Sphaeropsis sapinea, with Special Reference to its Occurrence on *Pinus* Spp. in South Africa*

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SYNOPSIS

Sphaeropsis sapinea (=*Diplodia pinea*) causes shoot blight, canker, collar rot, root disease and blue stain of *Pinus* spp. In South Africa, it has restricted the cultivation of *Pinus radiata* almost entirely to the South-Western Cape. It is also important on *Pinus patula* growing in the summer rainfall areas. Favourable conditions for infection are wet weather and high temperatures (25°C optimum) coinciding with new shoot growth. Hail and other injuries, and stress conditions (especially moisture stress) are important factors predisposing trees to infection. Control measures include sanitation, forest management practices to reduce stress and injury to trees, and the use of both inter and intra-specific host resistance. Fungicidal control is practical only in nurseries. Some research priorities are given.

INTRODUCTION

Sphaeropsis sapinea (Fr.) Dyko & Sutton, formerly *Diplodia pinea* (Desm.) Kickx (Sutton, 1980), was recorded as a pathogen of *Pinus* spp. in South Africa in 1912 by Fisher (Fisher, 1912) and in 1917 by Legat (1917). Since then, it has been particularly important on *Pinus radiata* D. Don in the summer rainfall areas where it causes extensive tree death after hailstorms (Kotze, 1935; Laughton, 1937; Lückhoff, 1964). *S. sapinea* also occurs on pines in other parts of the world, but most of its notoriety is based on the devastation it has caused in South African plantations (Gibson, 1979).

There has been a considerable amount of recent work on the taxonomy, morphology, etiology and epidemiology of *S. sapinea*. The present review summarises available information on *S. sapinea* to serve as a basis for future research on this fungus in South Africa.

SYNONYMY, MORPHOLOGY AND VARIABILITY

Since its initial description under the name *Sphaeria pinea* Desm. in 1842, *S. sapinea* has acquired at least 10 other synonyms (Saccardo, 1884; Punithalingam and Waterston, 1970) of which *Diplodia pinea* (Desm.) Kickx was the most common (Waterman, 1943b). Confusion in the synonymy of *S. sapinea* was attributed by Grove (1919) to variation in the maturity of spore-bearing material examined by collectors. Sutton (1980) reviewed the taxonomy of the coelomycetes on the basis of conidiogenesis and designated the name *Sphaeropsis sapinea* (Fr.) Dyko & Sutton to this fungus. Based on Sutton's classification, *Diplodia* and *Sphaeropsis* both belong to the suborder Blastopycnidineae, but whereas *Diplodia* has conidiophores and conidiogenous cells which form a single monoblastic conidium, *Sphaeropsis* lacks conidiophores, and conidiogenous cells proliferate annelidically. A teleomorph of *S. sapinea* is not known, though spermatia have been observed (Wingfield and Knox-Davies, 1980b). Detailed examination has revealed spermatiophores attached to pseudoparenchyma originating from pycnidium-like conidiomata (Sutton, personal communication). Spermatia have consistently been recovered from monoconidial isolates and attempts to induce them to germinate have been unsuccessful (present authors, unpublished data; Palmer, 1985). According to definition (Luttrell, 1979) this confirms their status as spermatia and not microconidia.

There are significant cultural and morphological differences between isolates of *S. sapinea* (Barker, 1979; Bachi and Peterson, 1982; Palmer and Stewart, 1982; Palmer, 1985). In 1937, Laughton found that isolates from the Eastern Transvaal and the South-Western Cape differed in pathogenicity, with Eastern Transvaal isolates being more virulent (Laughton, 1937). Careful investigation is needed to determine whether this variation can be reconciled with recent evidence based on scanning and transmission electron microscopy suggesting that there are two distinct strains of the fungus (Wang *et al.*, 1984; Palmer, 1985).

