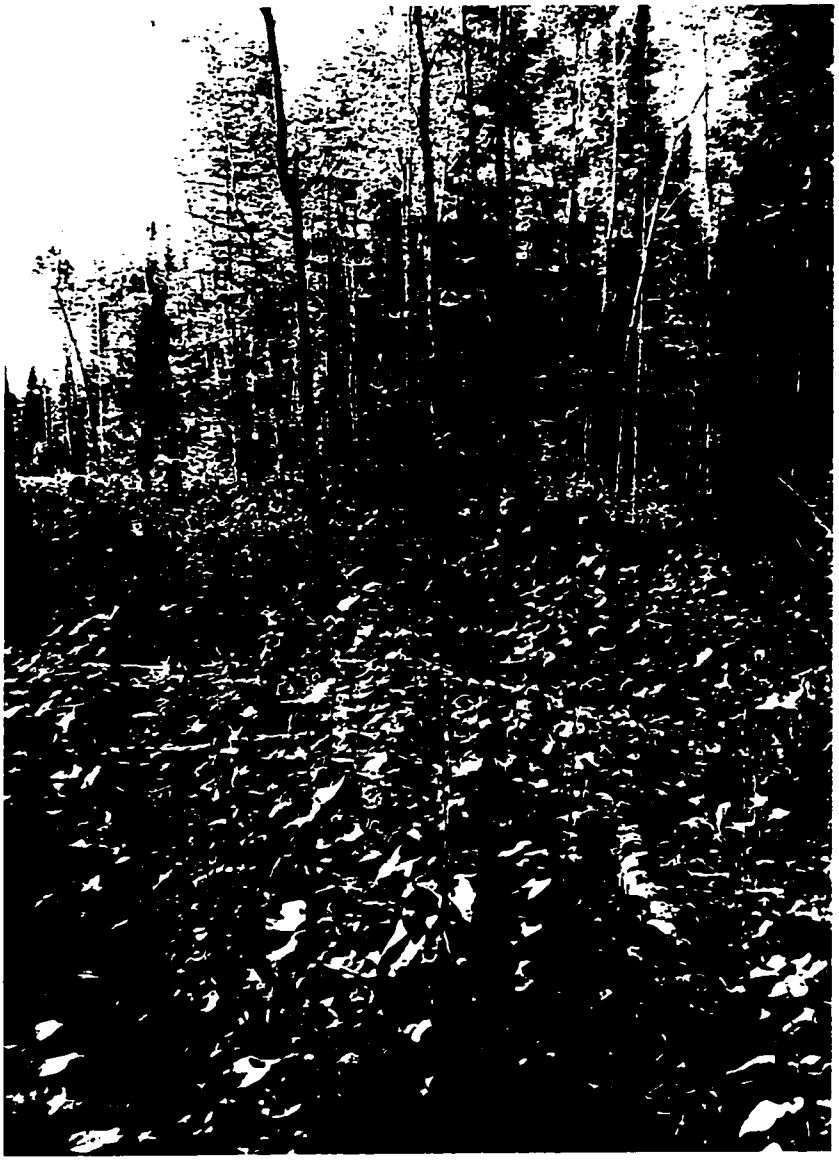

Figure 4. The MBD study site one growing season after poplar and birch harvest at the time of the *C. purpureum* sporocarp survey.

Figure 5. Birch Pile A (BPA), in the foreground, and Birch Pile B (BPB), from which sporocarps of *C. purpureum* were collected one growing season after the logs were cut.

MICROSCOPIC CHARACTERISTICS OF SOMATIC INCOMPATIBILITY IN *C. PURPUREUM*

Self and non-self pairings were conducted on coverslips dipped in water agar and placed on 1% MEA plates. Non-self pairing isolates BPA-34-A3/BPA-34-A4 and BPB-7-A1/BPB-7-B1were observed in five pairings each, while BPA-34-A3 and BPB-7-A1 were observed in five self-pairings each. Five mm round plugs of mycelium were used in all pairings, except in one set where 3 mm round plugs were used. Sets of pairings always used the same group of isolates, although coverslip width and length were varied. The isolate plugs to be paired were placed on opposing edges of the agar water coverslip, with part of the plug overhanging the MEA plate to provide the nutrient for growth. Following 3-6 days of incubation in the dark at 24°C, the coverslips and hyphae growing on them were cut from the surrounding growth and media. The coverslips were placed upside-down on glass slides, in a drop of 2% glutaraldehyde used as a cytoplasmic fixative. The interaction zones for the pairings were observed using brightfield microscopy at 400x and 1000x (oil immersion), and black and white photos were taken to document the results.

OVERWINTERING CAPABILITY OF *C. PURPUREUM* SPOROCARPS

Overwintered *C. purpureum* sporocarps were collected in the spring of 1998 and 1999 from the CCA study area. Sampling of sporocarps was not random, as it was biased towards overwintered sporocarps that had a healthy appearance. They were moistened and held over 1% MEA to collect any spores, as described earlier. The spores were observed microscopically (400x) for germination following overnight incubation at 24°C.

RESULTS

POPULATION STUDY OF *C. PURPUREUM*

Random pairings of isolates collected from the CCA study site in the fall of 1997 were all somatically incompatible, even among those collected from the same wood unit (Figure 6). However, one pairing between isolates found not far from each other had an ambiguous SI reaction that could not be determined even after several repetitions. This pairing was said to have indeterminate compatibility.

Plot 59 isolates collected in the fall of 1997 were collected from 9 of 12 wood units (stumps or logs) (Figure 7). No compatible isolates were found, even among isolates collected from the same wood unit (Figure 8). There were 1-8 sporocarps collected on the wood units in Plot 59, where each sporocarp represented a distinct somatic incompatibility group (SIG).

Isolates collected from MBD and WBD in the fall of 1998, paired against all isolates within their block were found to be incompatible except for one pairing between WBD isolates with indeterminate compatibility (Figures 9 and 10). Random pairing of isolates collected from WBD (by chance MBD was excluded) and the birch piles found compatible isolates in only three pairings where they were all from the same log in BPA (Figure 11).

Of the 102 birch logs in BPA and BPB censused in the fall of 1998, 50 logs, or 49% had *C. purpureum* sporocarps. The larger pile, BPA, with 86 logs, had 43% logs bearing the sporocarps. Conversely, of the small pile with 16 logs, 81% of the logs in BPB bore *C. purpureum* sporocarps (Table 1).

Of the 125 sporocarp isolates collected over the 37 *C. purpureum* infected logs in BPA, 93 different SIGs were observed (Table 2). And in BPB 43 SIGs were observed among 52

	X-C-2	C-A-13	C-A-11	C-A-9	C-A-5	1-A-1	1-C-2	1-C-5	1-C-8	5-A-2	5-A-3	5-B-1	12-B-1	12-C-1	19-A-2	20-A-2	23-A-1	K-A-1	K-B-5	P-A-2	P-B-5	P-D-2	P-D-3	P-E-7	P-E-9	P-F-4	P-I-1	P-I-7	P-I-8
X-C-2		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C-A-13			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C-A-11				-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C-A-9					-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C-A-5						-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1-A-1							-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1-C-2								-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1-C-5									-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1-C-8										-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5-A-2											-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5-A-3												-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5-B-1													-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12-B-1														-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12-C-1															-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19-A-2																-	-	-	-	-	-	-	-	-	-	-	-	-	-
20-A-2																	-	-	-	-	-	-	-	-	-	-	-	-	-
23-A-1																		-	-	-	-	-	-	-	-	-	-	-	-
K-A-1																			-	-	-	-	-	-	-	-	-	-	-
K-B-5																				-	-	-	-	-	-	-	-	-	-
P-A-2																					-	-	-	-	-	-	-	-	-
P-B-5																						-	-	-	-	-	-	-	-
P-D-2																							-	-	-	-	-	-	-
P-D-3																								-	-	-	-	-	-
P-E-7																									-	-	-	-	-
P-E-9																										?	-	-	-
P-F-4																											-	-	-
P-I-1																												-	-
P-I-7																													-
P-I-8																													

Figure 6. Pairings between randomly selected *C. purpureum* isolates collected from the Cascades Conservation Area study site. All pairings were incompatible, except for the indeterminate reaction between P-E-9 and P-F-4.

