

A worldwide perspective on the management and control of *Dothistroma* needle blight

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Summary

Dothistroma needle blight (DNB) caused by *Dothistroma septosporum* and *Dothistroma pini* is a damaging disease of pine in many countries. The disease led to the abandonment of planting susceptible *Pinus* species in parts of Africa, Asia, Australasia, Europe and North America. Although the disease can be effectively controlled using copper fungicides, this chemical is only routinely applied in forests in New Zealand and Australia. Other management tactics aimed at making conditions less favourable for disease development, such as thinning or pruning, may be effective on some, but not all, sites. Disease avoidance, by planting non-susceptible species, is the most common form of management in Europe, along with deployment of hosts with strong disease resistance. Although *D. septosporum* is present almost everywhere *Pinus* is grown, it is important that an effort is maintained to exclude introductions of new haplotypes that could increase virulence or enable host resistance to be overcome. A global strategy to exclude new introductions of *Dothistroma* and other damaging forest pathogens, facilitated by collaborative programmes and legislation, is needed.

1 | INTRODUCTION

Dothistroma needle blight (DNB) is one of the most economically important foliar diseases of *Pinus* species worldwide (Barnes, Crous, Wingfield, & Wingfield, 2004; Bradshaw, 2004), causing premature needle drop, reduced yield and, in some cases, tree mortality (Brown & Webber, 2008; Rodas, Wingfield, Granados, & Barnes, 2016). The causal agents of DNB, *Dothistroma septosporum* and *D. pini* are morphologically similar and best identified using molecular methods (Barnes et al., 2004, 2016). *Dothistroma septosporum* is found worldwide, while *D. pini* has, to date, only been recorded from North America and Europe (Drenkhan et al., 2016). Although *Pinus* is the major host, *D. septosporum* has been known to infect other genera, including *Abies*, *Cedrus*, *Larix*, *Picea* and *Pseudotsuga*. *Dothistroma pini* has only been reported from *Pinus* so far (Drenkhan et al., 2016).

Dothistroma needle blight has been found on all continents except Antarctica, across a huge climatic range from sea level to high elevation, and in tropical, subtropical and temperate climates (Drenkhan et al., 2016; Watt, Kriticos, Alcaraz, Brown, & Leriche, 2009). Outbreaks have been observed in various parts of the world since the 1950s, but most especially in the Southern Hemisphere on *Pinus radiata* (Gibson, 1974). The disease is known to have been present in Zimbabwe as early as 1943 (Gibson, Christensen, & Munga, 1964), but it was not until the late 1950s and early 1960s that it was observed in East Africa (Gibson et al., 1964), Chile (Dubin, 1965) and New Zealand (Gilmour, 1967). Before the late 1990s, outbreaks tended to be localized and episodic in the Northern Hemisphere (Parker & Collis, 1966; Peterson, 1967; Thompson, 1966). However, since the late 1990s, the disease has caused widespread and severe damage to planted and native stands of *Pinus contorta* subsp. *latifolia* in Canada and in *P. nigra* subsp. *laricio* plantations in the United Kingdom (Archibald & Brown, 2007) and France (Villebonne & Maugard, 1999). More recently, new records of the disease have been made in a number of Baltic and

Nordic countries (Hanso & Drenkhan, 2008; Drenkhan & Hanso, 2009; Markovskaja & Treigienė, 2009; Müller, Hantula, & Vuorinen, 2009; Solheim & Vuorinen, 2011).

In the USA, Kenya and New Zealand, DNB posed such a threat to the economic sustainability of commercial pine forestry that disease control had to be attempted. For example, in New Zealand, it caused an estimated loss of NZD \$19.8 million per year during the 2000s (Watt, Palmer, & Bulman, 2011). Chemical control was investigated first in these countries (Gibson et al., 1964; Gilmour, 1965; Thomas & Lindberg, 1954) and later on in Chile (Contreras, 1988) and Europe (Karadžić, 1987). In more recent years, other methods have been added to the toolkit of options available to tackle this serious disease.

This review was initiated through the EU COST Action FP1102 DIAROD (Determining Invasiveness and Risk of *Dothistroma*) Working Group 2, which was formed to determine the risk of DNB and evaluate different management strategies to mitigate those risks. In this review, we address past and present measures used to manage DNB around the world and discuss options that might be used in the future.

2 | EXCLUSION AND PREVENTATIVE MEASURES**2.1 | Exclusion**

In an ideal situation, the best way to manage a disease is to prevent the introduction of its causal agent. However, although the origin of both *Dothistroma* spp. is still uncertain, DNB is found almost everywhere that susceptible hosts grow (Drenkhan et al., 2016; Watt et al., 2009). *Dothistroma* spp. spread through both natural dissemination and anthropogenic pathways. Natural dissemination would either occur via air-borne ascospores, which are thought to travel considerable distances (Dale, Lewis, & Murray, 2011; Mullett, Tubby, Webber, & Brown, 2016), or via conidia present in mist and cloud (Gibson et al.,

1964). The main anthropogenic pathway is thought to be through the movement of infected planting material between regions and countries (e.g. Brasier, 2008; Barnes, Wingfield, Carbone, Kirisits, & Wingfield, 2014; Mullett, 2014). Gibson et al. (1964) suggested wind-borne conidia enabled the spread of the DNB pathogen across East Africa, as wind patterns matched the progression of disease over the years studied. Similarly, *D. septosporum* could have blown from New Zealand to Australia in moist air currents (Edwards & Walker, 1978) and from Estonia to Finland across the Gulf of Finland, a distance of 50–100 km (Lilja et al., 2011). This apparently free movement of the pathogen between and within countries suggests few, if any, countries could claim “pest-free status” (FAO, 1996) from *Dothistroma* spp. in the long term. Even in countries where *Dothistroma* spp. have not been recorded, it is probably only a matter of time before DNB is discovered. This could be the result of conditions becoming suitable for disease expression (through climate change or the increased presence of susceptible hosts), or, if *Dothistroma* spp. are not already present, by their spread from nearby infected areas. For example, DNB was first seen in England and Wales in the 1950s, in Scotland in 1985 and finally in Northern Ireland in 2011 (EFSA, 2013). In Northern Europe, *Dothistroma* was present in Denmark and Russia over one hundred years ago, but DNB was first recorded in Estonia, Finland, Sweden and Norway from only 2006 onwards (Musolin et al., 2014).