DISTRIBUTION AND HOST RANGE

S. sapinea has been reported from at least 25 countries in both hemispheres between the latitudes 30° to 50° north and south (Waterman, 1943b; Punithalingam and Waterston, 1970; Gibson, 1979). The principal countries of occurrence and important pine hosts of *S. sapinea* are given in *Table 1.*

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TABEL 1. Geographical distribution and major Pinus *hosts of* S. sapinea

COUNTRY	HOST	REFERENCES
NORTH AMERICA		
USA	*Pinus nigra* Arnold	Waterman, 1943b; Peterson & Wysong, 1968; Brookhouser & Peterson, 1971; Schweitzer & Sinclair, 1976; Peterson, 1977.
	P. sylvestris L.	Lancaster, 1939; Waterman, 1943b; Peterson & Wysong, 1968; Brookhouser & Peterson, 1971; Peterson, 1977; Palmer & Nicholls, 1983
	P. resinosa Ait.	Waterman, 1943b; Nicholls, 1977; Palmer & Nicholls, 1983; Palmer & Stewart, 1982.
	P. ponderosa Laws	Peterson & Wysong, 1968; Brookhouser & Peterson, 1971; Peterson, 1977; Walla, 1979; Johnson & Peterson, 1985.
	P. banksiana Lamb	Palmer & Nicholls, 1983; Palmer & Stewart, 1982.
Canada	*P. sylvestris* L.	Haddow & Newman, 1942.
SOUTH AMERICA	*P. radiata* D. Don; *P. halepsis* Mill.	Waterman, 1943b; Punithalingam & Waterston, 1970; Gibson, 1979.
EUROPE	*P. sylvestris; P. nigra*	Waterman, 1943b; Punithalingam & Waterston, 1970; Gibson, 1979; Van Dam & De Kam, 1984.
ASIA	*P. sylvestris; P. nigra*	Waterman, 1943b; Punithalingam & Waterston 1970; Gibson, 1979; Chen & Chang, 1966.
AUSTRALASIA		
Australia	*P. radiata*	Eldridge, 1957; Marks *et al.*, 1966; Stahl, 1968; Marks & Minko, 1969; Wright & Marks, 1970.
New Zealand	*P. radiata*	Chou, 1976a; Currie & Toes, 1978; Burdon *et al.*, 1980.
AFRICA		
South Africa	*P. patula* Schl. *et* Cham	Laughton, 1937; Lückhoff, 1964; Van der Westhuizen, 1968; Wingfield & Knox-Davies, 1980a.
	P. radiata	Fisher, 1912; Legat, 1917, 1917; Kotze, 1935; Laughton, 1937; Lückhoff, 1964; Wingfield & Knox-Davies, 1980a.
	P. taeda L.	Laughton, 1937; Wingfield & Knox-Davies, 1980b.
Other African countries	*P. radiata*	Punithalingam & Waterston, 1970; Gibson, 1979.

In South Africa, *P. radiata* is so susceptible that *S. sapinea* has virtually restricted its cultivation to the South-Western Cape where hail is rare. *P. pinaster* is only slightly less susceptible and plantings are also being restricted to hail-free areas. *P. patula, P. taeda* and *P. elliottii* are planted in the summer rainfall areas and of these *P. patula* is the most susceptible species (Laughton, 1937; Lückhoff, 1964; Van der Westhuizen, 1968; Poynton, 1979). In the worst hail belts of the Eastern Transvaal, hundreds of hectares once planted to *P. patula* have been converted to *P. elliottii*, which offers a higher degree of resistance (Poynton, 1979).

SYMPTOMS AND DAMAGE

S. sapinea is associated with so many different disease symptoms that it is generally more convenient to classify symptoms according to appearance and/or location on the host. On this basis we have distinguished the following: shoot blight, canker, collar rot, root disease and blue stain.

