Date of Publication:
March 2016

Cunninghamia

A journal of plant ecology for eastern Australia

The Royal
Botanic Garden
Sydney

ISSN 0727-9620 (print) • ISSN 2200-405X (Online)

Dieback of *Nematolepis ovatifolia* (Rutaceae), an endemic shrub in the alpine- subalpine heaths of the Snowy Mountains, is facilitated by climate change.

K. Green

NSW National Parks and Wildlife Service, Snowy Mountains Region, Jindabyne, 2627 AUSTRALIA
kenneth.green@environment.nsw.gov.au

Abstract: The shrub *Nematolepis ovatifolia* (F. Muell.) Paul G. Wilson (family Rutaceae) is endemic to the alpine and subalpine areas of the Snowy Mountains, Australia, where it dominates large areas of heath. Mass dieback was observed in the spring/summer of 2012. Damage at first was confined to the tips of branches, a symptom that could be due to frost damage and/or pathogen-induced water stress. Subsequently, whole stems and shrubs died and new areas of chlorosis appeared on smaller shrubs. Surveys of 186 sites covering the geographical range of the shrub in the summers of 2013/14 and 2014/15 found that 59 populations were definitely dieback affected, 92 had early symptoms and 35 were healthy. Two possible causes were investigated: killing frost and pathogens, with insect attack being a further cause of defoliation.

The root rot pathogen, *Phytophthora cambivora* was isolated from one washed root sample and from one of five soil/root samples. In 2014/15, in five sites where symptomatic plants were monitored, most plants recovered to a condition where they were considered unaffected in March 2015. It is possible that symptomatic plants had in fact suffered frost damage. Hence populations with early symptoms were grouped with healthy populations for analysis of proximity to trails. Compared with these, dieback affected populations were significantly closer to trails. It could not be determined when the pathogen was introduced, as it could have been imported on earthmoving equipment or by subsequent users of trails. It was apparently well spread before spring of 2012 but infection of plants was not evident. Its sudden eruption in spring of 2012 may have been facilitated by two warm and wet La Nina years, with mean growing season soil temperature up to 1.5°C higher than the long term mean and growing season rainfall double the long term mean. Plant death occurred in the hottest year on record in Australia, with the average alpine treeline growing season soil temperature of 9.2°C in 2012/13 being >2.0°C above the long term mean.

Cunninghamia (2016) 16: 1–9
doi:10.7751/cunninghamia.2016.16.001

Introduction

Shrubs and grasslands alternate in cycles throughout the Australian Alps, with senescence of shrubs and colonization by grasses being recorded from the alpine zone in the Snowy Mountains (Costin 1959) and in the subalpine zone in the Victorian Alps (Williams and Ashton1988). Generally large-scale shrub death in mountain areas is uncommon apart from large-scale senescence where shrubs are of a similar age after mass recruitment post-fire or in the aftermath of removal of grazing (Clarke *et al.* 2015). The most commonly recorded dieback in high mountains in Australia is insect related, for example defoliation of large areas of alpine grasslands in the Snowy Mountains by swiftmoths (Green & Osborne 2012). There have been few incidences reported from overseas, with more attention being focused on large areas of subalpine forests being killed by beetles, (*Dendroctonus* spp.) and their microbial associates with the elevational range of infestation increasing into the alpine treeline ecotone (Raffa *et al.* 2012; Donato 2013). Substantial dieback of native shrubs occurred in Barrington Tops in northern New South Wales due to an exotic pathogen, the soil-borne water mould *Phytophthora cinnamomi* (McDougall *et al.* 2003). Previously *Phytophthora cinnamomi* in the area had only been found at elevations below 800 m; its presence at 1560 m elevation was a cause of considerable concern for National Park management (NPWS 2015).

Causes of large-scale shrub death are not only biotic. Frosts have resulted in extensive damage to shrubs in the Snowy Mountains, particularly in years with shallow snow cover combined with very low minimum temperatures. At Kiandra in 1982 overnight temperatures fell to below –10 °C on eight nights with the coldest being –21.5°C. The shrub *Bossiaea foliosa* was killed and the cover of tall shrubs was reduced by 32% with no resprouting (Leigh *et al.* 1987). In the same year, at higher elevations where plants were usually afforded some protection from mid-winter frosts by snow cover, the frosts accompanied the shallowest recorded snow to that date in the Snowy Mountains with widespread damage to vegetation. Shrub genera including *Nematolepis*, *Tasmannia* and *Podocarpus* were affected and also the tree *Eucalyptus niphophila* (Green & Osborne 1994). Leigh *et al.* (1987) suggested that a frost as harmful as the one in 1982 would be a one in 50 year event. In summer of 2012-2013 another mass die off of shrubs was recorded, this time mainly affecting a single species.