It is important that an attempt is made to prevent the ingress and mixing of plant pathogen populations, even when countries harbour the same species. Should the original population include only one mating type, as is the case for *D. septosporum* in New Zealand (Barnes et al., 2014; Groenewald et al., 2007), variation in virulence might be very low. Introduction of other haplotypes might provide the opportunity for sexual recombination and thus the risk of creating more virulent phenotypes. When, for example, a second mating type of *Phytophthora infestans* was introduced to Europe and the USA, it resulted in the development of far more aggressive strains of the pathogen, leading to a resurgence in “late blight” of potatoes and tomatoes in the 1980s and 1990s (Fry & Goodwin, 1997). Similarly, when two phylogenetically related *Phytophthora* species came into contact in Central European forest nurseries, hybridization led to the formation of a group of extremely aggressive heteroploid pathogens of *Alnus* spp. that are now widespread in Europe (Husson et al., 2015). The risks associated with sexual recombination within *Dothistroma* spp. are not limited to the formation of more aggressive phenotypes. In axenic *D. septosporum* cultures, some strains differed in their levels of production of the virulence factor dothistromin (Bradshaw, Ganley, Jones, & Dyer, 2000), suggesting a possible genetic basis to this phenotype. However, it is not known if high dothistromin production in culture is replicated by high production *in planta*, nor has the relationship between dothistromin levels and virulence in the field been established. Sexual recombination may also result in the formation of ascospores, and these have a greater dispersal potential than conidia that are generally carried short distances by rain splash (Gibson et al., 1964; Peterson, 1973). Modern molecular methods, such as quantitative polymerase chain reaction (qPCR) and real-time PCR (West, Atkins, Emberlin, & Fitt, 2008; West, Atkins, & Fitt, 2009), could be

used to quantify sporulation of this pathogen. Methods for absolute quantification of *Dothistroma* using cutting edge techniques have been developed (Janoušek et al., 2012) and used (Mullett, Peace, & Brown, 2016). New quantification methods yet to be developed may improve epidemiological studies and help DNB management. Even if both mating types are already present, the addition of new genetic variants could potentially increase pathogen virulence. Further to this, because only *D. septosporum* is known in the Southern Hemisphere (Drenkhan et al., 2016), the introduction of *D. pini* to this region may have unanticipated impacts on forest health, although observations in Europe suggest this is unlikely (Fabre, Ios, Piou, & Marçais, 2012).

It is difficult to prevent natural dispersal of *Dothistroma* spp. Despite this, there are regional initiatives aimed at stopping their ingress through trade. It is difficult to detect *Dothistroma* spp. through visual inspection because the lag between infection and symptom expression can result in infected plants remaining symptom free for several months (Gadgil, 1977). Chemical treatment may also suppress symptom development without eliminating the pathogen. Detection using molecular methods or by holding material under quarantine in conditions suitable for symptom development is possible, but impractical. Despite these difficulties, some European countries attempt exclusion. For example, in Britain and Slovenia, all *Pinus* plants grown in tree nurseries are inspected for DNB during the peak infection period. If found, all affected stock is destroyed and restrictions are placed on the movement of stock from that nursery. In Switzerland, if DNB is identified in a nursery, distribution of *Pinus* is banned until no DNB has been detected for an entire growing season. Eradication of DNB on infected pines in urban areas is also being attempted in Switzerland to prevent spread to natural pine forests that are mostly disease-free. Other than that, exclusion of *Dothistroma* spp. is not currently attempted in Europe, nor elsewhere, despite legal commitments of the European Union.

2.2 | Avoidance by host species selection

Susceptibility between different hosts of *Dothistroma* spp. varies widely, at both species and subspecies levels (Drenkhan et al., 2016). In many cases, the impacts of DNB have been avoided by not planting susceptible species on high-risk sites. In some countries, DNB had such a devastating impact on certain tree species that a drastic change in forestry policy was required. For example, *P. radiata*, previously a very productive crop in Kenya, Tanzania and Zimbabwe, had become so heavily damaged by DNB in the 1960s (Christensen & Gibson, 1964; Gibson, 1974) that it was abandoned despite aerial and ground-based fungicide application being shown to reduce disease severity (Gibson, Kennedy, & Dedan, 1966). In 1974, *P. radiata* planting stopped and now the most common plantation species are *Cupressus lusitanica*, *Pinus patula* and *Eucalyptus* spp. (Sedjo, 2004). Similarly in South Africa, in response to the observed effects of DNB on *P. radiata* in Kenya and Zimbabwe, and severe damage from *Diplodia sapinea* on this species, the decision was made to plant the less favourable, but more resistant, *P. patula* instead (Gibson, 1972; Crous, Wingfield, & Swart, 1990). In the 1960s, planting of *P. radiata* was also curtailed in

TABLE 1 Country reports of DNB impact and management undertaken

Country	DNB impact ^a	Control type	Comments
Britain	Major	Chemical Silviculture Replacement	Species change away from <i>P. nigra</i> subsp. <i>laricio</i> . Provenance change (away from <i>P. contorta</i> var. <i>latifolia</i>). Thinning – heavier and earlier than traditionally practiced. Currently only experimental aerial and ground-based chemical control.
New Zealand	Major	Chemical Breeding Silviculture	Chemical application every 2-3 years, ca. 70,000 ha sprayed per year (5% of total area).
Canada	Medium	Silviculture Replacement	Chemical use not feasible because spraying would be required throughout rotation given lack of age-related resistance. Species change away from <i>P. contorta</i> in severely affected areas.
Chile	Medium	Chemical Silviculture	Chemical use in forests restricted. Pruning to 2.1 m from ground level when disease severity exceeds 60%. Chemical at nursery only.
France	Medium	Replacement	Replace <i>P. radiata</i> x <i>attenuata</i> with less susceptible species.
Serbia	Medium ^b	Chemical Silviculture	Chemical control every 3-4 years in <i>P. nigra</i> plantations and twice during spring (May–June) in nurseries.
Slovakia	Medium	Chemical Replacement	Annual chemical application in nursery <i>P. nigra</i> . Some growers replace <i>P. nigra</i> with other conifers.
Spain	Medium	None	Major severity in the North of Spain. Pitch canker is masking the effect of DNB.
Switzerland	Medium	Eradication	DNB not tolerated – trees removed if detected.
Turkey	Medium	Silviculture Sanitation	The disease was recently detected on <i>P. brutia</i> in 2011. Treatments are relatively new and based mainly on silvicultural practices. Badly affected individual trees are thinned to reduce humidity in the crowns. Thinning intensity has increased as DNB was recognized as a major problem. Residue is burned immediately after felling.
Bulgaria	Low	Chemical Silviculture	Chemical control only in nurseries where DNB is seen. Diseased trees selectively thinned, also allows better air circulation.
Estonia	Low	Chemical	Chemical control only in nurseries to control other pine diseases, no fungicide application to control DNB specifically. No chemical treatment in forests.
Latvia	Low	Chemical	Chemical control only in nurseries.
Lithuania	Low ^c	Chemical	Chemical control only in nurseries using systemic fungicides to control a wide spectrum of pine diseases.
Montenegro	Low	Chemical	Regular chemical treatments in forest nurseries against general needle pathogens.
Portugal	Low	Chemical	Chemical control only in nurseries.
Republic of Macedonia	Low	Chemical	Chemical control using copper-based fungicides only in nurseries.
Russia	Low	Chemical	Not economical to control in forest. Chemical control using wide-spectrum systemic fungicides only in nurseries in the Rostov region.
Slovenia	Low	Chemical Silviculture	Fungicide treatment in nurseries from spring to the first frost every 14 days, when rainfall is more than 20 mm additional treatment is applied; copper-based fungicides or dithiocarbamate fungicides. DNB forbidden in nurseries by law. Chemical use forbidden in forests, silvicultural measures applied.
Australia	Minor	Chemical Breeding Silviculture	Chemical control in forests most years at local level. Only 2,000 ha treated per year (0.25% of total susceptible area).
Czech Republic	Minor ^d	Chemical Replacement	No new plantings of <i>P. nigra</i> due to DNB. Important for amenity pines and some non-native spruces. No chemical treatment in stands and plantations, only nurseries and Christmas tree farms. Additional spraying in forest nurseries in May.
Hungary	Minor ^e	Chemical Silviculture	Chemical control not economical. Remove heavily infected trees or stands.
Italy	Minor	None	Not economical to control – so far DNB is not an issue.
Poland	Minor ^f	Replacement	Ban on planting <i>P. nigra</i> and all <i>P. nigra</i> subspecies since ca. 2005.