Sphaeropsis shoot blight

This is the most commmon symptom associated with *S. sapinea* infection (Laughton, 1937; Haddow and Newman, 1942; Waterman, 1943a, 1943b; Van der Westhuizen, 1955; Eldridge, 1957; Buchanan, 1963; Peterson and Wysong, 1968; Marks and Minko, 1969; Brookhouser and Peterson, 1971; Chou, 1976a; Peterson, 1977; Gibson, 1979; Poynton, 1979). It has been recorded in all forestry areas of South Africa (Laughton, 1937; Lückhoff, 1964; Van der Westhuizen, 1968; Poynton, 1979; Wingfield and Knox-Davies, 1980a).

The first indications of shoot blight are resin droplets on the growing shoots, and a few stunted needles (Peterson, 1977, 1978, 1981). Later, needles turn brown and the shoot tips become crooked or curled, with the woody tissue turning purplish-brown (Eldridge, 1957) (*Figure 1*). After about three weeks, black pycnidia appear on the surface of dead needles (*Figure 2*).

When terminal shoots are infected they exude large amounts of resin. They curl or are girdled and die, resulting in a condition known as leader dieback or dead top (Elridge, 1957; Marks *et al.*, 1966; Marks and Minko, 1969; Chou, 1976b; Gibson, 1979). Lateral branches then assume dominance, and a whorl of secondary leaders develops from the base of the dead shoot (*Figure 3*).

Shoot blight of seedlings (*Figure 4*) occurs sporadically in pine nurseries around the world, espcially those located close to infected mature trees in stands or windbreaks (Crandall, 1938; Slagg and Wright, 1943; Palmer, 1985).

The importance of shoot blight on tree growth and log quality depends on whether terminal or lateral shoots are infected. Infection of lateral shoots is generally less inclined to retard growth and cause deformation of the tree than infection of terminal shoots (Foster and Marks, 1968; Wright and Marks, 1970) The growth of dead-topped *P. radiata* trees can be reduced by as much as 40 % (Wright and Marks, 1970; Currie and Toes, 1978; Brown *et al.*, 1981). In young trees, death of even a few centimetrees of the leader can result in a lateral branch becoming dominant. This reduces the quality of the log because considerable amounts of compression wood are formed (Foster and Marks, 1968; Wright and Marks, 1970). Repeated branching following leader dieback also brings about a considerable loss in merchantable wood.

Sphaeropsis canker

Branch cankers originate from infected buds or shoots (Waterman, 1943b). The fungus moves down the pith where it avoids defence barriers laid down by the host (Marks and Minko, 1969). When the host is weakened by environmental stresses it passes through the medullary rays to infect the cambium and cortical tissues (Marks and Minko, 1969). This gives rise to elongated, depressed areas and resin exudation. When the surrounding bark is removed, olive-green streaks and brown resin-soaked wood are visible (Marks and Minko, 1969; Nicholls, 1981). Older infections have pronounced callus growth around the edges of the depression (*Figure 5*). Cankers can eventually girdle and kill the branches.

Whorl or bole cankers follow leader dieback or pruning injury (Waterman, 1943b; Gilmour, 1964). They often appear near the top of the tree at the base of secondary leaders. Resin exudes from the canker and runs down the bark (Waterman, 1943b; Marks and Minko, 1969). Infected pruning wounds also develop cankers which disfigure the bole, or girdle and kill the tree (Wright and Marks, 1970). Cross sections through bole cankers reveal dark blue wedges of infected tissue between the pith and cambium (*Figure 6*).

Sphaeropsis collar rot and root disease

Collar rot of nursery seedlings is often seen in other countries but has not been recorded in South Africa (Kotze, 1935; Laughton, 1937; Lückhoff, 1964; Gibson, 1979; Wingfield and Knox-Davies, 1980a). The root collar area becomes discoloured and resinous and pycnidia develop in surrounding tissue (Palmer and Nicholls, 1983; Palmer, 1985). The foliage becomes chlorotic and the needles die.