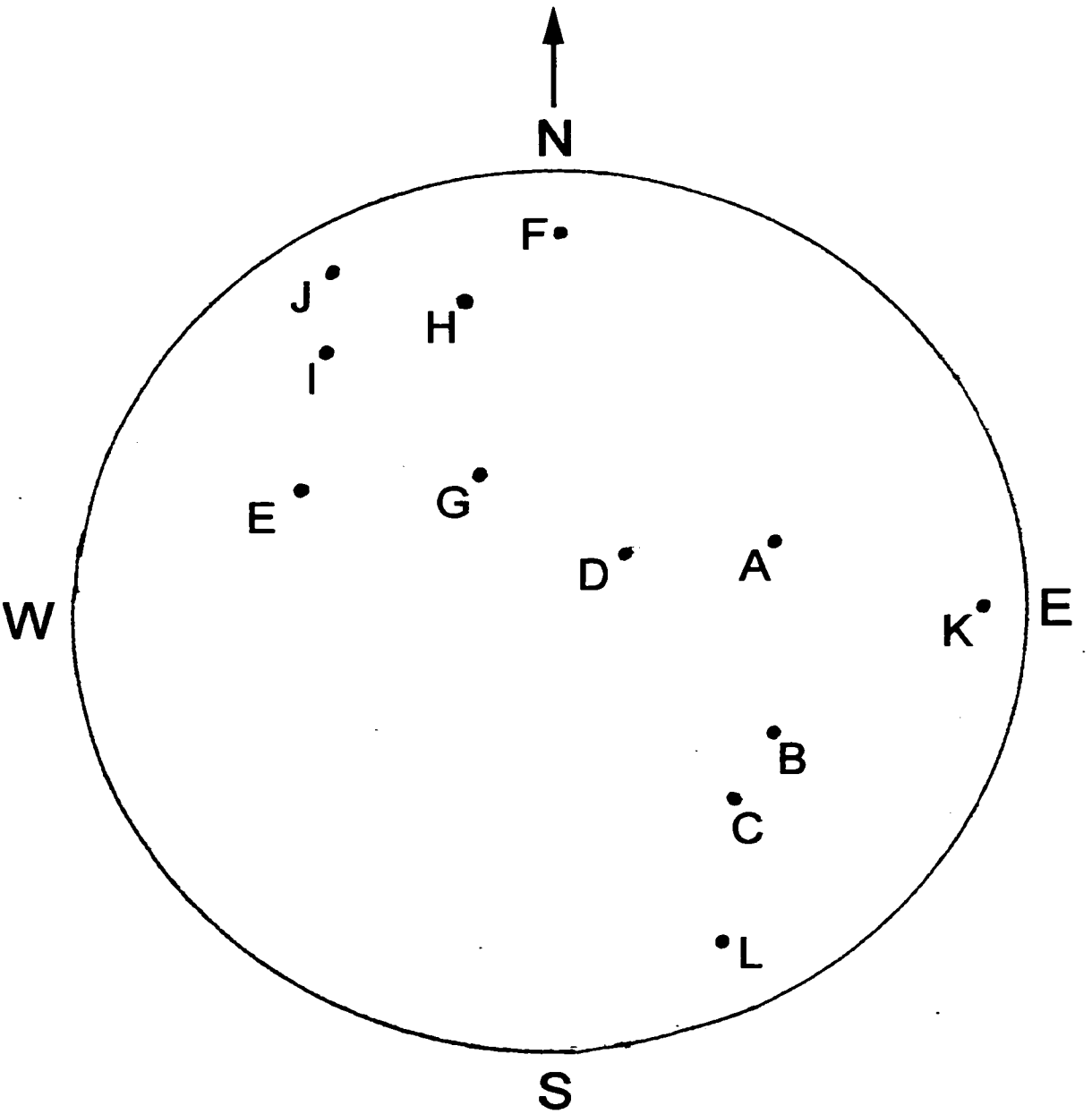

Figure 7. Map of Plot 59 with locations of 12 potential wood sites for *C. purpureum*. *C. purpureum* sporocarps were found on nine of them.

	B-1	C-1	D-1	E-1	E-2	E-3	E-4	E-5	E-6	E-7	E-8	F-1	G-1	H-2	I-1	I-2	I-3	I-4	K-1	K-2
B-1		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C-1			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D-1				-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E-1					-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E-2						-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E-3							-	-	-	-	-	-	-	-	-	-	-	-	-	-
E-4								-	-	-	-	-	-	-	-	-	-	-	-	-
E-5									-	-	-	-	-	-	-	-	-	-	-	-
E-6										-	-	-	-	-	-	-	-	-	-	-
E-7											-	-	-	-	-	-	-	-	-	-
E-8												-	-	-	-	-	-	-	-	-
F-1													-	-	-	-	-	-	-	-
G-1														-	-	-	-	-	-	-
H-2															-	-	-	-	-	-
I-1																-	-	-	-	-
I-2																	-	-	-	-
I-3																		-	-	-
I-4																			-	-
K-1																				-
K-2																				

Figure 8. Pairing results for *C. purpureum* isolates collected in Plot 59. They were all somatically incompatible.

MBD	1	2	3	4	5-1	6
1		-	-	-	-	-
2			-	-	-	-
3				-	-	-
4					-	-
5-1						-
6						

Figure 9. Results for pairings between *C. purpureum* isolates collected in Mills Block D. All of the six isolates were somatically incompatible.

WBD	1	2	3	4	5-1	5-2	5-3	6
1		-	-	-	-	-	-	-
2			-	-	-	-	-	-
3				-	-	-	-	-
4					-	-	-	-
5-1						-	-	-
5-2							-	-
5-3								?
6								

Figure 10. Pairing results of *C. purpureum* isolates from Williams Block D. All but one pairing was somatically incompatible; WBD-5-3 and WBD-6 had indeterminate compatibility.

	BPA-9-A-2	BPA-9-A-4	BPA-11-A-1	BPA-22-A-2	BPA-34-A-2	BPA-50-A-2	BPA-50-A-3	BPA-50-B-3	BPA-51-A2-1	BPA-51-S-1	BPA-52-A-2	BPA-52-A-3	BPA-52-S-1	BPA-52-S-4	BPA-52-S-6	BPA-55-S-1	BPA-57-A1-1	BPA-57-A1-2	BPA-57-B-1	BPA-57-B-3	BPA-69-A-2	BPA-73-A-1	BPA-75-A-3	BPA-75-B-5	BPA-84-B-3	BPB-2-S-1	BPB-7-B-1	BPB-10-B-3	BPB-11-A-1	BPB-11-B-2	BPB-13-A-2	BPB-13-B-3	WBD-4	WBD-5-1	WBD-5-2	WBD-6
BPA-9-A-2		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-9-A-4			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-11-A-1				-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-22-A-2					-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-34-A-2						-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-50-A-2							-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-50-A-3								-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-50-B-3									-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-51-A2-1										-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-51-S-1											-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-52-A-2												-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-52-A-3													-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-52-S-1														+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-52-S-4															+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-52-S-6																-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-55-S-1																	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-57-A1-1																		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-57-A1-2																			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-57-B-1																				-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-57-B-3																					-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-69-A-2																						-	-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-73-A-1																							-	-	-	-	-	-	-	-	-	-	-	-	-
BPA-75-A-3																								-	-	-	-	-	-	-	-	-	-	-	-
BPA-75-B-5																									-	-	-	-	-	-	-	-	-	-	-
BPA-84-B-3																										-	-	-	-	-	-	-	-	-	-
BPB-2-S-1																											-	-	-	-	-	-	-	-	-
BPB-7-B-1																												-	-	-	-	-	-	-	-
BPB-10-B-3																													-	-	-	-	-	-	-
BPB-11-A-1																														-	-	-	-	-	-
BPB-11-B-2																															-	-	-	-	-
BPB-13-A-2																																-	-	-	-
BPB-13-B-3																																	-	-	-
WBD-4																																		-	-
WBD-5-1																																			-
WBD-5-2																																			
WBD-6																																			

Figure 11. Random pairing results of *C. purpureum* isolates collected from both birch piles in and study site WBD (MBD was randomly excluded). The three compatible isolates originated from the side of the same log in BPA.

Table 1. Number of logs in each birch pile, and number and percentage with *C. purpureum*.

	# of Logs	# of Logs with *C. purpureum*	% of Logs with *C. purpureum*
Birch Pile A	86	37	43
Birch Pile B	16	13	81
	102	50	49

Table 2. The number of *C. purpureum* sporocarps collected, number of somatic incompatibility groups (SIGs), A and B face compatibility, and intransitivity of SI reactions for each *C. purpureum* infected log in Birch Pile A. (Y = yes).