(Continues)

TABLE 1 (continued)

Country	DNB impact ^a	Control type	Comments
Romania	Minor ^g	Silviculture Chemical	Chemical control rare, only experimental or in special cultures (orchard, arboretum) at the local level. Silviculture by thinning or sanitary culling.
South Africa	Minor	Replacement	Resistant <i>P. patula</i> replaced plantings of <i>P. radiata</i> .

^aMinor, low, medium, major, severe (average foliage loss of less than 10%, 11–25%, 26–50%, 51–75%, and over 75%) according to geo-database in Drenkhan et al. (2016).

^bMedium DNB severity in *Pinus nigra* plantations and natural stands after age 20–35. Severe in young and middle aged *P. nigra* plantations and nurseries.

^cLow or medium impact.

^dMinor in forest stands, however, dramatically increasing impact in young *P. sylvestris* stands in some areas. Very important in plantations of *P. nigra*.

^eMajor significance after wet springs and summers.

^fNo impact on *P. sylvestris*.

^gGenerally minor, sometimes major (10–25 year-old plantations of *P. nigra* subsp. *nigra*).

parts of North America (Parker & Collis, 1966; Cobb, Uhrenholdt, & Krohn, 1969) and India (Bakshi & Singh, 1968). The arrival of *D. septosporum* in New Zealand led to the abandonment of *P. ponderosa* and *P. nigra* subsp. *laricio* as forestry species in that country.

In 2006, a moratorium on planting *P. nigra* subsp. *laricio* in the United Kingdom was imposed due to its extreme susceptibility to DNB (Ray, Morison, & Broadmeadow, 2010). Planting of the same subspecies was also curtailed in high-risk locations in the Czech Republic (Table 1) and in France (Piou, Saintonge, & Marçais, 2015). Highly susceptible provenances of another species, *Pinus contorta*, have not been used in the United Kingdom since 2010 (see Fraser, Woodward, & Brown, 2016; for current information on species and provenance variation in susceptibility). In northwest British Columbia, planting of *P. contorta* var. *latifolia*, formerly a favoured management species, has been greatly reduced since the early 2000s. A stand establishment aid (McCulloch & Woods, 2009) was developed to help manage DNB in areas where more favourable weather had increased disease levels in stands of susceptible provenances of *P. contorta* (Woods, Coates, & Hamann, 2005). This guidance includes recommendations for decreasing the *Pinus* component of species mixtures and replacing *P. contorta* with other native conifers in the area.

3 | DISEASE MANAGEMENT

3.1 | Surveillance, monitoring and modelling

Forest health surveillance forms the basis of any management programme, and trained observers are key members of any forest disease management team. An example of good practice is the early recruitment of pathologists and entomologists during the development of exotic conifer plantations in East Africa and New Zealand (Allen, 1973; Bulman & Gadgil, 2014; Gibson, 1972). Regular surveys were established alongside research programmes on the biology and control of known pests and diseases, with the aim of early detection and the development of workable biosecurity legislation (Kershaw, 1989). Countries wishing to trade plant material are obliged to carry out surveys for specific pests and diseases to retain their “pest-free status” with respect to, for example, *Ceratocystis platani* on *Platanus* spp. and *Cryphonectria parasitica* on *Castanea* spp. For pathogens that are

already widely distributed across Europe and further afield, for example *Dothistroma* spp., the focus shifts to monitoring disease distribution and intensity to help target and fine-tune management options. In Britain, trained forestry professionals have performed regular DNB surveys of the public forest estate since 2006 (Brown & Webber, 2008), and the data are used for planning local forest management tactics. In New Zealand, annual aerial DNB surveys are carried out to define a copper fungicide spray programme for disease control (Bulman, Gadgil, Kershaw, & Ray, 2004) and similar surveys occur in Australia (Smith, Smith, Collett, & Elms, 2008). The Département de la santé des forêts conducts forest health surveys in France and reports of an increase in DNB severity prompted research on disease management (Aumonier, 2002; Piou et al., 2015). Annual DNB surveys are carried out in Belgium, Czech Republic, Slovenia and Switzerland and sporadically in other European countries (i.e. Austria, Estonia, Hungary, Latvia, Lithuania and Romania) (EFSA, 2013). European forest monitoring (financed by ICP-Forests, EU Scheme, Forest Focus Scheme and LIFE+) gives some information on DNB occurrence in Europe.

At a landscape level, models can be used to predict disease risks which can help foresters decide on disease management tactics, such as species deployment, silviculture or amended rotation length. For instance, Gonthier and Thor (2013) listed 20 predictive models for heterobasidion root rot and suggested they could be used for comparative analyses to determine the best management strategies for that disease. Likewise, Jactel et al. (2012) described a multicriteria risk analysis and a ranking method that evaluated the effect of four forest management approaches on forest health. Several models have also been developed for DNB. Iturrutxa, Mesanza, and Brenning (2015) described the use of generalized linear mixed effects models to predict the spatial risk for three *P. radiata* needle diseases (including DNB) in Spain to focus management strategies. Watt, Ganley, Kriticos, and Manning (2011) developed a multiple regression model to predict the distribution and severity of DNB under climate change in New Zealand to assist long-term management decisions such as future species selection on particular sites. Models have been developed to predict disease outbreaks (Dvorak, Drapela, & Jankovsky, 2012; Welsh, Lewis, & Woods, 2014; Woods et al., 2016) and growth loss (Van der Pas, 1981). These can guide decisions on when, and how often, to apply

chemical control, or whether to plant a susceptible species or an alternative that underperforms the susceptible species on disease-free sites.

3.2 | Site and host manipulation

3.2.1 | Factors contributing to disease development

Several environmental variables affect the severity of DNB. Moisture is generally considered the most important variable because rainfall is needed for conidia dispersal (Peterson, 1973) and the duration of foliage wetness influences infection and disease development (Gadgil, 1974, 1977). In New Zealand, Gilmour (1981) showed that peaks in disease severity coincided with periods of rainfall, with little or no infection during dry periods. Other studies in Britain, Bulgaria, Hungary, Canada, USA, Chile, Colombia and Kenya also noted a clear link between high summer rainfall and high disease severity (Archibald & Brown, 2007; Dubin, 1967; Fraser, Mullett, Woodward, & Brown, 2016; Gibson et al., 1964; Koltay, 2015; Murray & Batko, 1962; Rodas et al., 2016; Rogerson, 1953; Woods et al., 2005; Zlatanov, 1977).