S. sapinea causes late damping-off or root rot of conifer seedlings (Darvas *et al.*, 1976) and a serious root disease of mature *P. elliottii* and *P. taeda* in some parts of South Africa (Wingfield and Knox-Davies, 1980b). Symptoms on mature trees are dark blue or black radial lesions in young roots (*Figure 7*) extending into larger roots and sometimes into the bole. Needles become chlorotic and are usually shed. The disease occurs under stress conditions. Symptoms on drought-stressed *P. taeda*, and similar to those described by Wingfield and Knox-Davies (1980b), have been reported from Hawaii (Hodges, 1983a) and Venezuela (Hodges, 1983b). The fungi associated with these symptoms in Hawaii and Venezuela were, however, *Botryosphaeria dothidea* and *Lasiodiplodia theobromae* respectively. Both fungi are taxonomically and ecologically related to *S. sapinea*.

Sphaeropsis blue stain

Besides attacking living pines, *S. sapinea* also causes blue stain, a greyish or dark blue discolouration in the sapwood of pine timber (Da Costa, 1955; Eldridge, 1957). Infection occurs through bark abrasions caused during felling and extraction, through branch butts after pruning and through the exposed ends of newly cut logs. Lignified cell walls are not damaged and the discolouration is due to the presence of dark hyphae in the parenchyma and rays. *Sphaeropsis* blue stain does not adversely affect the structural properties of timber but it is aesthetically undesirable (Eldridge, 1957).

Damage caused by *Sphaeropsis* diseases

Damage caused by *S. sapinea* can be both direct and indirect (Lückhoff, 1964):

* Destruction of young trees before they reach merchantable age.
* Loss of increment due to defoliation and death of leading shoots and branches.
* Degrade due to blue stain.
* Losses associated with exploiting diseased trees and stands before they reach maturity and attain maximum value.

FIGURE 1. S. sapinea *infected lateral shoot of* Pinus radiata *with characteristic crooked tip.*

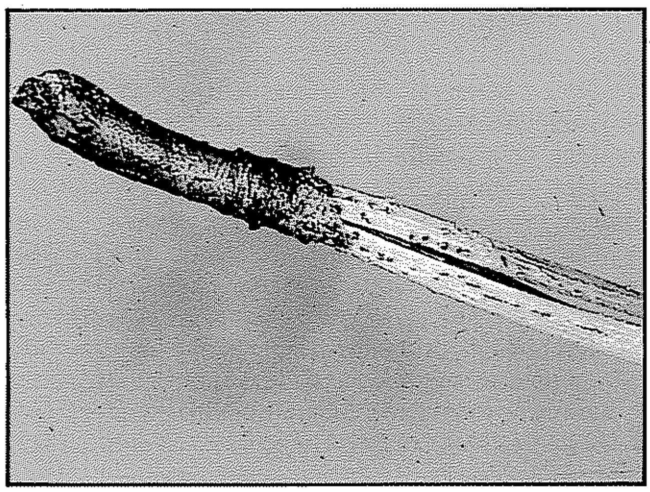

FIGURE 2. Dead pine needles bearing pycnidia of S. sapinea.

FIGURE 3. Terminal shoot of P. radiata *killed by* S. sapinea *with whorl of secondary leaders*