Ovate Phebalium, *Nematolepis ovatifolia* (F.Muell.) Paul G.Wilson (previously *Phebalium ovatifolium*) (family Rutaceae) is a Snowy Mountains endemic shrub (Doherty *et al.* 2015), one of 21 species endemic to this region (Costin *et al.* 2000). Mass dieback in *Nematolepis ovatifolia* across the Snowy Mountains appeared in the spring of 2012. The damage, at first, was confined to tips of branches of taller shrubs. This resembled damage noted in spring 1982 (see Green & Osborne 2012-page 48). However, as summer 2012/13 progressed, whole stems and shrubs subsequently died and new areas of chlorosis appeared on both smaller shrubs and previously unaffected tall shrubs, with large areas of the shrub becoming chlorotic and then turning a chestnut brown before dying (Fig. 1). In spring/summer 2013/14 there was a recurrence of the dieback with the early symptoms, those confined to the tips of branches, appearing across the entire geographical range of *Nematolepis ovatifolia* in the central portion of Kosciuszko National Park.

At first, damage was confined to the tips of branches suggested that killing frost could explain the die off. However, as the damage spread from the tips of branches to engulf whole shrubs, pathogens were also suspected. At the same time, shrubs over large areas in the north of Kosciuszko National Park were being defoliated and dying from insect attack (McDougall *et al.* 2015). To determine the cause of the *Nematolepis* dieback, three possible agents were investigated: killing frost, pathogens and insect attack. To assess the extent and possible causes of the dieback of *Nematolepis ovatifolia* data were collected on (1) the geographic extent and condition of populations of *Nematolepis ovatifolia*, (2) climatic conditions in the alpine/subalpine area including frosts, (3) soil pathogens and treatment, and (4) insect damage.

Figure 1. Part of a patch of *Nematolepis ovatifolia* at the alpine treeline in summer 2012/13 where 676 mainly mature shrubs suffered from dieback, showing the stages of infection from normal green to chlorotic, yellow, brown and defoliated.

Methods

Geographic extent of Nematolepis ovatifolia

The geographic range of *Nematolepis ovatifolia* was initially obtained from online records from the Australian National Herbarium (2015), the collection of the National Herbarium of New South Wales (2015) and the Office of Environment and Heritage Atlas of NSW Wildlife (2015), together with specimen vouchers from the Kosciuszko National Park Herbarium. This was then followed up by a field survey aimed to encompass the entire range of *Nematolepis ovatifolia* based on these herbarium records as the core distribution (Fig. 2). The range of *Nematolepis ovatifolia* was traversed in summer 2013/14 and 2014/15 and populations were assessed as affected (chlorosis or death of leaves over entire branches), symptomatic (chlorosis or death of leaves at the tips of branches) and unaffected. The search for the limits of populations of *Nematolepis ovatifolia* included a vehicle traverse of all adjacent fire-trails to the west and along the northern boundary with the eastern distribution undertaken on foot as was the high level western distribution and the area south of the Thredbo River (Fig. 2). Population locations were recorded on a hand-held Global Positioning System (GPS) unit, and the distance to the nearest fire trail, access track or road for each population was calculated in Arc GIS (Esri ArcMap 10.1). To determine if affected populations were closer to trails or roads, the distances to trails (log transformed) were compared between affected populations and symptomatic/unaffected populations using a Student's t test. Other environmental factors recorded included position on slope and presence of other dead or dying plant species.