The effect of moisture on disease levels is also seen at a microsite level. Decades of field observations from a number of countries have determined that disease levels tend to be high in gullies and low-lying areas where trees remain wet for prolonged periods (Brown & Webber, 2008; Bulman et al., 2004; Crisan, Chira, Isaia, & Marcu, 2015; Marks, Smith, & Cook, 1989; Petkov, 1993). The same effect is often seen where low clouds, or fog, sits on ridge tops. The foggy micro-climate found in East Anglia in England, combined with extensive planting of highly susceptible *P. nigra* subsp. *laricio* may explain the severe damage caused by DNB observed in this area during the last decade (Brown & Webber, 2008). Active management techniques to shorten foliage wetness period and thus minimize the risk of significant disease development have been developed based on a combination of experimental and field observations. These and other management techniques are outlined below.

3.2.2 | Silvicultural management – thinning

As early as 1965, it was suggested that DNB was more severe in densely stocked stands. A group of Australian foresters who visited New Zealand in December 1965 observed that *P. radiata* at 2000–4000 stems ha⁻¹ at 15 years of age was heavily diseased, but a nearby area with much lower stocking was uninfected (Marks, 1966). Reducing stand density by planting at a lower initial stocking, along with thinning, has been shown to reduce disease levels in several studies in Australia (Marks & Smith, 1987; Marks et al., 1989; Neumann, Collett, & Smith, 1993), Chile (Alzamora, Hauer, & Peredo, 2004), Kenya (Gibson et al., 1964), New Zealand (Bulman et al., 2013; Van der Pas, Bulman, & Horgan, 1984) and the USA (Van Haverbeke & Boldt, 1968).

There are several reasons why thinning a stand should reduce disease severity. Improved air circulation in thinned stands allows the foliage to dry at a faster rate than in unthinned stands, and thinning may improve tree vigour and thus increase resistance (Mitchell, Waring, &

Pitman, 1983). Reduced leaf wetness period slows infection and disease development (Gadgil, 1974, 1977; Gibson et al., 1964; Peterson, 1973; Peterson & Harvey, 1976). Rain-splashed spores usually travel only short distances (Marks & Smith, 1987; Peterson, 1973; Petkov, 1993), so wider spacing reduces the amount of inoculum to which neighbouring trees are exposed. Highly susceptible trees, which are often heavily diseased and smaller than average, are removed in preference to less susceptible trees during thinning operations (Bulman et al., 2013), thereby lowering inoculum. In keeping with the effect of thinning, disease levels are sometimes lower in stands where crown closure does not occur. In an Australian study on 5-year-old *P. radiata*, disease severity was 50% when tree crowns were less than 1 m apart, but less than 5% when crowns were over 2.5 m apart (Marks & Smith, 1987).

Preliminary results from ongoing experiments in Britain suggest that thinning has had a significant impact on reducing the severity of DNB in the heavily diseased *P. nigra* subsp. *laricio* forests of East Anglia. This species is normally progressively thinned from around 2250 to 350–450 stems ha⁻¹. Disease levels in “conventionally” thinned stands were compared with no thinning and heavy thinning (down to 750 and then 450 stems ha⁻¹ at first and second thinning, respectively). Initially, heavy thinning reduced tree mortality and increased increment, but little treatment difference was apparent 3–4 years later as the canopy began to close. It remains to be seen whether the small overall increment gains due to thinning are offset by the overall decrease in marketable timber. However, thinning operations in this part of Britain are also designed to keep the crop alive, to avoid unmanageable volumes of timber being sent to saw mills and to maintain shelter for other understorey species (T. Jennings, personal communication 2015). Similar operational trials are being conducted on *P. contorta* and *P. sylvestris* stands in Scotland. In north western, British Columbia thinning and pruning may have slowed the disease to some extent in some areas, but, in general, on sites where environmental conditions are very favourable for disease, tree stocking or species composition did not affect disease development (A. Woods, personal communication).

3.2.3 | Silvicultural management – pruning

Pruning has much the same effect as thinning; airflow is increased and inoculum levels are reduced because the lower branches that are removed tend to be the most heavily infected. In unthinned, unpruned stands of the long-needed *P. nigra* subsp. *laricio*, many infected needles that have fallen from higher up in the crown are intercepted, which then act as a further source of inoculum (Mullett, Peace et al., 2016). Pruned foliage is generally left in situ but needles on the ground are rapidly colonized by other fungi (Gadgil, 1970; Gibson et al., 1964; Mullett, Tubby et al., 2016), so the inoculum available to infect foliage on the tree is reduced through competition. The distance from pruned branches on the ground to attached branches is such that few conidia will reach the foliage on the tree (Gadgil, 1970).

In New Zealand, pruning can delay the need to spray by several seasons (Bulman et al., 2004). A 6-year trial confirmed that pruning

reduced disease severity in a *P. radiata* plantation for up to 2 years (Bulman, 1997) and Van der Pas et al. (1984), also working in New Zealand, showed that pruning suppressed disease levels for at least one season. In Australia, pruning reduced disease severity on 7-year-old *P. radiata* trees at the edge of a stand, but had less effect on trees within the stand (Marks & Smith, 1987). They concluded that control by pruning, spacing and thinning is worthwhile. In the southern part of Chile (around Valdivia Province), where the highest disease levels are frequently observed, *P. radiata* is planted at about 1,250 stems ha⁻¹ with an early pruning when 5 years old, to 2.1 metres high, if disease levels exceed 60% (R. Ahumada, personal communication). This is the only known example of pruning being initiated specifically to remove infected branches.

Disease severity was not reduced by thinning and pruning in two studies. Hood and Ramsden (1996) found that effects of thinning and pruning treatments decreased with time, and they could not demonstrate a treatment response after 2 years in a trial of 5-year-old *P. radiata* in Queensland, Australia. In the central North Island of New Zealand, a trial to examine the effect of pruning and tree density showed no difference in disease levels between plots stocked at 830 stems ha⁻¹ and plots at 430 stems ha⁻¹ at age 8 years (Bulman et al., 2013). Both trials used small treatment blocks of less than 0.2 ha, and it is probable that the area was too small to affect airflow or reduce inoculum and disease levels. Crown closure had not occurred in the high stocking treatment so possibly tree density in both treatments was too low to show an effect.

3.2.4 | Shade

The severity of DNB is known to increase with increasing light intensity (Gadgil & Holden, 1976; Gibson, Kennedy, & Dedan, 1967; Ivory, 1970). Field observations in the Kenya Highlands showed that DNB severity was low on individual *P. radiata* growing in shade compared with severely diseased neighbouring unshaded trees. Experiments comparing disease severity on 1-year-old seedlings growing under artificial shade or in the open confirmed that shade suppressed disease. The effect was attributed to reduced sporulation on infected tissues under shade. However, height of the shaded trees was also seriously reduced, making this form of control economically unviable (Gibson et al., 1967). The experiment in Kenya did not measure light intensity. It involved small seedlings growing in artificial conditions, and results should not be compared with the thinning trials described above. The effect of interactions between light intensity, inoculum pressure, stand densities and tree age on disease development on individual trees has not been studied.