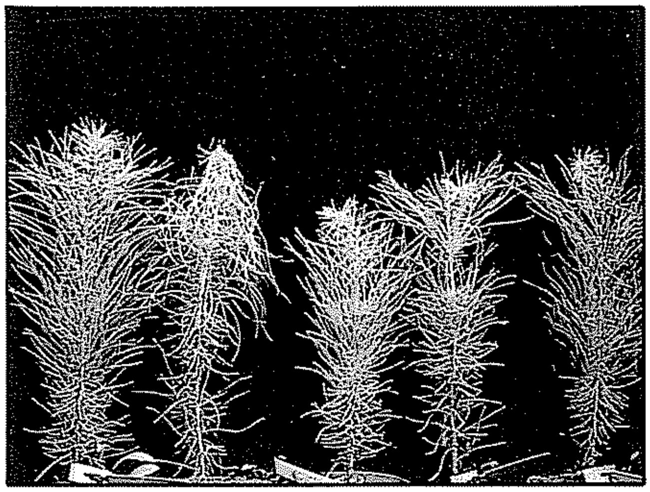

FIGURE 4. S. sapinea *shoot blight of* P. radiata *seedlings.*

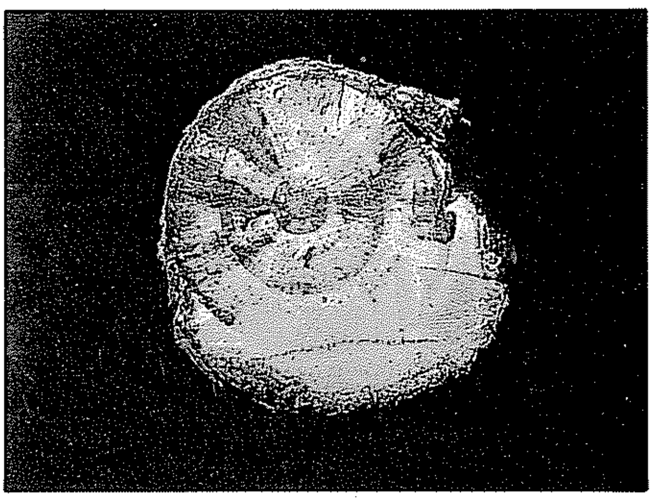

FIGURE 5. Transverse section through a branch canker on P. radiata *showing callus formation and wedges of* S. sapinea *infected tissue.*

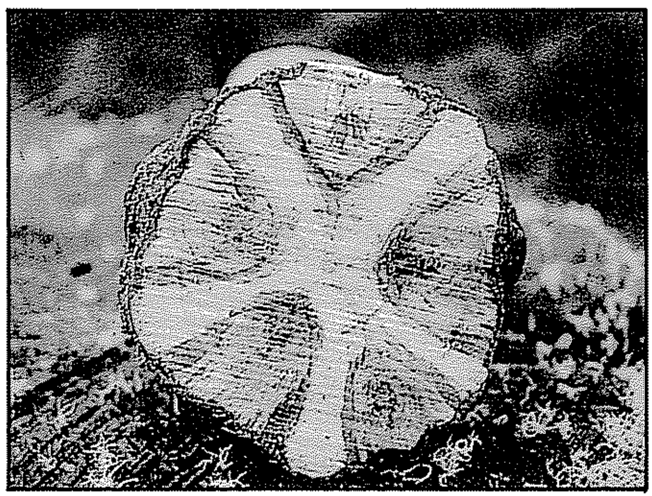

FIGURE 6. Transverse section through bole of P. radiata *showing* S. sapinea *infection of pruning wounds.*

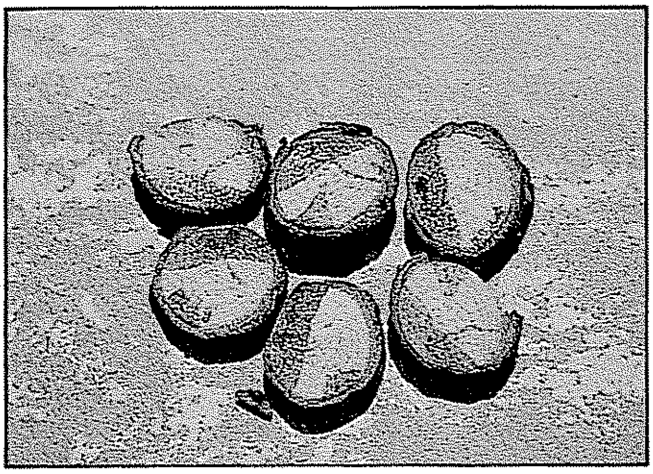

FIGURE 7. S. sapinea *infected tissue in young roots of* P. elliottii.