Log #	# of *C. purpureum* isolates	# of SIGs	A/B compatibility	Intransitive
BPA-9	5	5		
-11	4	3		
-15	2	1	Y	
-21	1	1		
-22	3	2		
-23	1	1		
-27	2	2		
-30	5	4	Y	
-34	4	4		
-35	3	1		
-36	1	1		
-39	3	1		
-41	1	1		
-42	5	5		
-43	2	1		
-47	3	1	Y	
-48	6	5		
-50	9	4	Y	Y
-51	8	6	Y	Y
-52	12	4		
-53	1	1		
-55	6	4		
-56	1	1		
-57	6	5		Y
-58	2	2		
-59	1	1		
-63	2	2		
-66	1	1		
-67	3	3		
-69	2	2		
-71	2	2		
-72	2	1		
-73	3	3		
-75	8	7		
-79	1	1		
-82	2	2		
-84	2	2		
37	125	93	5	3

isolates in just 13 *C. purpureum* infected logs (Table 3). Compatibility among isolates from both A and B faces of logs appears to be less common than for isolates from A and B to be incompatible, as over both piles, and 50 infected logs, only nine, or 18% had A/B compatibility (Tables 2 and 3).

Most of the pairings were easy to score after one month of incubation because of the intensity of the reaction, although several were re-evaluated after further incubation, and if still ambiguous the pairing was repeated up to two more times. Intransitive pairings were also repeated twice. While most pairings between isolates collected from the same log were found to be fully transitive, three logs in BPA and one in BPB, had isolates that did not meet this criterion (Tables 2 and 3). Intransitive isolates were determined to belong to separate SIGs. Of 1640 unique pairings there were only 8 (<1%) intransitive or indeterminate pairings overall. The number of SIGs per log ranged from 1-9, with 68% of the *C. purpureum* infected logs in both birch piles containing 1-3 SIGs (Table 4). Pairing charts for isolates collected from the birch piles can be found in Appendix III.

MICROSCOPIC CHARACTERISTICS OF SOMATIC INCOMPATIBILITY IN *C. PURPUREUM*

The macroscopic somatic incompatibility reaction varied in its appearance. It appeared as a zone of scant mycelia separating the two colonies, such as between isolates BPA-34-A3 and BPA-34-A4, and manifested as a zone of built up hyphae with accompanying pigmentation, as is seen between BPB-7-A1 and BPB-7-B1 (Figure 12). There were interaction zones observed that had macroscopic appearances intermediate to these manifestations of SI. Hyphal characteristics

Table 3. The number of *C. purpureum* sporocarps collected, number of somatic incompatibility groups (SIGs), A and B face compatibility, and intransitivity of SI reactions for each *C. purpureum* infected log in Birch Pile B. (Y = yes).

Log #	# of *C. purpureum* isolates	# of SI Groups	A/B Compatibility	Intransitive
BPB-1	11	9		Y
-2	7	5	Y	
-3	5	5		
-4	4	2	Y	
-7	2	2		
-8	1	1		
-10	6	5	Y	
-11	5	4		
-12	2	2		
-13	4	4		
-14	3	2	Y	
-15	1	1		
-16	1	1		
13	52	43	4	1

Table 4. The number and percentage of logs in Birch Piles A and B having one to nine somatic incompatibility groups (SIGs) per log.

# of SIGs/log	# of logs	% of logs
1	18	36
2	12	24
3	4	8
4	6	12
5	7	14
6	1	2
7	1	2
8	-	-
9	1	2
	50	

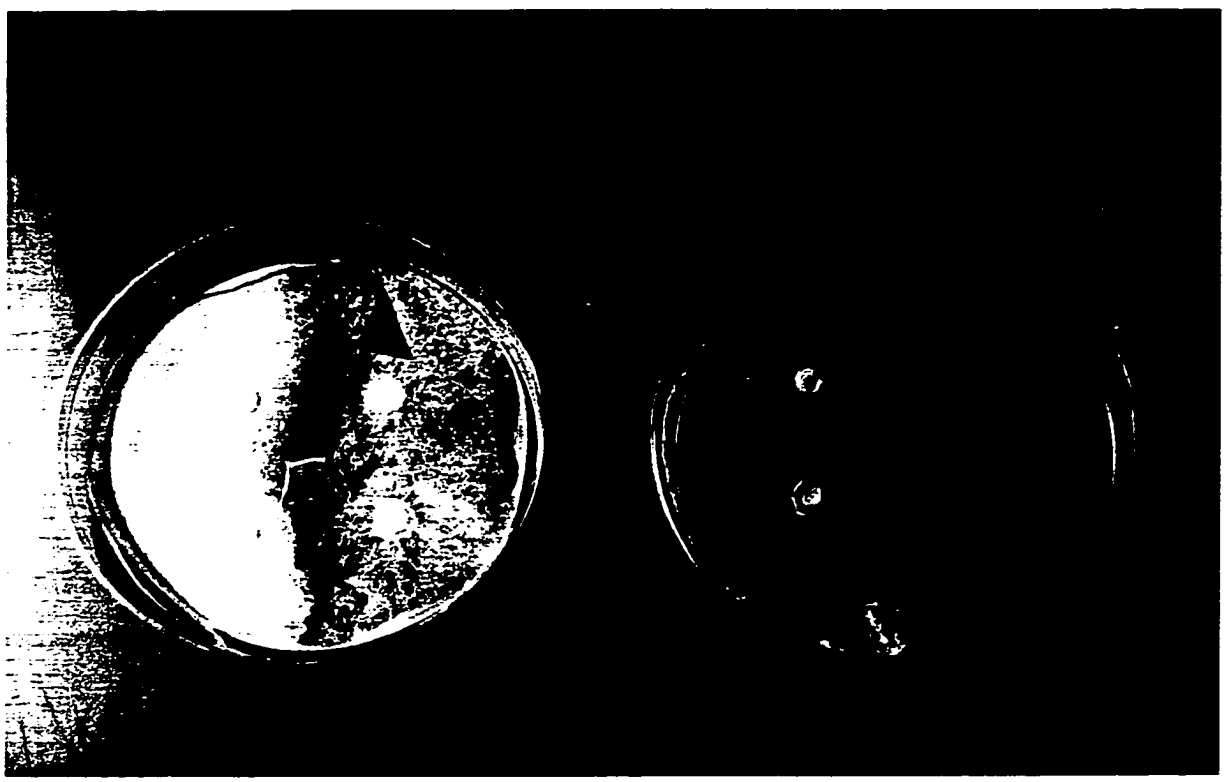

Figure 12. Two differing types of *C. purpureum* interaction zone. Isolates BPA-34-A3 and BPA-34-A4 interacted to form a sparse zone of scanty mycelia (arrowhead), and BPB-7-A1 and BPB-7-B1 developed massed hyphae with accompanying pigmentation (arrow) at the interaction zone.

observed microscopically of *Chondrostereum purpureum* in culture included vesicles, irregularly spaced clamp connections, and hyphal whorls with and without clamp connections.

Microscopically, initial anastomosis appeared similar in self and non-self fusions (Figure 13). Subsequent microscopic reactions within the interaction zone seem to differ among pairings of isolates of *C. purpureum*. In the interaction zone of pairings of BPA-34-A3 and BPA-34-A4 were found inflated cells that could be described as "spindle" shaped (Figure 14), arising from a darkened cell (Figure 15), and occasional degraded hyphal cells. The interaction zone of BPB-7-A1 x BPB-7-B1 exhibited distorted and deformed hyphae and hyphal coiling frequently forming hyphal knots. Hyphal coiling with a random and disorganized appearance may occur as an artifact of slide preparation.

OVERWINTERING CAPABILITY OF *C. PURPUREUM* SPOROCARPS

Of the sporocarps collected in April of 1998, 10 of 11 produced spores that germinated on 1% MEA. In April of 1999, 12 of 15 sporocarps produced viable spores. First, Second and Third Collection sporocarps from April 1999, Collections A and B from May 1999, and Collections A_2 and B_2 from June 1999 were all collected from the same group of sporocarps at the base of a balsam poplar stump and were found to produce viable spores (Figure 16). In total 32 of 37, or 86% of the overwintered sporocarps collected in the spring of 1998 and 1999 produced spores that germinated (Table 5). The average temperature for this period was higher than normal. Rainfall was lower than normal from April to September 1998, especially April, and higher than normal in October 1998 (Table 6).