3.2.5 | Fertilizers

Trees growing under stressful conditions have reduced ability to prevent the growth of pathogens within their tissues (Schoeneweiss, 1975, 1981). Thus, DNB severity may be greater in forests established on nutrient-deficient soils. The application of fertilizer to control DNB in *P. radiata* plantations has been tested in a number of studies, but

has either had only short-lived success, no effect or was even detrimental. For example, Lambert (1986) tested the effect of sulphur and nitrogen on DNB severity in New South Wales, Australia. Nitrogen fertilizer resulted in high arginine concentrations in the needles due to sulphur (and phosphorus) deficiencies and led to higher disease severity compared with the control or sulphur fertilizer treatments 2 years after application. In British Columbia, repeated applications of nitrogen fertilizer were also associated with increased DNB incidence and severity (R. Brockley, personal communication). Eldridge, Turner, and Lambert (1981) found disease was most severe in plantations on sulphur-deficient basalt soils in New South Wales. In Chile, Contreras (1988) found that triple superphosphate, boronatrocalcite, potassium nitrate and magnesium sulphate applied in a single treatment at planting did not affect DNB during later stages of growth. In New Zealand, two heavy applications of NPK plus Mg, and Mg alone, were applied in June 1965. In February 1966, disease severity in the treated plots was about 15% lower than in controls, but only 4 months later, in June 1966, mean defoliation was 40% in all treatments (Gilmour, 1967). Overall, it appears that stands with inadequate sulphur, either from naturally low sulphur soils or from excessive nitrogen fertilization, are more susceptible to DNB and addition of fertilizer will not reduce disease levels.

3.2.6 | Breeding for increased disease resistance

Deployment of tree species, varieties or clones that are resistant to *Dothistroma* spp. offers a socially acceptable and potentially long-term control option. The reader is referred to other reviews in this issue for more information on differences in susceptibility between host species (Drenkhan et al., 2016) and potential mechanisms of resistance (Fraser, Martín-García et al., 2016). Here, we summarize research on selection for resistance to *Dothistroma* spp. undertaken in a number of countries over many years. We use the term "resistance" to imply quantitative resistance or tolerance, as complete resistance is probably an unattainable goal. Variation in susceptibility to *Dothistroma* spp. exists within and between pine species, and this trait has moderate heritability (h^2 ca. 0.3) (Ivcović et al., 2010; Kennedy, Yanchuk, Stackpole, & Jefferson, 2014). Selection for resistance started with *P. radiata* in Africa in 1963 (Paterson, 1966) and showed initial success. In a subsequent report, however, Paterson (1968) highlighted the difficulties in selecting for improved resistance, with only 216 such trees (one in 69,000) identified after a 5-year search of 10,000 ha of plantation forests in East Africa. Later, Ivory and Paterson (1969) demonstrated that it was possible to select resistant *P. radiata* based on phenotype and this was transmissible; scions from trees selected for resistance had a greater degree of resistance than scions from non-selected trees. Resistant trees were more vigorous than randomly selected trees, but trees selected for vigour were not more resistant. Less than 20% of the progeny from trees selected for vigour were found to possess enhanced resistance.

In the USA, attempts to identify resistant species and varieties started in the late 1960s. Selection trials with 8-month to 2-year-old potted seedlings placed in an infected *P. radiata* stand in California

showed that *P. muricata* was apparently resistant, while Guadalupe Island and Cedros Island *P. radiata* had intermediate resistance and could be suitable for hybridization with the more susceptible mainland *P. radiata* (Cobb & Libby, 1968). Libby, Bannister, and Linhart (1968) also showed in preliminary tests that pines from Guadalupe and Cedros islands were much less susceptible to *Dothistroma* spp. than mainland populations and were of high value in a breeding programme. Despite being more susceptible, Año Nuevo *P. radiata* provenance was the main source of genetic material in Spain (Aragonés, Barrena, Espinel, Herrán, & Ritter, 1997) and most selection and breeding was within existing landrace plantations derived from Año Nuevo and Monterey sources in Australia and New Zealand (Burdon, 2001).

Resistance varied greatly between individual trees in 30- to 32-year-old plantations of *P. nigra* and *P. ponderosa* in Nebraska, with some trees remaining free of disease symptoms (Peterson, 1967). The *P. nigra* clones used as Hungarian elite propagation material were evaluated for resistance in 1996 and showed considerable differences in susceptibility to *Dothistroma* spp. (Koltay, 1999). In New Zealand, 66 phenotypically "resistant" trees were selected from plantations with severe DNB in 1966. When clonally propagated, cuttings from 21 of these retained resistance, but only five had acceptable growth, branching and stem straightness. In another study, large variation in resistance was found in hedged clonal archives. Resistance was shown to be a moderately heritable trait (Wilcox, 1982), and Carson (1989) identified DNB resistant families with moderately high heritabilities from all assessments on *P. radiata* in nine progeny trials from 2 to 10 years old.

Estimates of benefits from deployment of DNB resistant lines vary. Dick (1989) predicted that if a DNB resistant line provided a 15% decrease in average stand infection then spray costs would reduce by 56%. However, there was uncertainty as to whether this would provide gains in yield. Carson, Dick, and West (1991) calculated genetic gain to be about 11–12% and suggested that the actual disease reduction with disease resistant stock may be greater because of the epidemiological effect which would occur when all trees in a stand have improved resistance. However, more recent work suggested gain may not be as high as previously thought (H. Dungey, personal communication); this study demonstrated that DNB resistance was moderately heritable and well correlated across three sites tested, but the maximum predicted gain from selection was around 9%, which dropped to 6–7% with inbreeding constraints.

3.2.7 | Deployment of cuttings

There is a suggestion that cuttings are less susceptible to DNB than seedlings. A clonal stand in Zimbabwe propagated from a single 7-year-old tree showed complete resistance to DNB at 21 months, whereas seedlings planted nearby were severely diseased after the same period (Barnes, 1970). Garcia and Kummerow (1970) assessed 10-month-old seedlings that were grafted with scions taken from 5-, 10-, 15- and 25-year-old trees and artificially inoculated with *Dothistroma*. Disease decreased with increasing age of the trees that provided the scions. In Australia, Ades and Simpson (1990) compared

juvenile cuttings with seedlings, and 6 years after planting mean disease severity of the cuttings was 21% compared with 30% for seedlings. This difference was attributed to the greater maturation age of the cuttings. They estimated that selection of the best 10% of clones could have reduced disease to 12%, making other disease control measures unnecessary. Increasing resistance to DNB with increasing host age has been well documented for *P. radiata*, but less so for other *Pinus* spp. (Fraser, Martín-García et al., 2016). Changes to *P. radiata* needle morphology with age, that is smaller stomata, increase in stomatal wax occlusion (Franich, Gadgil, & Shain, 1983) and to physical characteristics of the tree, such as natural lower crown loss due to suppression, may increase DNB resistance. Increased physiological age of cuttings may in part explain the observations that *P. radiata* cuttings are less susceptible.