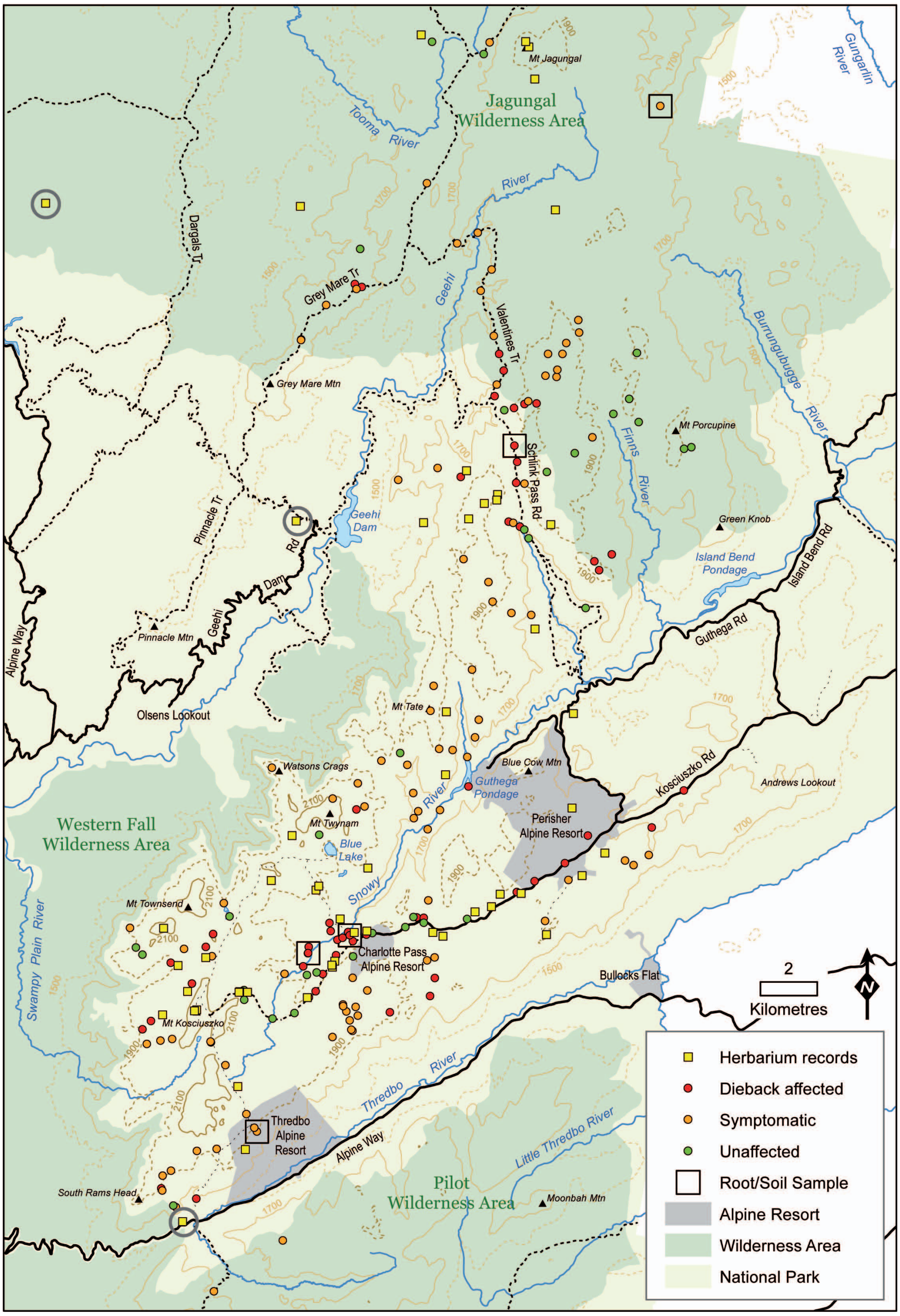

Figure 2. Map of the extent of *Nematolepis ovatifolia* from online herbarium records (three erroneous records circled) and 186 locations assessed either as unaffected, those with apparent early symptoms of dieback, and those seriously affected by dieback in the summers of 2013/14 and 2014/15. Locations where populations were sampled for *Phytophthora cambivora* are boxed. *Phytophthora* was actually confirmed through baiting results at the sites at Charlotte Pass and Thredbo.

Climatic and microclimatic data

To examine the thermal conditions in both air and soil in the period up to and including the death of plants, temperature data were collected from a number of loggers used in other studies. Air temperature data came from a Tinytag Plus temperature logger (Gemini Data Loggers, Chichester, England) recording at 60-minute intervals that was located in the Stevenson meteorological screen at Charlotte Pass. Soil temperature data were obtained from identical loggers at 10 cm depth in the soil at the alpine treeline ecotone on the lower slopes of Mt. Clarke, a permanently monitored site and a part of the international GLORIA network (A Global Observation Research Initiative in Alpine Environments).

To examine the potential exposure of plants to thermal conditions not buffered by snow cover, snow depth data were collected from long-term snow measuring sites associated with hydrological or vegetation monitoring. Snowpack depth data came from the Snowy Hydro snowcourse located at Spencers Creek and the Kostex site (Kosciuszko treeline experiment), where seedlings of *Eucalyptus niphophila* had been planted above the alpine treeline in March 2007.