Figure 13. Anastomosis (arrow) between genetically dissimilar hyphae in a non-self pairing between isolates BPA-34-A3 and BPA-34-A4. (1000x).

Figure 14. Atypical spindle-shaped cells with abnormally thickened septa in the interaction zone of a non-self pairing of isolates BPA-34-A3 and BPA-34-A4. (1000x).

Figure 15. The dark hyphal cell at the disjunction between spindle-shaped cells and normal cells in the interaction zone of a non-self pairing of BPA-34-A3 and BPA-34-A4 (1000x).

Figure 16. Base of a suckering balsam poplar stump, pictured in May 1999, from which overwintered *C. purpureum* sporocarps were collected. Viable spores were produced from sporocarps collected in April, May and June 1999.

Table 5. Sporulation and germination of overwintered sporocarps. (Y = yes).

Collection Date	Isolate	Sporulation	Germination
April 30 1998	Sp1	Y	Y
	Sp2		
	Sp3	Y	Y
	Sp4	Y	Y
	Sp6	Y	Y
	Sp7	Y	Y
	Sp8	Y	Y
	Sp9	Y	Y
	Sp10	Y	Y
	Sp11	Y	Y
	Sp12	Y	Y
April 26 1999	1st coll.	Y	Y
	2nd coll.	Y	Y
	3rd coll.	Y	Y
	WP-1	Y	Y
	WP-2	Y	Y
	WP-3	Y	Y
	WP-4	Y	Y
	WP-5	Y	Y
	WP-6	Y	Y
	WP-7	Y	Y
	WP-8		
	WP-10		
	WP-11	Y	Y
	WP2-S-1	Y	Y
	WP2-N-3		
May 23 1999	Coll. A	Y	Y
	Coll. B	Y	Y
	$WP\text{-}1_2$	Y	Y
	$WP\text{-}4_2$	Y	Y
	$WP\text{-}5_2$	Y	Y
	$WP\text{-}6_2$	Y	Y
	$WP\text{-}8_2$		
	WP-20	Y	Y
	TA	Y	Y
June 14 1999	Coll. A_2	Y	Y
	Coll. B_2	Y	Y
	37	32	32

Table 6. Relevant Thunder Bay weather data* for winter 1997/98, spring/summer/fall 1998, and winter 1998/99.

	Temperature (°C)			Average snow	Rainfall (mm)		Relative humidity (%)	
	Average	Normal#	Low	on ground (cm)	Total	Normal#	Maximum	Minimum
Nov. '97	-4.2	-2.6	-24.8	7.5				
Dec. '97	-5.5	-11.3	-25.9	19.9				
Jan. '98	-11.5	-15.0	-28.2	39.9				
Feb. '98	-3.9	-12.8	-25.2	36.8				
Mar. '98	-3.7	-5.6	-20.0	20.4				
Apr. '98	5.4	2.7			1.6	33.0	84	31
May '98	10.9	9.0			45.6	67.2	94	40
June '98	14.7	13.9			66.6	84.0	98	58
July '98	18.4	17.7			40.4	79.9	96	46
Aug. '98	18.0	16.4			46.8	88.5	99	52
Sept. '98	13.4	11.2			59.6	86.0	96	52
Oct. '98	7.0	5.4			162.8	56.5	91	61
Nov. '98	-1.2	-2.6	-21.8	8.3				
Dec. '98	-9.4	-11.3	-31.1	14.6				
Jan. '99	-15.6	-15.0	-37.9	50.5				
Feb. '99	-7.9	-12.8	-26.5	62.7				
Mar. '99	-4.9	-5.6	-27.0	54.9				
Apr. '99	4.4	2.7	-6.7	10.6				

*from Tranquillo Ridge Climatological Station, courtesy of Graham Saunders.
Environment Canada 30 Year Normals.

DISCUSSION

POPULATION STUDY OF *C. PURPUREUM*

The genetic variability at the somatic incompatibility loci appears to be high over both the CCA study area, including Plot 59, and the birch piles. Within the limited samples available at the MBD and WBD sites, there also seems to be high SI variability. The number of individual SI genotypes detected approached the number of isolates, representing the number of discrete fruiting clusters representative of the study areas. Where isolates were found to be compatible they originated from the same wood unit and although may only represent individuals of the same SIG, they most likely were isolates representing the same individual. Similar to the studies by Gosselin *et al.* (1995; 1999) the large number of SIGs detected in this study indicates that local populations of *Chondrostereum purpureum* are composed of many individual genotypes, which may reflect a high genetic diversity within the species. This is supported by the literature, which indicates that within populations seeded by wind-blown basidiospores there is high genetic diversity, with frequent genets occupying small areas (Chamuris and Falk 1987; Kay and Vilgalys 1992; Marçais *et al.* 1998; Murphy and Miller 1993; Rayner and Todd 1982a; Williams *et al.* 1981).

As indeterminate or intransitive reactions occurred in less than 1% of the pairings, the SI reaction in *C. purpureum* seems fairly reliable. The intransitive pairings between some isolates may be attributable to close relatedness among the intransitive set of isolates. Similarly, the indeterminate pairings may be due to only small differences at the SI loci (Malik 1996, cited in Worrall 1997) when isolates differing at only a single SI gene (Anagnostakis 1984) or a few SI genes (Kile 1983) may have a reaction almost indistinguishable from a somatically compatible reaction. Because there is a higher likelihood of neighbouring fungal individuals to be closely

related (Lane 1981; Wolfenbarger 1959, cited in Kay and Vilgalys 1992), it may be expected that intransitive and indeterminate reactions would occur more frequently between isolates found close to each other, as was the case here.

Like genetic markers that are not variable enough, markers that show too much differentiation may not be useful in revealing relationships (Leung *et al.* 1993). When the SI character shows high variability, as seen here with *C. purpureum*, the genetic relationship among the isolates is unclear (Leung *et al.* 1993). The polygenic and multiallelic character of somatic incompatibility may lead to situations where inevitable rejection between isolates is the norm (Rayner and Boddy 1986).

Although 144 samples were collected over the whole CCA study area, 20 in Plot 59, 6 from MBD, 8 from WBD, no more than 29, 20, 6, and 8, respectively, were paired against one another. Of the 191 pooled isolates from BPA, BPB, MBD and WBD, 36 samples were paired. The birch pile isolates were also paired in all combinations with others collected from the same wood unit with no pairing set exceeding 13 samples. All of these pairing experiment sample sizes fell well below the sample size limit of 60 for detection of a genotype that has a frequency of 10 % with 95% confidence (Leung *et al.* 1993). This may explain why so few somatically compatible isolates were detected. A larger study could resolve this dilemma. Conversely, the large number of SIGs detected may be representative of a wealth of possible SI genotypes within the *C. purpureum* population.

Although all isolates used in this study were subcultured up to two times, changes in SI reactivity in previous studies were usually noted after several multiple subcultures (Hawker 1950), hence it is unlikely that the high number of SIGs observed in this study was the result of degradation of the somatic response. Some studies indicate somatic incompatibility remains stable *in vitro* (Leslie 1993; Murphy and Miller 1993) and *in vivo* (Barrett and Uscuplic 1971), yet

progressive changes in characteristics, such as virulence, fecundity, growth rate, and fermentation or metabolic activity, have been documented following successive subculturing (Hawker 1950). Although serial transfer of developing colonies is common practice (Kay and Vilgalys 1992), it is possible that multiple subculturing events could diminish the ability to form a stable anastomosis product (Barrett and Uscuplic 1971; Hyakumachi and Ui 1987), or decrease the intensity of the SI reaction (May 1988) thus producing the erroneous appearance of a high or low number of SIGs.