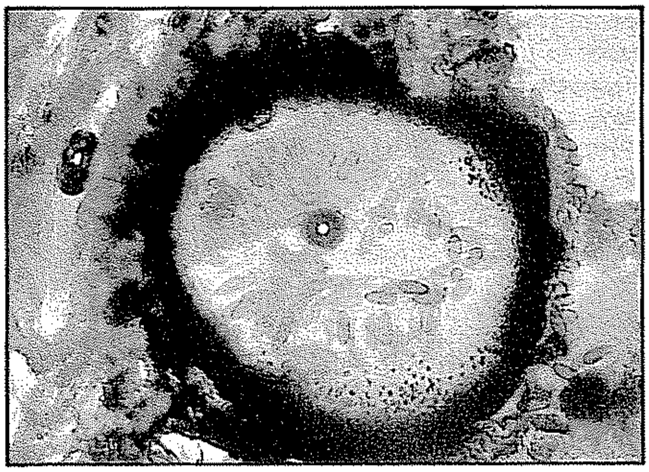

FIGURE 8. Section through a pycnidium of S. sapinea.

SPORE FORMATION AND DISPERSAL

Pycnidia (*Figure 8*) develop on dead needles, on bark and on scales of second-year cones (Peterson, 1981; Palmer, 1985). *S. sapinea* is also abundant on forest litter (Kotze, 1935; Laughton, 1937; Waterman, 1943a, 1943b). Conidia (*Figure 9*) take about two months to mature (Waterman, 1943b; Peterson, 1977, 1981). They pass through three distinct stages of maturation. Young conidia are hyaline and non-septate, then pale brown and non-septate and, finally, dark brown and occasionally uninseptate when fully mature. Free water is essential for their discharge (Eldridge, 1957; Brookhouser and Peterson, 1971). In water they ooze slowly through the ostiole as long cirri. They are scattered by the impact of raindrops and are mainly dispersed during rainy weather (Eldridge, 1957; Brookhouser and Peterson, 1970). Wind is essential for long distance dispersal (present authors, unpublished data). Little is known of the role of insects and birds in dispersing *S. sapinea* conidia.

SPORE GERMINATION AND INFECTION

Environmental conditions

Relative humidities over 90 % and temperatures of 25°C are optimal for spore germination and penetration of the host (Van der Westhuizen, 1968; Brookhouser and Peterson, 1971; Chou, 1978; 1982a). Under these conditions, infection occurs within 8 hours and the first symptoms can appear after four to ten days (Peterson, 1977; 1981). Shoots growing vigorously are particularly susceptible (Chou, 1982b). This explains why infection is heaviest in the summer rainfall regions as noted by Laughton (1937).

Host susceptibility

Some *Pinus* spp. are more susceptible than others to *S. sapinea* (*Table 1*). Burdon *et al.* (1980) has recorded differences in susceptibility between progenies of *P. radiata*.

FIGURE 9. Conidia of S. sapinea.

Wounding and stress conditions

Unwounded new shoots are susceptible to infection if climatic conditions are favourable and large amounts of inoculum are present (Laughton, 1937; Waterman, 1943b; Marks *et al.*, 1966; Brookhouser and Peterson, 1971; Chou, 1976a, 1976b; Nicholls, 1977; Nicholls and Ostry, 1977; Bega *et al.*, 1978; Wingfield and Knox-Davies, 1980a; Johnson and Peterson, 1985; Palmer, 1985). In general, though infection takes place only through wounds caused by hail, insects or other agents (Van der Byl, 1933; Laughton, 1937; Haddow and Newman, 1942; Eldridge, 1957; Stahl, 1968; Marks and Minko, 1970; Nicholls, 1977; Wingfield and Palmer, 1983). Chou (1977) could find no evidence that the level of dieback was affected by tree age.