To determine the potential for plants to project above the snow, plant heights were measured across a range of affected and unaffected populations of *Nematolepis ovatifolia* at elevations from 1720 m to 2020 m. In each population, shrubs were selected by throwing a pole into the population and measuring the height of the nearest 30 individuals.

Pathogens

To assess if plant pathogens were causing the dieback of *Nematolepis ovatifolia,* soil and root samples were collected and analysed. One lesioned root sample from a dying *Nematolepis ovatifolia* shrub exhibiting dieback symptoms was collected below Charlotte Pass in December 2012 and sent for testing to the Plant Disease Diagnostic Unit at the Royal Botanic Gardens Sydney and subsequently material was forwarded to the Centre of Phytophthora Science and Management diagnostic laboratory at Murdoch University for molecular confirmation of the identity of the pathogen. For confirmation of *Phytophthora cambivora* from baiting results, five more root samples with attached soil were collected from symptomatic plants throughout the range of the species in 2013 (Fig. 2), with a further 20 soil samples collected in 2014 (not shown). The five soil/root samples taken in 2013 were sent to Murdoch University for analysis and the 20 soil samples taken in 2014 were sent to the Royal Botanic Gardens Sydney.

Monitoring sites

At four populations along the Kosciuszko Road across four elevations 30 plants were monitored per elevation in one of a number of preliminary trials of a phosphite-based systemic fungicide (Aus-Phoz 600, Australian Agricultural Chemicals). Because nothing is known about side effects or toxicity of phosphite in Australian alpine vegetation and wetting agents might also be phytotoxic (Hardy *et al.* 2001) a precautionary approach was taken and phosphite and wetting agents were tested separately. In paired field trials, two shrubs of similar size and with similar symptoms in close proximity were randomly allocated to either treatment or control. 60 symptomatic shrubs were sprayed with 0.5% phosphite, with the paired nearby shrub being sprayed with tap water from a separate, clean spraypack. Shrubs were marked with flagging tape and each shrub photographed to record the symptoms. At the end of February 2015 the shrubs were resurveyed and the status of the plants recorded.

Plants with extensive damage were not used in the phosphite trial. To monitor seriously affected plants a population of *Nematolepis ovatifolia* at Whites River just west of the Schlinks Pass Road was assessed (Fig. 2). The site had 75 permanently marked points where vegetation regrowth was monitored annually from the fires of 2003. In December 2014 each site that contained *Nematolepis ovatifolia* was assessed for condition as above and re-assessed in March 2015.

Insect damage

Plants were searched for any evidence of insects, either larvae or silk. Shrubs known to be attacked by insects, mainly Asteraceae family were also investigated during the survey of the geographic range of *Nematolepis ovatifolia.*

Results

Geographic extent

The survey in the summers of 2013/14 and 2014/15 found *Nematolepis ovatifolia* at elevations from 1610 to 2140 metres. There were four erroneous herbarium records lower than this, one in Victoria and three circled in Figure 2. One was listed as “Thredbo Village” but could have been at the top of the chairlift rather than the bottom (a 575 m difference in elevation) because *Nematolepis ovatifolia* does not occur in the valley around Thredbo Village (pers. obs; Euan Diver pers. comm.). A second site marked just off the Geehi Dam Road actually gives a written description of “Windy Creek” which is the sampling site of the marked location due east of this, so it appears that the longitude was incorrectly entered on the voucher label. The third site is at low elevation to the north-west in rainforest conditions on the steep slopes falling away from the Dargals Trail and is likely to be wrong.

Of the 186 sites surveyed across the range limit of *Nematolepis ovatifolia* in 2013/14 and 2014/15, 59 populations were definitely affected, 92 were symptomatic and 35 were considered healthy (Fig. 2). There were 12 other plant species with death recorded, but only two of these were found dead in more than 10 sites: the shrubs *Orites lancifolia* (14 sites) and *Grevillea australis* (32 sites). Areas of affected plants commonly spread downhill from trails and along water courses.

Following heavy and continued rains through January 2015, some sites were re-assessed. Newly affected shrubs were only seen in locations such as Charlotte Pass where a high number of plants had already died. Elsewhere, apparent recovery had occurred in populations originally classified as having symptoms. Twigs that had previously held chlorotic or browned leaves had shed these leaves and other twigs or branches did not exhibit new symptoms. It appears that the populations with affected shrubs were correctly categorized as such, but some of those with suspicious symptoms in the 2013/14 survey would be considered unaffected in 2015. Hence for analysis the populations categorized as symptomatic and unaffected were combined into one group and the distance to the nearest trail was compared between these sites and the seriously affected sites. Affected populations were found to be significantly closer to the trails ($t = 2.65$, $df = 184$, $p < 0.01$) than unaffected populations and those with some early symptoms. The distribution of affected plants had two large centres, at Charlotte Pass and the Valentines Trail, with isolated areas radiating from there. There was overall a diminishing incidence northwards to the limit of *Nematolepis ovatifolia* just to the north-west of Mt Jagungal and also overall a diminishing incidence with elevation above the alpine treeline.