Any mitochondrial effect on the SI results cannot be accounted for, as precautions against mitochondrial incompatibility were not taken in this study. The mitochondrion is suspected to play a role in cell death, and thus be involved in the mechanism of somatic incompatibility (Rayner 1991a; 1991b). Mitochondria do not co-migrate with exchanged nuclei in homokaryon pairings (Casselton and Economou 1985; Hintz *et al.* 1988; May and Taylor 1988; Specht *et al.* 1992) and in di-mon pairings (May and Taylor 1988); therefore it seems unlikely that they co-migrate in somatic reactions between heterokaryons. May (1988) found that 2 of 8 pairings between heterokaryons with common nuclei but differing mitochondrial populations were intolerant of this difference and were somatically incompatible. Rizzo *et al.* (1995b) produced sib-related heterokaryons by pairing single spore cultures against a standard single spore culture, and producing stock cultures only from the side of the standard culture to negate any possible mitochondrial influence on subsequent somatic compatibility tests. Although this seems prudent, it was not done here, and may account for the high number of somatically incompatible individuals observed. This phenomenon needs to be researched in *C. purpureum,* as it may be a serious confounding factor in this population study.

Multiple pairing is commonly practiced in somatic incompatibility studies, and has thus far been found to have no effect on SI results (Chamuris and Falk 1987). In this study with

Chondrostereum purpureum an interaction effect resulting from multiple pairings on single plates seems unlikely as many pairings were repeated in different arrangements with the same outcome.

There appears to be no correlation between the number of individuals on a wood unit and A and B face compatibility. Thus A/B compatibility does not indicate that one individual dominated the resource unit deterring infection by other individuals. The number of isolates per log within the birch piles was as high as 9 isolates per log. Yet over 68% of the logs bearing *C. purpureum* sporocarps were limited to 1-3 SIGs per log. That *C. purpureum* gains its primary occupation advantage by arising from previously compartmentalized infections has been suggested (Coates 1984, cited in Rayner and Boddy 1986; Fritz 1954). That there was a low number of SIGs in most of the infected logs, and that within the first growing season following resource availability *C. purpureum* became active, suggests that it was pre-established in the living tree (Boddy and Rayner 1982; Rayner 1979b). Although these results do not conclude that infection of the birch logs was latent, they do not preclude this.

Over both birch piles 49% of the logs had *C. purpureum* sporocarps. Yet, if broken down into the two piles, BPA had a sporocarp incidence of 43%, while BPB had an incidence of 81%, almost twice that of BPA. The difference may be that BPA had more logs thus the pile consisted of many logs with less available surface area exposed and available as infection sites for airborne spores, pointing towards spores as the most significant source of infection. Study of the birch piles would have yielded more information if the *C. purpureum* population could have been observed over several years, as Fritz (1954) found *C. purpureum* fruiting on poplar logs in storage reached almost 100% within the first two seasons following cutting.

Both birch piles and study sites MBD and WBD were in their first season following harvest, yet they had differing population sizes of *C. purpureum*, with MBD and WBD having low numbers of the fungus. The larger population on the birch piles may be the result of the increased

levels of inoculum due to previous harvesting on the CCA site providing much infected woody debris as a spore source.

From this study, one can conclude that local populations of *Chondrostereum purpureum* are composed of high numbers of individuals with different alleles for somatic incompatibility. Population studies of this small size are significant as "in sexual organisms the unit of greatest importance is the breeding population which can be defined as that group of individuals which, because of their proximity in space and time, are potentially capable of interbreeding" (Rayner and Todd 1979, p. 346). It is important to reiterate that population studies based on the SI criterion are inherently underestimates of genotypic frequency.

MICROSCOPIC CHARACTERISTICS OF SOMATIC INCOMPATIBILITY IN *C. PURPUREUM*

Verticillate or "whorled" clamp connections were observed as well as hyphal whorls with hyphae arising from them. Clamp connections occurring in whorls have been extensively reported in *Stereum* spp. (Ainsworth 1987; Boidon 1971; Boddy and Rayner 1982; Rayner and Turton 1982), and little reported in *Chondrostereum purpureum* (Chamuris 1988; Nakasone 1990; Stalpers 1978), except by Cartwright and Findlay (1958). This phenomenon is not associated with the somatic incompatibility reaction as it was observed in both unpaired and paired cultures of the fungus and is mentioned here only because it seems under-reported. Boddy and Rayner (1982) have postulated that whorled clamp connections may be "an adaptation to rapid radial spread" (p. 345), which would be fitting in such a fast-growing species as *C. purpureum*.

The BPA-34-A3 and BPA-34-A4 interaction zone macroscopically appeared as a sparse zone between the two isolates. In the interaction zone, sparse populations of spindle-shaped hyphal cells, such as was described for *C. versicolor* and *B. adusta* by Rayner and Todd (1982b), were

observed in chains. Degraded hyphae were also observed and were most likely the remnants of hyphae in later stages of the incompatibly reaction. The degradation of the hyphal cells and subsequent cessation of growth into the interaction area may lead to the sparse interaction zone between these two isolates. In each pairing, hyphae were observed at different stages of the somatic incompatibility reaction, and because the hyphae were fixed prior to microscopic observation the sequence of SI events was inferred.

The macroscopic appearance of the interaction zone between isolates BPB-7-A1 and BPB-7-B1 was a barrier composed of hyphae at the interface. Where there is dense mycelium at the interaction zone, this may indicate a mutual deadlock in which the hyphal interaction involves "gross mycelial contact" (Rayner and Webber 1984, p. 402). Microscopic features found in the somatic interaction zone were vesicles and distorted hyphae that may be undergoing an initial somatic reaction. These hyphae may follow an antagonistic SI pathway leading to hyphal coiling where the hyphae become entangled in a relatively ordered manner. Hyphal coiling may lead to hyphal knotting and may be analogous to the hyphal knots in the SI interaction zone of *P. schweinitzii* (Barrett and Uscuplic 1971) and *M. oreades* (Mallett and Harrison 1988). It seems likely that interacting hyphae die ensuring mycelial discontinuity between somatically incompatible isolates.

It must be acknowledged that the hyphal coiling phenomenon could result from twisting of the hyphae during slide preparation; thus disorderly wrapping may be an artifact, while deliberate coiling may be the result of a somatic reaction. Cooke and Rayner (1984, cited in Rayner and Webber 1984) suggest that combat hyphal interactions, like hyphal coiling, are used in defense of territory, or for secondary resource capture or replacement. However Rayner and Boddy (1988, p. 249) suggest it may occur as self or non-self parasitism when there is a low nutrient supply. Although low nutrients are an unlikely factor here because the bulk of the mycelium was growing

on MEA, the mycelium in the interaction zone was growing along water agar to facilitate observation of the reaction. Further studies using low nutrient agar need to be done.

The somatic incompatibility reaction in *C. purpureum* occurred with variation that ranged between the two extremes examined here, yet in all pairings the reaction occurred equally on both sides, giving the appearance of the interaction zone manifestation being dependent upon the two isolates initiating equal responses. The initial confronting self and non-self hyphae of *C. purpureum* isolates anastomose in the same way, probably to allow somatic compatibility to be assessed. Subsequent somatic reactions differed among somatically incompatible pairings, possibly depending upon which SI loci are dissimilar. Anagnostakis (1987) postulates that each SI gene may regulate a different mechanism by which SI is effected, hence the macroscopic appearance of the interaction zone may correspond with differing modes of asserting somatic incompatibility.

Barrett and Uscuplic (1971) suggest two independent mechanisms for somatic incompatibility, with one early mechanism "restricting close association of opposing hyphae", and the other following intermingling "resulting in the death of certain hyphae" (p. 596). The existence of such systems may explain the rarity of observations of non-self hyphal interactions in *C. purpureum*, and other species that may practice non-self hyphal avoidance over hyphal interaction (Hansen *et al.* 1993b; Wilson 1991). However, the low numbers of interactions seen in this study might have been a function of the small number of non-self pairings (10) observed microscopically. The conclusions reached in this preliminary study are speculative, thus further studies are needed to determine if different mechanisms of somatic incompatibility are the cause of the differences seen at the *C. purpureum* SI interaction zone.

OVERWINTERING CAPABILITY OF *C. PURPUREUM* SPOROCARPS

Chondrostereum purpureum sporocarps can successfully overwinter as 86% of the sampled sporocarps produced viable spores. Sampling was not random, as sporocarps that were extremely weathered in appearance or were parasitized by other fungi were not collected. As sporocarps with this type of appearance seemed in the minority, it may be that many that did not survive the winter were "sloughed off" as described by Wall (1991). Spore production in *C. purpureum* has been reported to last 12 (Spiers 1985) to 16 months (Dye 1974, cited in Spiers 1985), with the number of spores produced decreasing with sporocarp age (Spiers 1985). The spore germination rate approached 100% in those sporocarps that did produce spores; hence when the life of the sporocarp is interrupted by winter weather and it survives, viable spore production is likely.