The heaviest infection involves trees that have been under physiological stress. Drought is generally given as a predisposing factor (Laughton, 1937; Millikan and Anderson, 1957; Stahl, 1968; Hunt, 1969; Wright and Marks, 1970; Minko and Marks, 1973; Bega *et al.*, 1978; Evans, 1978; Wingfield and Knox-Davies, 1980a; Brown *et al.*, 1981). Other stress factors cited are overstocking, poor site conditions and nutrient stress (Van der Byl, 1933; Lückhoff, 1964; Wingfield and Knox-Davies, 1980a; Brown *et al.*, 1981). The role of predisposition in the host-pathogen interaction needs to be clarified. It has been suggested that pine oleoresin, containing monoterpenes toxic to *S. sapinea*, plays a role in host resistance (Chou and Zabkiewicz, 1976; Brown *et al.*, 1981; Chou, 1981). Evidence in support of this is the fact that high stocking and nutrient and moisture stresses reduce oleoresin flow in *P. taeda* (Mason, 1971).

CONTROL

The most practical disease control measure is the replacement of susceptible cultivars with more resistant species or cultivars (Lückhoff, 1964; Wright and Marks, 1970; Gibson, 1979; Burdon *et al.*, 1980). The planting of different species is not always feasible as there is still insufficient information on interspecific resistance to *S. sapinea* and how this is affected by site and climatic conditions. Nevertheless, in South Africa *P. patula* is being phased out in favour of *P. elliottii* (Poynton, 1979). Selecting for resistance within the more popular *Pinus* spp. (*P. radiata, P. pinaster* and *P. patula*) deserves more attention.

Maintenance and sanitation of stands and nurseries are both effective and economical ways of controlling *Sphaeropsis* diseases. It is claimed that premature thinning reduces *Sphaeropsis* infection (Gibson, 1979), presumably by reducing atmospheric humidity and competition for water and nutrients (Bega *et al.*, 1978). The prevention of wounding in thinning operations is important, but difficult in older thinnings where the larger trees cause more damage as they fall. Restricting pruning damage will reduce losses from whorl canker (Gilmour, 1964). Infection will also be reduced if trees are pruned during periods when dispersal of the fungus is minimal and conditions are unfavourable for spore germination, i.e. during dry and/or cold periods. Physiological stress due to nutrient deficiencies can be alleviated by fertilising at planting and/or following thinning (Brown *et al.*, 1981). Slash from thinning and pruning provides an abundant source of inoculum and should be removed where possible. Sanitation measures also apply to nurseries where dead or dying seedlings are best removed from nursery beds to prevent further spread of inoculum (Nicholls, 1977, 1981, 1982, 1983, 1984).

Attention has been given to chemical control of *S. sapinea* in nurseries and plantations (Peterson and Wysong, 1968; Van der Westhuizen, 1968; Brookhouser and Peterson, 1971; Schweitzer and Sinclair, 1976; Nicholls, 1977, 1981; Palmer *et al.*, 1981; Palmer and Nicholls, 1983). In South Africa the cost and practical problems involved in aerial spraying of plantations limit the use of fungicides to nurseries.

The potential for biological control was investigated by Liang and Li (1982) who found that prior colonisation of young shoots by *Pestalotia cryptomeriae* and *Gluconobacter* sp. reduced infection by *S. sapinea*.

CONCLUSION

S. sapinea is an important opportunistic pathogen of pines in South Africa. It is particularly important in the summer rainfall areas. Immediate priorities in research programmes to reduce the impact of *Sphaeropsis* diseases in local pine plantations should include:

1. Formulating procedures to evaluate host resistance (including an evaluation of the genetic variability within the fungus).
2. Evaluating forest management priorities to reduce stress conditions and injury to the trees.

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