Insect damage

Lepidopteran larvae were frequently found in shelters of leaves bound together by silk at the tips of branches from shrubs of the family Asteraceae. Collections, from similar shelters at the tips of twigs of *Nematolepis ovatifolia* from the north-eastern extent of the range also found similar lepidopteran larvae at different developmental stages superficially resembling a Leaf Rolling Moth species from the family Tortricidae or Oecophoridae. (Thomas Wallenius pers. comm.). Large areas of insect defoliation of Asteraceae were commonly found during the survey of *Nematolepis ovatifolia*, however similar defoliation of *Nematolepis* was rare and confined only to just above the alpine treeline at Thredbo.

Killing frost

Snow depth at the Snowy-Hydro snowcourse at Spencers Creek did not exceed one metre until after the coldest period of the winter of 2012 and on 5 July the average depth was 85.3 cm. The average hourly temperature in the Stevenson Screen at Charlotte Pass (<2 km away to the south-west) for the period 5-7 July was -7.6ºC, with 6 July being the coldest day with an average temperature of <-10ºC, over the full 24 hours with the minimum temperature falling close to -17ºC. In spring 2012 at Spencers Creek there were 50+ symptomatic *Nematolepis ovatifolia*. Snowgums, *Eucalyptus niphophila*, also showed evidence of foliage death; mature tree canopies were unaffected as were seedlings, with most of the leaf die off on saplings in a band at or above about 75-80 cm. This height band of dead leaves on snowgum saplings was found at a number of sites throughout the spring.

Shrubs at the three highest elevations measured all averaged less than 70 cm in height and showed no evidence of leaf damage from this cold period (Fig. 3). On 4 July 2012 at the Kostex site, snow depth averaged 75.3 cm and the top leaves of *Eucalyptus niphophila* seedlings were exposed above the snow, but *Nematolepis ovatifolia* (average 62 cm height) were buried. On 28 December when the site was monitored, seedlings of *Eucalyptus niphophila* had dead leaves at a height of 65-70 cm but *Nematolepis ovatifolia* were unaffected. At a slightly lower elevation, and just within the treeline ecotone, shrubs averaged >73 cm in height and were badly affected. Below this, populations at the same elevations, two centred on 1720 m and two on 1750 m had affected and unaffected shrubs (Fig. 3).

Pathogens

Out of the 26 samples tested, *Phytophthora cambivora* (Petri) Buisman, (1927) was isolated from the one washed root sample with lesions from Charlotte Pass sampled in 2012, and one of the five root/soil samples (from Thredbo) in 2013. Laboratories were unable to isolate any *Phytophthora* species from the 20 soil samples taken in 2014.

Monitoring sites

Of the 120 plants monitored in the preliminary paired phosphite trials, 117 plants were re-located and 105 were assessed as having recovered regardless of whether they were in the control or treatment. Most monitored plants shed their affected leaves and no new leaves appeared to be affected. Of the 12 plants that continued to decline in health, 10 originally had advanced symptoms and only two plants proceeded from minor symptoms to major. Recovery of *Nematolepis ovatifolia* was also evident at the Whites River population. Of 74 plants recorded as either symptomatic or affected in December 2014, 28 were still assessed as affected in March 2015, 46 had recovered. Only three plants recorded as unaffected in December 2014 were recorded as affected in March 2015.

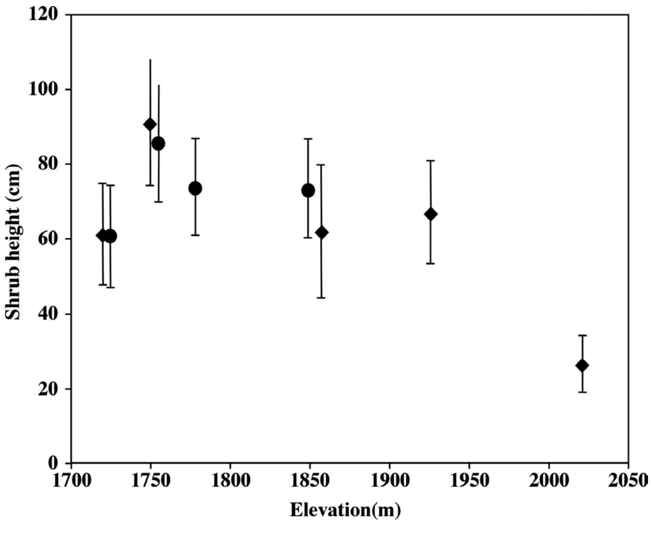

Figure 3. Shrub height ± SD of *Nematolepis ovatifolia* at locations with suspected frost damage (Circles) and without damage (Diamonds).