3.3 | Biological control

Fungal and bacterial agents have been screened for antagonistic activity towards *D. septosporum*. Some *Trichoderma* and *Bacillus* species were shown to kill *D. septosporum* or inhibit its growth in vitro (McDougal, Schwelm, & Bradshaw, 2011), indicating potential as biocontrol agents for DNB. A strain of the bacterium *Aneurinibacillus migulanus* reduced DNB severity from 6% to 1% and also lowered conidial abundance and germination when artificially inoculated into 2-year-old *P. contorta* trees (Alenezi et al., 2016). Ridout and Newcombe (2015) carried out inoculations on *P. ponderosa* in Idaho, USA, with six fungi that naturally occur on hosts infected by *Dothistroma* spp. They found that five of the six fungi increased disease severity and one reduced disease. Although there is considerably more research to be performed, biocontrol has shown some potential for management of other foliar forest diseases. A mixture of endophytic fungi conferred resistance to white pine blister rust in *Pinus monticola* (Ganley, Sniezko, & Newcombe, 2008). The complexity of endophytic species residing naturally in pine needles (Ganley, Brunsfeld, & Newcombe, 2004) make this a difficult field of research but one that shows potential as an additional tool to manage foliar diseases such as DNB. Russulaceae ectomycorrhizae also had an antagonistic effect in vitro against *D. septosporum* in Chile (Garrido et al., 1982). The frequency and extent of disease modification by non-pathogen symbionts in forest systems may have significant implications for DNB management, not only for application in biocontrol, but also for understanding the biotic drivers of disease severity both within and outside the native range of pathogens and their hosts. Investigating microbial modification of DNB severity in both its native and introduced ranges might provide insights leading to better control and management of the pathogen (Ridout & Newcombe, 2015). Fraser, Martín-García et al. (2016) provides further discussion on the effect of endophytes, mycorrhizae and other agents on DNB severity.

3.4 | Chemical control

Chemical control of DNB has been shown to be effective in several countries with extensive research having been carried out since the

1950s. The first trials showed that three to five applications of copper as a Bordeaux mixture in summer gave the most effective control of DNB on *P. nigra* in the United States (Thomas & Lindberg, 1954). Similar success with copper compounds was reported by Peterson (1967) who found two hand-sprayed applications three to six weeks apart gave almost complete disease control for one growing season. In Georgia, three hand-sprayed applications of 1% Bordeaux mixture, 20 days apart, reduced infection levels from 83% (unsprayed controls) to 33% in *Pinus brutia* var. *pityusa* (Shishkina & Tsanova, 1966). Further research demonstrated that copper acted against the pathogen in two ways. Firstly, copper deposits on conifer needles are slowly dissolved in water, distributing copper ions over the needle surface. This kills spores released during periods of rain and protects the foliage from new infection (Franich, 1988). Secondly, copper stops fruiting bodies producing and releasing spores. The second action appears to be the most significant for disease control (Bulman et al., 2013).

In response to increasing DNB severity on *P. radiata* in East Africa and the African Central Highlands in the 1960s, extensive screening of a number of systemic and contact fungicides applied by hand sprayers, mist sprayers or fixed-wing aircraft was carried out by Gibson et al. (1964, 1966), Etheridge (1965) and Hocking (1967). Aerial spray trials in Kenya demonstrated that copper fungicides had the potential to provide economically beneficial control of DNB (Gibson et al., 1966). These early trials were followed by laboratory and field tests of 38 fungicides (Hocking, 1967) where triphenyl tin and copper compounds gave good protection, with two ground-based applications per year for areas with heavy rainfall. Gibson (1971) recommended aerial spraying for East Africa after showing that young *P. radiata* were protected by light copper fungicide application. Copper at 4 kg ha^{-1} applied in two operations annually was economically justified (Gibson, 1972). However, by 1974, it was concluded that while control was beneficial in New Zealand, aerial application was inefficient and impractical in Africa, primarily because fixed-wing aircraft at that time was not capable of carrying large payloads at high altitude and the topography made spraying close to ground level difficult and dangerous (Gibson, 1974).

Trials in New Zealand (Gilmour, 1965) led to the first operational spraying in the summer of 1965–1966 (Olsen, 1971). An analysis of the spray programme from 1966 to 1973 found that only 10.6% of 13,560 ha sprayed in one large plantation required a second spray seven years later and concluded that one or two applications per 30-year rotation may be sufficient to control the disease (Gilmour, Leggat, & Fitzpatrick, 1973). Woollons and Hayward (1984) demonstrated that the application of copper oxychloride (50% copper active ingredient) at an application rate of 4.16 kg ha^{-1} in 50 L of water significantly decreased mortality and increased increment, but Van der Pas et al. (1984), and Alzamora et al. (2004) in Chile, could not demonstrate growth response to spraying in other trials undertaken in thinned stands. Late spring, just before the start of the infection cycle, was found to be the optimum time to spray (Bulman et al., 2004).

Current practice in New Zealand is to use helicopters for applying copper fungicide from the air. Advances in spray technology allowed the rate of copper and carrier to be reduced from 2.08 kg ha^{-1} active

ingredient in 50 L ha^{-1} of water to 0.855 kg ha^{-1} active ingredient in 2 L of oil made up to 5 L ha^{-1} with water (Bulman et al., 2004). Trials established in 2009 indicate that the spray volume can be further reduced to 3 L ha^{-1} without any loss of efficacy (Bulman, 1997). An annual disease survey carried out from the air in winter is used to determine whether spraying is needed or not. Stands are usually sprayed when average disease severity reaches 20%, but the trigger level varies between companies, based on their appetite for risk. In Australia, copper is applied most years, but to only a very small area of *P. radiata* grown there, generally 2000–3000 ha in wetter parts of New South Wales or South Australia.

In Europe, aerial application of a systemic benzimidazole fungicide suppressed DNB in plantations of *P. nigra* on Mt. Suvobor (2006–2007) and Subotica sand (2007) in Serbia. Treatments were performed during the main sporulation periods of May and June and gave good disease suppression (Golubović-Ćurguz, Karadžić, Gvozdić, Milenković, & Radojičić-Antić, 2013; Pap et al., 2009). In Hungary, copper fungicides were applied to 12-year-old *P. nigra* in late spring and again one month later using a ground-based sprayer. Systemic active substances used alone (70% thiophanate-methyl at 1 kg ha^{-1} and chloroethanol 50% at 3 L ha^{-1}) were less effective than copper. The copper products lowered disease severity from 71% in the untreated controls to less than 4%, but at least two treatments were required to reduce the risk of secondary infection (Koltay, 2001; Koltay, Tóth, Kondár, & Szabó, 2009). While the results from Hungary showed that chemical control is effective against DNB in *P. nigra*, it is necessary to determine accurate treatment costs and overall economic gains to decide on best practice. For example, considering that *P. nigra* stands are found in large blocks in Hungary, aerial application would be more economical than ground-spraying. However, a number of mainland European countries currently practice chemical control only in forest nurseries (Table 1, ESFA, 2013), often because chemical use in forests is considered uneconomic and sometimes prohibited or discouraged. The European Union is encouraging cost-effective and environmentally friendly methods to minimize the use of chemicals, that is Directive 2009/128/EC (2009): Establishing a framework for community action to achieve the sustainable use of pesticides. Of the 23 countries listed in Table 1, 13 carry out chemical control in nurseries. Only New Zealand and Australia routinely practice chemical control in forests. None of the countries that list DNB as a medium impact disease use chemicals for the control of DNB in forests.