Spore production is stimulated following rainfall, and continues as long as the temperature is between 0°C and 25°C, and the relative humidity does not fall below 90%, according to de Jong *et al.* (1990), or 75% according to Spiers (1985). These weather conditions were found to be not uncommon in spring in the Thunder Bay area.

The finding that *C. purpureum* overwintered sporocarps can successfully produce viable spores, indicates their potential for causing spring infection of winter-wounded trees. This may be significant if tree susceptibility is high in the spring due to high xylem nutrient levels, as has been postulated by Beever (1970). This also increases the amount of inoculum thought to be produced by *C. purpureum* sporocarps in the forest environment, occurring at a time when winter damage is freshly exposed. These factors should be considered when assessing the mycoherbicidal uses of this fungus.

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APPENDIX I

SAMPLE INVENTORY FOR CCA, PLOT 59, MBD, AND WBD

CASCADES CONSERVATION AREA (CCA)		
Isolate	Date Collected	Source
1-A-1	October 5 1997	Poplar stump -just above root collar
1-A-2	"	Poplar stump -just above root collar
1-B-2	"	Poplar stump -side -superior to 1B1
1-B-3	"	Poplar stump -side -superior to 1B2
1-C-1	"	Poplar stump -cut surface
1-C-2	"	Poplar stump -cut surface
1-C-3	"	Poplar stump -cut surface
1-C-4	"	Poplar stump -cut surface
1-C-5	"	Poplar stump -cut surface
1-C-6	"	Poplar stump -cut surface
1-C-7	"	Poplar stump -cut surface
1-C-8	"	Poplar stump -side -inferior to 1C2
1-C-10	"	Poplar stump -side -inferior to 1C1
1-D-2	"	Poplar stump - just above root collar -inferior to 1D1
1-E-1	"	Poplar stump -just above root collar
1-E-2	"	Poplar stump -just above root collar -superior to 1E1
2-A-1	"	Poplar stump -cut surface
2-B-1	"	Poplar stump -cut surface
2-B-3	"	Poplar stump -cut surface
4-A-1	"	Poplar stump -cut surface
4-A-3	"	Poplar stump -just above root collar -inferior to 4A2
4-A-4	"	Poplar stump -side -inferior to 4A1
5-A-1	October 7 1997	Poplar stump -cut surface
5-A-2	"	Poplar stump -cut surface
5-A-3	"	Poplar stump -cut surface
5-A-4	"	Poplar stump -side
5-A-5	"	Poplar stump -just above root collar
5-B-1	"	Poplar stump -cut surface
5-B-2	"	Poplar stump -cut surface
5-B-3	"	Poplar stump -cut surface
5-B-4	"	Poplar stump -root collar
5-C-1	"	Poplar stump -cut surface
5-C-2	"	Poplar stump -side
11-A-1	November 5 1997	Poplar stump -cut surface
11-B-1	"	Poplar stump -cut surface
11-C-1	"	Poplar stump -cut surface
11-C-2	"	Poplar stump -cut surface
11-C-3	"	Poplar stump -cut surface
11-C-4	"	Poplar stump -cut surface
11-C-5	"	Poplar stump -cut surface

Isolate	Date Collected	Source
12-A-1	November 5 1997	Poplar stump -side
12-B-1	"	Poplar stump -cut surface
12-B-2	"	Poplar stump -side
12-B-3	"	Poplar stump -side
12-C-1	"	Poplar stump -side
12-C-2	"	Poplar stump -side
17-A-1	November 3 1997	Poplar stump -side
17-A-2	"	Poplar stump -side
18-A-1	"	Poplar stump -side
18-A-2	"	Poplar stump -side
19-A-1	"	Poplar stump -side
19-A-2	"	Poplar stump -side
19-A-3	"	Poplar stump -side
20-A-1	"	Poplar stump -cut surface
20-A-2	"	Poplar stump -side
20-A-5	"	Poplar stump -side
20-A-6	"	Poplar stump -side
21-A-1	"	Poplar stump -side
21-B-1	"	Poplar stump -cut surface
22-A-1	"	Poplar stump -east side
22-A-2	"	Poplar stump -west side
23-A-1	"	Poplar stump -side
23-B-1	"	Poplar stump -side
24-A-1	"	Poplar stump -cut surface
24-A-2	"	Poplar stump -side
24-B-1	"	Poplar stump -side
A-A-1	November 2 1997	Poplar stump -side
B-A-1	"	Poplar stump -cut surface
B-A-2	"	Poplar stump -side
B-A-3	"	Poplar stump -side
B-A-4	"	Poplar stump -side
B-B-1	"	Poplar stump -cut surface
C-A-1	"	Poplar stump -cut surface
C-A-2	"	Poplar stump -cut surface
C-A-3	"	Poplar stump -cut surface
C-A-4	"	Poplar stump -cut surface
C-A-5	"	Poplar stump -cut surface
C-A-6	"	Poplar stump -side
C-A-7	"	Poplar stump -side
C-A-8	"	Poplar stump -side
C-A-9	"	Poplar stump -side
C-A-10	"	Poplar stump -side
C-A-11	"	Poplar stump -side
C-A-12	"	Poplar stump -side
C-A-13	"	Poplar stump -side

Isolate	Date Collected	Source
J-A-1	November 3 1997	Poplar stump -root collar
J-B-1	"	Poplar stump -side
K-A-1	"	Poplar stump -just above root collar
K-B-1	"	Poplar stump -cut surface
K-B-2	"	Poplar stump -cut surface
K-B-3	"	Poplar stump -cut surface
K-B-4	"	Poplar stump -side
K-B-5	"	Poplar stump -cut surface
P-A-1	October 13 1997	Poplar stump -cut surface
P-A-2	"	Poplar stump -cut surface
P-A-5	"	Poplar stump -side
P-A-6	"	Poplar stump -side
P-A-7	"	Poplar stump -just above root collar
P-B-1	"	Poplar stump -cut surface
P-B-2	"	Poplar stump -cut surface
P-B-3	"	Poplar stump -cut surface
P-B-4	"	Poplar stump -cut surface
P-B-5	"	Poplar stump -cut surface
P-C-1	"	Poplar stump -cut surface
P-C-2	"	Poplar stump -cut surface
P-C-3	"	Poplar stump -cut surface
P-D-1	"	Poplar stump -cut surface
P-D-2	"	Poplar stump -side
P-D-3	"	Poplar stump -side
P-D-4	"	Poplar stump -side
P-E-1	"	Poplar stump -cut surface
P-E-2	"	Poplar stump -cut surface
P-E-3	"	Poplar stump -cut surface
P-E-4	"	Poplar stump -cut surface
P-E-5	"	Poplar stump -cut surface
P-E-6	"	Poplar stump -cut surface
P-E-7	"	Poplar stump -side
P-E-8	"	Poplar stump -side
P-E-9	"	Poplar stump -side
P-E-10	"	Poplar stump -side
P-E-11	"	Poplar stump -side
P-E-12	"	Poplar stump -just above root collar
P-E-13	"	Poplar stump -cut surface
P-F-1	October 17 1997	Poplar stump -side
P-F-2	"	Poplar stump -side
P-F-3	"	Poplar stump -side
P-F-4	"	Poplar stump -side
P-F-5	"	Poplar stump -side
P-G-1	"	Poplar stump -side
P-H-1	"	Poplar stump -side

Isolate	Date Collected	Source
P-I-1	October 17 1997	Poplar stump -cut surface
P-I-2	"	Poplar stump -cut surface
P-I-3	"	Poplar stump -side
P-I-4	"	Poplar stump -side -inferior to PI3
P-I-5	"	Poplar stump -side -inferior to PI4
P-I-6	"	Poplar stump -side -inferior to PI5
P-I-7	"	Poplar stump -side -inferior to PI6
P-I-8	"	Poplar stump -side
P-I-10	"	Poplar stump -side
P-I-12	"	Poplar stump -root collar
P-J-1	"	Poplar stump -cut surface
X-A-1	November 2 1997	Poplar stump -cut surface
X-C-1	"	Poplar stump -cut surface
X-C-2	"	Poplar stump -cut surface