Discussion

Following the initial discovery of advanced dieback symptoms in shrubs, early symptoms of dieback were found across almost the entire range of *Nematolepis ovatifolia.* However, there appeared to be more than one agent responsible. Later, after a wet summer, most shrubs with suspicious symptoms in monitored sites were assessed as unaffected, whereas definitely affected shrubs proceeded towards complete death. For most shrubs in monitored sites the leaves on the affected tips were shed and the plants recovered with no hint of chlorosis. So the suspicious symptoms have not proven to be unequivocally due to *Phytophthora*, nor necessarily to lead to death. The suspicious symptoms could in some cases have been frost damage after shallow snow early in the winter season. Insect attack was noted on many shrubs, predominantly in the family Astercaeae but the same lepidopteran larvae were also collected from *Nematolepis ovatifolia.* Above and around Thredbo, large areas of *Nematolepis ovatifolia* had been stripped of all leaves except a few bound together by silk at the top of the branch, these leaves were commonly still green and hence the loss of leaves could not be confused with those damaged by frost or having early symptoms of *Phytophthora* infection.

Killing frost

Conditions in early July 2012 of low air temperature with shallow snow (65-70 cm) were conducive to the killing of leaves exposed above the snow surface and in all cases damage to *Eucalyptus niphophila* was at this height. High elevation populations of *Nematolepis ovatifolia* were mainly protected beneath the snow surface but at lower elevations where shrubs were taller they were exposed to frost damage. Shrubs above the winter snowline affected by frost in 1982 mainly recovered (pers. obs.). Similarly, seedlings of *Eucalyptus niphophila* can survive many years at about shrub height, despite repeated frost-killing of exposed leaves above the snow (Wimbush & Forrester 1988). By contrast, in a montane frost hollow *Bossiaea foliosa* was killed by frost (Leigh *et al.* 1987), but the plant would not have had its base protected by snow cover at montane elevations. The *Nematolepis ovatifolia* which had affected tips that then progressed through death of the branch and then the shrub were unlikely to have reached that condition as a result of frost. However, those in which the affected leaves dropped and the plant itself was unaffected were possibly a result of some damage acquired just above the snow surface, most likely frost damage.

Pathogens

Phytophthora cambivora was isolated from two populations of *Nematolepis ovatifolia* in which plant death rapidly followed early symptoms of infection. *Phytophthora cambivora* is hosted by at least 30 genera in 19 families (USDA 2014). In Australia it adversely affects apple, almond and cherry trees (Bumbieris & Wicks1980; Wicks & Hall 1990). It has also been isolated from eucalypt plantations (Shearer & Smith 2000).

Although pathogen infection and plant death were mapped from Thredbo through to south of Jagungal, *Phytophthora cambivor*a was found in only two of 26 samples. It is possible that in the Snowy Mountains *Phytophthora cambivor*a may be rare in the soil because dispersing zoospores are less persistent than chlamydospores or oogonia in the soil (Vannini *et al.* 2012). Vettraino *et al*. (1999) suggested that difficulty in isolating *Phytophthora cambivora* from soil may be due to the lack of resting structures such as chlamydospores, which *Phytophthora cambivora* is not known to produce (Vannini *et al*. 2012). As *Phytophthora cambivora* generally exists mainly as a single mating type it would also be unable to produce oospores (Vannini *et al.* 2012). It is apparent from the sudden infection and death across such a widespread area that *Phytophthora cambivora* in the Snowy Mountains had survived for some years along roads and trails but, apart from along water courses below these, did not disperse greatly in the soil. Even where it has dispersed it has proven difficult to isolate from soil beneath symptomatic *Nematolepis ovatifolia* which suggests that the high elevation rhizosphere is not a favoured environment for *Phytophthora cambivora* and it may only survive in host tissues, possibly dispersing among roots of adjacent plants that are in contact rather than through the soil (Ristaino and Gumpertz 2000).