In Britain, where DNB is listed as having a major impact (Table 1), a number of fungicides are used widely in tree nurseries, but not in forests, partly because of cost, but also because of political pressure to reduce chemical use. The UK Forestry Standard (Forestry Commission, 2011) states that the use of artificial pesticides and fertilizers is generally a last resort in practising sustainable forestry and use on special sites such as ancient woodland is particularly discouraged. However, the standard does recognize that use may be necessary under some circumstances. Recently, the ultra-low-volume “Micronair” application technology used in New Zealand has been used to apply copper oxychloride to stands of *P. sylvestris* at a rate of 1.66 kg ha^{-1} in 5 L of water/oil carrier in experimental trials. These applications were



FIGURE 1 Aerial copper spray and silviculture trial in Valdivia, Chile. (a) pruning with copper, (b) pruning with no copper, (c) no pruning with copper, (d) no pruning and no copper

politically very sensitive and high profile, necessitating extensive public liaison and environmental monitoring pre- and post-application. Trials are ongoing to demonstrate proof of concept, establish working protocols and to determine efficacy.

Until recently, aerial copper fungicides were routinely applied to about 10,000 hectares of *P. radiata* plantations in Chile on an annual basis, from the south province of Arauco to the province of Valdivia. Since 2013, DNB has been managed by silviculture and deployment of *P. radiata* lines that have some resistance to DNB (R. Ahumada, personal communication). While copper spray provided the best control, pruned unsprayed stands had less disease than unpruned unsprayed stands (Fig. 1). The change of practice was mainly due to environmental regulations and FSC restrictions.

4 | FUTURE PERSPECTIVES

4.1 | How might disease risk change in the future?

4.1.1 | Evolution of the pathogen

An important consideration for future DNB control and management is the spread and evolution of the pathogens involved. There is a risk, for example, that the DNB pathogens will develop resistance to the current chemical control products used or, as a result of changes in pesticide legislation and economic and environmental issues, that effective products might be prohibited. The capacity of *Dothistroma* spp. to evolve traits that directly increase virulence is also a concern, particularly in countries where both mating types are known to occur (Drenkhan et al., 2016). Furthermore, in those regions where only one mating type is present, the risk of an introduction of the other mating

type is high as a result of plant trade (Eschen, Roques, & Santini, 2015). These risks are being assessed using increasingly sophisticated molecular techniques which help researchers gain a better understanding of both the population biology and the molecular basis of virulence in *D. septosporum* (Barnes et al., 2014; Bradshaw et al., 2016; Kabir, Ganley, & Bradshaw, 2015).

4.1.2 | Climate change

As outlined in the review by Drenkhan et al. (2016), the known distribution of DNB has increased over the last two decades. In the review by Woods et al. (2016), it is suggested that this increase may, in part, be related to climate change. CLIMEX modelling of future climate trends suggests that the DNB pathogens could extend their range and pose a threat to even more parts of the world (Watt et al., 2009), a pattern already demonstrated for other invasive and native forest pathogens including *Phytophthora cinnamomi* on *Castanea* and *Quercus* spp., *Biscogniauxia mediterranea* on *Quercus suber* and *Cryphonectria parasitica* on *Castanea* spp. (Desprez-Loustau et al., 2007, 2010; La Porta et al., 2008).

In future, the changing climate might not only affect the behaviour and potential range of *Dothistroma* spp. and many other pests and pathogens, but may also affect the ability of many tree species to thrive in their current range (Anderegg, Kane, & Anderegg, 2013; Ray et al., 2010). The effect of climate change may be positive, negative or neutral, depending on the host-pathogen interaction (Luck et al., 2011). If the expected changes outstrip the ability of local tree populations to adapt, a permanent increase in tree stress, with consequent impacts on susceptibility to pest and diseases, may result. A large body of literature links physiological stress with reduced ability to resist necrotrophic or opportunistic organisms (e.g. reviewed by Kliejunas

et al., 2009), and there is no reason to suspect that this will be different for the hosts of the DNB pathogens. Stress induced by changes in climate could even widen the range of species on which DNB becomes a problem, especially if the climate becomes more suitable for both *Dothistroma* spp. in the same region. It is important to note that even if climate change is beneficial for host trees, those conditions may be even more favourable for the pathogen (Woods et al., 2005). In a study comparing pine plantation management systems in New Zealand and Scotland, a forecast into the 2080s showed that DNB associated with a climate change effect could cause a large reduction in recoverable volume of *P. radiata* and resulting economic loss (Meason & Mason, 2014).

4.2 | What are key options for improved disease management in the future?

4.2.1 | Exploration of new species/provenances

Adoption of new plantation species or provenances will make an important contribution to the management of DNB. A key and potentially very effective option for future DNB control is the judicious choice of planting stock, although DNB resistance/tolerance is not the only factor to consider. In many countries, the forest industry is having to consider alternative tree provenance/species because of climate change effects. The experience with DNB emphasizes the importance of developing integrated mitigation strategies that include a consideration of disease susceptibility as well as silvicultural and climatic “preferences” of such alternative species. For example, initial recommendations for the south of Britain considered *P. nigra* subsp. *laricio* to be one of the most promising candidates to thrive in an increasingly arid climate (Ray et al., 2010), but this was later reversed given the extremely severe impact of DNB.

Any exploration of new provenances and species brings with it the consideration of where to source such stock. Large-scale movement of plant material within and between countries is common. *Dothistroma* spp. may spread long distances via natural means, but the plant trade has also had a very significant role in dissemination (Barnes et al., 2014; EFSA, 2013). A DNB outbreak in England in the 1980s can be traced back to *P. contorta* and *P. nigra* subsp. *laricio* planting stock from a nursery where infection had been found in the 1950s (Murray & Batko, 1962; M. S. Mullett personal communication). Similarly, spread of DNB in Europe (Bednářová, Palovčíková, & Jankovský, 2006) and New Zealand (Bulman et al., 2013) was attributed to movement of nursery stock. The rise in global plant trade has been cited as one of the most significant biosecurity threats of modern times (Santini et al., 2013). Ultimately, such movement provides opportunities for recombination, either through mating or interspecific hybridization, allowing pathogens to adapt to new hosts and new environments. The extent to which such adaptation could occur in *Dothistroma* spp., and the resultant effects thereof, are unknown. The current legislation on plant movement exists to minimize this threat, but there are large differences in countries' approaches (Eschen et al., 2015) and policies can prove ineffective (e.g. Brasier, 2008). A thorough revision of current

legislation is needed, not only from an ecological point of view, but also for economic reasons (Epanchin-Niell & Liebhold, 2015; Keller & Springborn, 2014). At the very least, there needs to be greater clarity over the origin of plants for planting to enable regulators and customers to make informed choices on consequent risk of exposure to new pest and pathogen species and genotypes.