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Isolate	Date Collected	Source
B-1	October 3 1997	Poplar stump -root collar
C-1	"	Poplar stump -just above root collar
D-1	"	Poplar stump -cut surface
E-1	"	Poplar slash
E-2	"	Poplar slash
E-3	"	Poplar slash
E-4	"	Poplar slash
E-5	"	Poplar slash
E-6	"	Poplar slash
E-7	"	Poplar slash
E-8	"	Poplar slash
F-1	"	birch log
G-1	"	birch stump -cut surface
H-2	"	birch stump -root collar
I-1	"	birch slash
I-2	"	birch slash
I-3	"	birch slash
I-4	"	birch slash
K-1	"	birch slash
K-2	"	birch slash

MILLS BLOCK D (MBD)		
Isolate	Date Collected	Source
MBD-1	October 2 1998	Poplar stump
MBD-2	"	Poplar stump
MBD-3	"	Poplar stump
MBD-4	"	Poplar stump
MBD-5-1	"	Poplar slash
MBD-6	"	Poplar stump

WILLIAMS BLOCK D (WBD)		
Isolate	Date Collected	Source
WBD-1	October 3 1998	Poplar stump
WBD-2	"	Poplar stump
WBD-3	"	Poplar stump
WBD-4	"	Poplar stump
WBD-5-1	"	Poplar slash
WBD-5-2	"	Poplar slash
WBD-5-3	"	Poplar slash
WBD-6	"	Poplar slash

APPENDIX II

SAMPLE INVENTORY FOR BIRCH PILES

Log #	Isolate #	Date collected	Source/Comments
BPA-1	-	October 17 1998	no *C. purpureum*
BPA-2	-	"	no *C. purpureum*
BPA-3	-	"	no *C. purpureum*
BPA-4	-	"	no *C. purpureum*
BPA-5	-	"	no *C. purpureum*
BPA-6	-	"	no *C. purpureum*
BPA-7	-	"	no *C. purpureum*
BPA-8	-	"	no *C. purpureum*
BPA-9	A-1	"	sapwood
"	A-2	"	sapwood
"	A-3	"	sapwood
"	A-4	"	heartwood
"	B-1	"	sapwood
BPA-10	-	"	no *C. purpureum*
BPA-11	A-1	"	sapwood
"	A-2	"	sapwood
"	A-3	"	sapwood/heartwood
"	A-4	"	sapwood/heartwood
BPA-12	-	"	no *C. purpureum*
BPA-13	-	"	no *C. purpureum*
BPA-14	-	"	no *C. purpureum*
BPA-15	A-1	"	sapwood
"	B-1	"	heartwood
BPA-16	-	"	no *C. purpureum*
BPA-17	-	"	no *C. purpureum*
BPA-18	-	"	no *C. purpureum*
BPA-19	-	"	no *C. purpureum*
BPA-20	-	"	no *C. purpureum*
BPA-21	B-2	"	sapwood
BPA-22	A-1	"	sapwood
"	A-2	"	sapwood
"	A-3	"	heartwood
BPA-23	B-1	"	sapwood
BPA-24	-	"	no *C. purpureum*
BPA-25	-	"	no *C. purpureum*
BPA-26	-	"	no *C. purpureum*
BPA-27	A-1	"	sapwood/heartwood
"	B-3	"	sapwood/heartwood
BPA-28	-	"	no *C. purpureum*
BPA-29	-	"	no *C. purpureum*
BPA-30	A-1	"	sapwood

Log #	Isolate #	Date collected	Source/Comments
BPA-30	A-2x1	October 17 1998	heartwood
"	A-2x2	"	heartwood
"	B-1	"	sapwood
"	B-3	"	sapwood
BPA-31	-	"	no *C. purpureum*
BPA-32	-	"	no *C. purpureum*
BPA-33	-	"	no *C. purpureum*
BPA-34	A-1	"	sapwood
"	A-2	"	sapwood
"	A-3	"	sapwood
"	A-4	"	sapwood
BPA-35	S-1	"	side
"	S-2	"	side
"	S-3	"	side
BPA-36	B-1	"	no comment
BPA-37	-	"	no *C. purpureum*
BPA-38	-	"	no *C. purpureum*
BPA-39	A-1	"	heartwood
"	A-2	"	sapwood
"	A-3	"	sapwood
BPA-40	-	"	no *C. purpureum*
BPA-41	B-1	"	sapwood
BPA-42	A-1	"	sapwood
"	A-2	"	sapwood
"	B-1	"	sapwood
"	B-5	"	sapwood
"	B-7	"	sapwood
BPA-43	B-1	"	sapwood
"	B-2	"	sapwood
BPA-44	-	"	no *C. purpureum*
BPA-45	-	"	no *C. purpureum*
BPA-46	-	"	no *C. purpureum*
BPA-47	A-1	"	sapwood
"	A-3	"	sapwood
"	B-2	"	sapwood
BPA-48	A-1	"	sapwood
"	A-2	"	sapwood
"	A-3	"	sapwood
"	B-1	"	sapwood
"	B-2	"	sapwood
"	B-3	"	heartwood
BPA-49	-	"	no *C. purpureum*
BPA-50	A-1	"	sapwood
"	A-2	"	sapwood
"	A-3	"	sapwood

Log #	Isolate #	Date collected	Source/Comments
BPA-50	A-4	October 17 1998	sapwood
"	B-1	"	sapwood
"	B-3	"	sapwood
"	B-4	"	sapwood
"	B-5	"	heartwood
"	B-6	"	sapwood
BPA-51	A1-2	October 23 1998	sapwood
"	A1-3	"	sapwood
"	A1-4	"	sapwood
"	A2-1	"	heartwood
"	B-1	"	heartwood
"	B-2	"	sapwood/bark
"	B-3	"	sapwood/bark
"	S-1	"	wound in side
BPA-52	A-1	"	sapwood/bark
"	A-2	"	sapwood
"	A-3	"	heartwood
"	S-1	"	side
"	S-2	"	side
"	S-3	"	side
"	S-4	"	side
"	S-5	"	side
"	S-6	"	side
"	S-7	"	side
"	S-8x1	"	side
"	S-8x2	"	side
BPA-53	A-1	"	sapwood
BPA-54	-	"	no *C. purpureum*
BPA-55	B-1	"	sapwood/bark
"	B-2	"	sapwood
"	B-3	"	sapwood
"	B-4	"	sapwood
"	S-1	"	side
"	S-2	"	side
BPA-56	B-1	"	sapwood
BPA-57	A1-1	"	sapwood/bark
"	A1-2	"	sapwood
"	A1-3	"	heartwood
"	B-1	"	sapwood
"	B-2	"	sapwood
"	B-3	"	sapwood
BPA-58	A-1	"	heartwood
"	A-2	"	heartwood
BPA-59	A-1	"	sapwood
BPA-60	-	"	no *C. purpureum*

Log #	Isolate #	Date collected	Source/Comments
BPA-61	-	October 23 1998	no *C. purpureum*
BPA-62	-	"	no *C. purpureum*
BPA-63	A-1	"	heartwood
"	B-1	"	heartwood
BPA-64	-	"	no *C. purpureum*
BPA-65	-	"	no *C. purpureum*
BPA-66	A-1	"	heartwood
BPA-67	A-1	"	sapwood
"	A-2	"	heartwood
"	B-1	"	sapwood/heartwood
BPA-68	-	"	no *C. purpureum*
BPA-69	A-2	"	sapwood
"	B-1	"	heartwood
BPA-70	-	"	no *C. purpureum*
BPA-71	A-1x1	"	sapwood
	A1x2		sapwood
BPA-72	A-2	"	sapwood
"	A-3	"	sapwood
BPA-73	A-1	"	sapwood
"	A-2	"	sapwood
"	A-3	"	sapwood
BPA-74	-	"	no *C. purpureum*
BPA-75	A-1	"	heartwood
"	A-2	"	sapwood
"	A-3	"	sapwood
"	B-1	"	heartwood
"	B-2	"	heartwood
"	B-3	"	sapwood
"	B-4	"	sapwood
"	B-5	"	sapwood
BPA-76	-	"	no *C. purpureum*
BPA-77	-	"	no *C. purpureum*
BPA-78	-	"	no *C. purpureum*
BPA-79	A-1	"	sapwood/heartwood
BPA-80	-	"	no *C. purpureum*
BPA-81	-	"	no *C. purpureum*
BPA-82	A-1	"	sapwood
"	A-2	"	heartwood
BPA-83	-	"	no *C. purpureum*
BPA-84	B-1	"	heartwood
"	B-3	"	heartwood
BPA-85	-	"	no *C. purpureum*
BPA-86	-	"	no *C. purpureum*
BPB-1	A-1	"	sapwood
"	A-2	"	sapwood