The fact that affected populations were found to be significantly closer to trails suggest that dispersal was along these access routes. Earthmoving machinery may have carried mud during the construction of these trails and most of the trails still receive some vehicle movement, a major vector for the spread of *Phytophthora cambivora* in southern Europe (Vannini *et al.* 2012). However, of four major concentrations of symptomatic plants, two (Schlinks Pass Road and the Kosciuszko Road) are surfaced with imported gravel making it difficult for current vehicles to transport mud, which is more likely on the Grey Mare Trail and Valentines Trail which are mainly just graded trails. Animals may use the trails preferentially and mud could be carried on the hooves of pigs, horses or cattle. Two of the heavily affected areas, at Charlotte Pass (gravel surface) and the Valentines Trail (soil surface), are also on the 655 km long Australian Alps Walking Track. However areas affected two or more km to the west and east of Schlinks Pass road are rarely visited by walkers; there are no nearby trails but there is evidence of past cattle grazing and current pig rooting. Similarly affected populations on the west and north side of Mt Kosciuszko show evidence of feral horse presence in recent years, particularly in muddy areas. With such widespread infection and so many possible vectors, the origin of the infestation is now difficult to determine.

Conditions high in the Snowy Mountains are generally not favourable for the survival of some *Phytophthora* species*,* although soils are in the same pH range of 3.65 - 4.39 as found in forest soils where oak trees were infected by *Phytophthora cambivora* (Jung *et al*. 1999). Vegetation studies undertaken from the 1940s onwards did so in the belief that the soils in the higher elevations of the Snowy Mountains were too cold for *Phytophthora cinnamomi* (Alec Costin pers. comm.). In Tasmania, Podger *et al.* (1990) concluded that *Phytophthora cinnamomi* is unlikely to be pathogenic where the annual mean temperature is < 7.5ºC. If this or a similar temperature limitation applies to *Phytophthora cambivora,* for which the optimal growth temperature is 22 to 24°C (Jung 1998), then it too would be unlikely to be pathogenic in thermal conditions high in the Snowy Mountains. At the upper limits of the montane zone the annual mean temperature was calculated for Kiandra (1395 m asl) at 6.8ºC and the Kosciusko Hotel (now Sponars, 1530 m asl) at 6.1ºC and temperatures would be lower at higher elevations in the subalpine and alpine zones (Costin 1954). Nitrogen levels in Snowy Mountains soils are also low, with concentration of nitrate of 2.8 ± 1.5 mg.kg^{-1} for a location (GLORIA 5), associated with symptomatic shrubs (Pickering & Green 2009). By contrast, Jung *et al.* (1999) found mean nitrate concentrations in soils of infected oak stands of 35.6 ± 40.5 mg.kg^{-1}. Unlike many mountain areas worldwide, alpine humus soils are the dominant soil type at high elevation in the Snowy Mountains (Costin 1954) and alpine soils contain a high diversity of root endophytes (Davies & McLean 2002). Such soils with high biodiversity can suppress soil-borne fungal diseases through competition (Altieri 1999). So high elevations in the Snowy Mountains are generally not suitable for *Phytophthora* infection and the question remains, why did dieback erupt in spring 2012?

Climate

Given the widespread locations of affected populations it appears that *Phytophthora cambivora* has been present for some time, but has been held in check by some factor. Disease due to *Phytophthora* induced dieback is not usually associated with high mountain environments (McDougall *et al.* 2003). Essentially the soils are too cold. At the alpine treeline, the growing season mean shaded soil temperature at 10 cm depth is virtually identical to the seasonal mean treeline air temperature (Körner 2012, p. 36) at 6.4 ±0.7°C (SD) (Körner and Paulsen, 2004). The growing season mean air temperature (October to May) at the alpine treeline (Charlotte Pass) was recorded as 6.6°C (Costin 1954) and shaded soil temperatures above the alpine treeline in the Snowy Mountains are normally below about 7°C (Green & Stein 2015). An abundance of soil moisture favours *Phytophthora cambivora* (Day 1938). However, the infected plant may not require much water uptake in wet periods. The first signs of dieback in *Nematolepis ovatifolia* were found retrospectively from photographs taken in May 2011. Backgrounds to these photographs contained large areas of *Nematolepis ovatifolia* with limited occurrence of symptoms on plants that were subsequently to show signs of infection, chlorosis and die. If they were already infected at that time the reason that major observable symptoms of water stress were not exhibited was possibly due to the abundance of water.