4.2.2 | Breeding for increased resistance

Desirable traits such as resistance can be identified and incorporated into breeding programmes. As outlined earlier, breeding for DNB resistance has been successful in a number of countries and may reduce disease levels by 10–15%. Resistance to DNB is polygenic and moderately heritable (Carson, 1989; Ivčović et al., 2010), and it makes sense for breeders to have selected for it. Single-gene resistance may be considered more risky for tree crops compared with annual agricultural crops, where the former have to contend with pathogen pressure for a long time before reaching harvest age. A screening programme to evaluate clonal material resistant to *D. septosporum* started in Chile in 2015 (R. Ahumada, personal communication). Future efforts in breeding for improved resistance are likely to be informed by molecular studies and genomic selection, rather than traditional phenotypic selection, which is time-consuming and expensive. Gains could be realized by molecular technologies such as genetic engineering, although there are considerable scientific and social challenges involved. As reviewed by Fraser, Martín-García et al. (2016), the mechanisms of resistance to DNB are complex, not well understood and are also influenced by other heritable traits and external abiotic and biotic factors. The genome sequence of *D. septosporum* revealed the presence of effectors that are recognized by immune receptors from tomato (De Wit et al., 2012) and this fuelled current research on molecular host–pathogen interactions in the *Dothistroma-Pinus* pathosystem (Bradshaw et al., 2016). However, genomic studies of the Pinaceae hosts are in their infancy due to their immense size, with the first pine genome only recently published (Zimin et al., 2014). Groups such as the Forest Stewardship Council are at present inhibiting adoption of genetic engineering, but the next decade is anticipated to bring considerable advances in the applications of molecular technologies to forest health and increased acceptance thereof.

4.2.3 | Forest diversification

As well as alternative species or improved breeds for forest planting, it is important to consider forest diversity. Forest management globally has tended towards simplification, despite warnings about the risks of creating monocultures or, at the most extreme level, clonal forests (e.g. Ennos, 2015; Woods et al., 2005). Reduced species diversity may create a greater risk compared with mixed-species stands (Pawson et al., 2013) and, combined with suitable climate, is probably a key driver in the development of some recent epidemics. The role of species diversity on DNB outbreaks was reported in British Columbia (Woods, 2003). Increasing planting distance between *P. contorta* trees through mixed-species plantations and overall reduction in use of this species for

regeneration in wet areas of British Columbia are the best strategies to reduce DNB and enhance future productivity (Boateng & Lewis, 2015). Other examples include white pine blister rust (*Cronartium ribicola*) on five-needle *Pinus* species in Europe and North America and fomes root and butt rot (*Heterobasidion annosum*) in *Pinus* and *Picea* species (Korhonen & Stenlid, 1998). Ennos (2015) alludes to a holistic approach to pest management that is premised by avoiding environmental conditions that favour disease development, including host stress and a narrow genetic pool. Although species mixtures in commercial forestry may be considered uneconomic, diversity at the species or even genetic level at a landscape scale might be feasible and beneficial (Felton et al., 2016; Jactel et al., 2009; Pautasso, Holdenrieder, & Stenlid, 2005; Wingfield, Brockerhoff, Wingfield, & Slippers, 2015).

4.2.4 | An integrated global perspective is paramount for future forest health

Initiatives aimed at ensuring that traded plant material is pest and pathogen-free include the European Food Safety Authority risk assessment relating specifically to *D. septosporum* (EFSA, 2013), biosecurity guidance in the 1951 International Plant Protection Convention of the FAO and the World Trade Organisation's Sanitary and Phytosanitary Standards Agreement. Such initiatives face a huge challenge with the year-on-year increase in the movement of plants that has resulted in increasing numbers of biosecurity threats to countries previously declared pest-free (Brasier, 2008; Roy et al., 2014; Santini et al., 2013; Tubby & Webber, 2010).

Wingfield et al. (2015) stated that globalization has sped up the emergence of new pests in plantation forests, and these forests are now under threat. The same can be said for natural forests, and the current DNB situation is an example of a forest health issue that affects both plantation and natural pine forests worldwide (Drenkhan et al., 2016). At a national scale, DNB can be managed by deployment of a variety of management tools, but, in hindsight, it could have been better managed by avoiding its spread to New Zealand, Chile, UK and other countries. For that to have happened, a will to limit movement of pests and pathogens was needed at the global scale, because countries were not able to exclude pests by their individual efforts. The formation of such global strategies is facilitated by collaborative programmes such as the EU COST Action FP1102 DIAROD (Determining Invasiveness and Risk of *Dothistroma*). The networks forged have helped facilitate accurate diagnosis of the pathogen and assessment of distributions and impact and opened up a toolkit of potential management options that can now be drawn on worldwide. Together we need to take heed of Brasier (2008), Wingfield et al. (2015) and many others, learn from the DNB experience and try to avoid devastating forest pathogen epidemics in future.

5 | RECOMMENDATIONS

There is no single control method for DNB that will be suitable, and at a global level, control is not necessary everywhere. Where DNB is

a problem, forest managers should make conditions less favourable for disease development by thinning and increasing host diversity and deploy lines with increased DNB resistance to mitigate DNB risk for susceptible hosts on low to medium risk sites. For high-risk sites, deployment of non-susceptible hosts is recommended. Copper sprays can control outbreaks if regulatory or social barriers can be dealt with.

Researchers need to focus on development of trees with desirable traits, including improved DNB resistance. New techniques available that speed up identification and adoption of those genotypes, such as genomic selection and genetic modification should be used. Regulators should strengthen legislation that helps shut down anthropogenic pathways that allow the movement of *Dothistroma*-infected material between countries. This needs to be performed in a unified manner at a global scale.

6 | CONCLUSIONS

Currently, in many countries where suitable hosts are grown, DNB does not reach levels that justify specific management strategies to control the disease. However, management and control measures are required in countries in which the disease is currently a serious problem, such as in New Zealand, the United Kingdom, Canada and some other European countries. As with many other damaging forest diseases, there is no single "silver bullet" for controlling DNB and a number of options have been adopted (Table 1). All management interventions come at a cost, not only in monetary terms (e.g. Dick, 1989; Van der Pas et al., 1984), but also in terms of political resistance or concern from environmental bodies. These factors must be weighed up against the final use of the crop, available markets and its estimated value.

Apart from avoiding the problem by planting species that are not susceptible to DNB, chemical control has been shown to be one of the most effective control measures available and has been adopted to control DNB and other diseases in nurseries in Europe and elsewhere. Nevertheless, it is rarely used in plantations, apart from those in New Zealand and Australia, a decision largely based on economics, along with social or political drivers. In some cases, thinning and/or pruning reduced disease levels and suppressed development for several seasons, but it seems that silvicultural management generally does not provide long-term control. However, in the UK, earlier and more frequent thinning has reduced mortality, perhaps more significantly in some areas, and may allow susceptible crops to be "salvaged" and carried through to commercial harvest. Fertilizer application and biological control using *Trichoderma* spp. or other antagonistic microorganisms have been attempted, but consistent reliable control has not yet been demonstrated.

The decision on whether or how to intervene to attempt to control DNB may have to be the result of extensive consultation between many different stakeholders at local, national and regional scales. Usually, DNB will be best managed by an array of strategies that suit the region and the current conditions in that region, as well as needs and circumstances of the manager or guardian of that forest.

Dothistroma needle blight is a disease that affects a large number of hosts over a large part of the world. It is an excellent example of a disease that could have been managed, at least in Southern Hemisphere pine plantations where DNB was not present, by allocating resources and promoting collaborative efforts aimed at avoiding the introduction of the pathogens. Pathogen exclusion is not easy but the best chance of succeeding with it is to collaborate at a global scale.

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