Log #	Isolate #	Date collected	Source/Comments
BPB-1	B-1	October 23 1998	sapwood
"	B-3	"	sapwood
"	B-4	"	sapwood
"	S-1	"	side
"	S-2	"	side
"	S-3	"	side
"	S-4x1	"	side
"	S-4x2	"	side
"	S-5	"	side
BPB-2	A-1	"	sapwood
"	A-2	"	sapwood
"	A-3	"	heartwood
"	B-2	"	sapwood
"	B-3	"	heartwood
"	S-1	"	side
"	S-2	"	side
BPB-3	A-1	"	sapwood
"	A-2	"	sapwood
"	B-1	"	sapwood
"	S-1	"	side
"	S-2	"	side
BPB-4	A-1	"	sapwood
"	A-2	"	sapwood
"	A-3	"	sapwood
"	B-1	"	sapwood
BPB-5	-	"	no *C. purpureum*
BPB-6	-	"	no *C. purpureum*
BPB-7	A-1	"	sapwood
"	B-1	"	sapwood
BPB-8	B-1	"	sapwood
BPB-9	-	"	no *C. purpureum*
BPB-10	A-1	"	sapwood
"	A-2	"	sapwood
"	A-3	"	heartwood
"	B-1	"	sapwood
"	B-2	"	sapwood
"	B-3	"	sapwood
BPB-11	A-1	"	heartwood
"	B-1	"	sapwood/heartwood
"	B-2	"	heartwood
"	S-1	"	side
"	S-2	"	side
BPB-12	B-1	"	sapwood
"	B-2	"	sapwood
BPB-13	A-2	"	heartwood

Log #	Isolate #	Date collected	Source/Comments
BPB-13	B-1	October 23 1998	sapwood
"	B-3	"	sapwood
"	B-4	"	heartwood
BPB-14	A-1	"	sapwood
"	B-1	"	sapwood
"	B-2	"	heartwood
BPB-15	B-1	"	heartwood
BPB-16	B-1	"	heartwood

APPENDIX III

PAIRINGS BETWEEN ISOLATES COLLECTED FROM BIRCH LOGS

BPA-9	A-1	A-2	A-3	A-4	B-1
A-1		-	-	-	-
A-2			-	-	-
A-3				-	-
A-4					-
B-1					

BPA-11	A-1	A-2	A-3	A-4
A-1		-	-	-
A-2			-	-
A-3				+
A-4				

BPA-15	A-1	B-1
A-1		+
B-1		

BPA-22	A-1	A-2	A-3
A-1		-	+
A-2			-
A-3			

BPA-27	A-1	B-3
A-1		-
B-3		

BPA-30	A-1	A-2x1	A-2x2	B-1	B-3
A-1		-	-	+	-
A-2x1			-	-	-
A-2x2				-	-
B-1					-
B-3					

BPA-34	A-1	A-2	A-3	A-4
A-1		-	-	-
A-2			-	-
A-3				-
A-4				

BPA-35	S-1	S-2	S-3
S-1		+	+
S-2			+
S-3			

BPA-39	A-1	A-2	A-3
A-1		+	+
A-2			+
A-3			

BPA-42	A-1	A-2	B-1	B-5	B-7
A-1		-	-	-	-
A-2			-	-	-
B-1				-	-
B-5					-
B-7					

BPA-43	B-1	B-2
B-1		+
B-2		

BPA-47	A-1	A-3	B-2
A-1		+	+
A-3			+
B-2			

BPA-48	A-1	A-2	A-3	B-1	B-2	B-3
A-1		-	-	-	-	-
A-2			-	-	-	-
A-3				-	-	-
B-1					-	-
B-2						+
B-3						

BPA-50	A-1	A-2	A-3	A-4	B-1	B-3	B-4	B-5	B-6
A-1		-	-	-	-	+	+	-	-
A-2			*	-	+	-	-	+	+
A-3				-	+	-	-	+	+
A-4					-	-	-	-	-
B-1						-	-	+	+
B-3							+	-	-
B-4								-	-
B-5									+
B-6									

* Intransitive reaction

BPA-51	A1-2	A1-3	A1-4	A2-1	B-1	B-2	B-3	S-1
A1-2		-	-	-	-	-	-	-
A1-3			-	+	+	+	-	-
A1-4				-	-	-	-	-
A2-1					*	+	-	-
B-1						+	-	-
B-2							-	-
B-3								-
S-1								

BPA-52	A-1	A-2	A-3	S-1	S-2	S-3	S-4	S-5	S-6	S-7	S-8x1	S-8x2
A-1		-	-	+	+	-	+	+	+	+	-	-
A-2			-	-	-	-	-	-	-	-	-	-
A-3				-	-	-	-	-	-	-	+	+
S-1					+	-	+	+	+	+	-	-
S-2						-	+	+	+	+	-	-
S-3							-	-	-	-	-	-
S-4								+	+	+	-	-
S-5									+	+	-	-
S-6										+	-	-
S-7											-	-
S-8x1												+
S-8x2												

BPA-55	B-1	B-2	B-3	B-4	S-1	S-2
B-1		-	-	-	-	+
B-2			-	-	-	-
B-3				+	-	-
B-4					-	-
S-1						-
S-2						

BPA-57	A1-1	A1-2	A1-3	B-1	B-2	B-3
A1-1		-	-	-	-	-
A1-2			+	-	*	-
A1-3				-	+	-
B-1					-	-
B-2						-
B-3						

BPA-58	A-1	A-2
A-1		-
A-2		

*Intransitive reaction

BPA-63	A-1	B-1
A-1		-
B-1		

BPA-67	A-1	A-2	B-1
A-1		-	-
A-2			-
B-1			

BPA-69	A-2	B-1
A-2		-
B-1		

BPA-71	A-1x1	A-1x2
A-1x1		-
A-1x2		

BPA-72	A-2	A-3
A-2		+
A-3		

BPA-73	A-1	A-2	A-3
A-1		-	-
A-2			-
A-3			

BPA-75	A-1	A-2	A-3	B-1	B-2	B-3	B-4	B-5
A-1		-	-	-	-	-	-	-
A-2			-	-	-	+	-	-
A-3				-	-	-	-	-
B-1					-	-	-	-
B-2						-	-	-
B-3							-	-
B-4								-
B-5								

BPA-82	A-1	A-2
A-1		-
A-2		

BPA-84	B-1	B-3
B-1		-
B-3		

BPB-1	A-1	A-2	B-1	B-3	B-4	S-1	S-2	S-3	S-4x1	S-4x2	S-5
A-1		-	-	-	-	-	-	-	-	-	-
A-2			-	-	-	+	+	-	-	+	+
B-1				-	-	-	-	-	-	-	-
B-3					-	-	-	-	-	-	-
B-4						-	-	-	-	-	-
S-1							+	-	-	*	*
S-2								-	-	+	+
S-3									-	-	-
S-4x1										-	-
S-4x2											*
S-5											

BPB-2	A-1	A-2	A-3	B-2	B-3	S-1	S-2
A-1		-	-	-	-	+	-
A-2			-	-	-	-	-
A-3				-	+	-	-
B-2					-	-	-
B-3						-	-
S-1							-
S-2							

BPB-3	A-1	A-2	B-1	S-1	S-2
A-1		-	-	-	-
A-2			-	-	-
B-1				-	-
S-1					-
S-2					

BPB-4	A-1	A-2	A-3	B-1
A-1		-	-	+
A-2			+	-
A-3				-
B-1				

BPB-7	A-1	B-1
A-1		-
B-1		

BPB-10	A-1	A-2	A-3	B-1	B-2	B-3
A-1		-	-	-	+	-
A-2			-	-	-	-
A-3				-	-	-
B-1					-	-
B-2						-
B-3						

*Intransitive reaction

BPB-11	A-1	B-1	B-2	S-1	S-2
A-1		-	-	-	-
B-1			-	-	-
B-2				-	-
S-1					+
S-2					

BPB-12	B-1	B-2
B-1		-
B-2		

BPB-13	A-2	B-1	B-3	B-4
A-2		-	-	-
B-1			-	-
B-3				-
B-4				

BPB-14	A-1	B-1	B-2
A-1		-	+
B-1			-
B-2			