The diminishing incidence of symptomatic plants with elevation above the alpine treeline suggests that at higher elevations lower soil temperatures are still holding infection in check, whereas at lower elevations rising soil temperature has made conditions suitable for infection. From 2010/11 onwards, climate patterns Australia-wide were characterised by both unusually high rainfall and temperatures. The growing seasons 2010/11 and 2011/12 were covered by the period April 2010 to March 2012, which was Australia's wettest two-year period on record and 2011 and 2012 were both in the three warmest La Nina years on record (BOM 2012). Precipitation at Thredbo over the growing season (October to May) averaged 791±192 mm (SD) in the 13 years immediately preceding the La Nina years and virtually doubled that with 1460 mm and 1456 mm in the two La Nina growing seasons (BOM 2015). At 10 cm soil depth beneath *Nematolepis ovatifolia* that was subsequently infected, temperature from growing season 2004/05 to 2009/10 averaged 7.75±0.6°C (SD), but were 8.6°C and 8.3°C in the two La Nina growing seasons (2010/11 and 2011/12). Ink disease, caused by *Phytophthora cambivora*, develops rapidly in excessively wet soils (Černý *et al.* 2008). Hence the summer period when soil temperatures were high would have corresponded with a period of high soil moisture, a situation that similarly preceded shrub dieback at Barrington Tops (McDougall *et al.* 2003).

From September 2012 precipitation declined, but the period to August 2013 was the warmest 12 month period on record in Australia (1.11°C above the long term average), a record that was exceeded the following month with the hottest September on record bookending a new record warmest 12 month period (1.25°C above the long term average). By the end of May 2014 the warmest 24 months on record in Australia had been achieved (BOM 2014). These temperature records were reflected locally with a growing season mean soil temperature of 9.2°C, recorded from the GLORIA site in 2012/13. So a wet and warm period, when conditions were suitable for rapid development and infection by *Phytophthora cambivora*, was followed by a hot, dry period when plants, deprived of root hairs, were placed under severe water stress and died rapidly.

It has been suggested that, with predicted further climatic warming and loss of snow at lower elevations (Whetton 1998; Hennessy *et al.* 2008), shrub cover may increase in alpine and subalpine areas currently dominated by herbs and graminoids, within one to two decades (Pickering & Green 2009). Because of climatic warming, a number of long-term monitoring sites have been established to measure vegetation response ranging from experimental warming of shrubs and herbs (Itex) (Wahren *et al.* 2013) and tree establishment above treeline (Kostex) (Green unpublished data) to observational (GLORIA) (Pickering & Green, 2009). However, elevational tree or shrub advance cannot be taken as inevitable because there are some factors whose actions occur infrequently, such as summer drought in 1965 and 1978 (Wimbush & Costin 1979) and 2002/03 (Morgan 2004) or drought following severe frosts in 1982/83 (Williams 1990). Frost damage and possible death of shrubs, due to cold nights without cloud cover accompanied by lack of snow, is one condition that could become exacerbated by climate change. It is unlikely that shrubs would be able to survive in areas where they are more likely to be affected adversely by severe frosts. In tundra areas in general, heath is more dependent upon the protection of deeper snow than are herbs (Billings 1973).

Higher soil temperature in the growing season allowing growth of *Phytophthora* species is another consequence of climate change. In Europe, for example, outbreaks of *Phytophthora cambivora* in the late 20th and early 21st century may have been facilitated by climate change (Vannini *et al*. 2012). Even in the subantarctic, dieback of the cushion plant *Azorella macquariensis* on Macquarie Island is believed to be due to increased infection by a pathogen with ongoing climate change (Whinam *et al.* 2014). Podger *et al.* (1990) in Tasmania concluded that an increase in mean annual temperature of 4.8°C would be required to make the highest Tasmanian alpine plants vulnerable to *Phytophthora cinnamomi*. Similar calculations have not been made for the high alpine plants in the Snowy Mountains, nor for *Phytophthora cambivora.* However, the Snowy Mountains treeline temperature in 2012/13 was ~3.8°C higher than the long term (1921–1995) growing season mean treeline temperature for Tasmania (Green & Stein 2015) and it appears that the temperature range required for *Phytophthora cambivora* to become infectious has already been achieved at these lower elevations. Hence the long-term future of high elevation shrubs will be more complex than previously thought.

Acknowledgements

Thanks to Brett Spunner for GIS and drawing Figure 2, Wayne Robinson for providing statistical advice and Thomas Wallenius for identifying Lepidopteran larvae. Thanks to Alec Costin and Dane Wimbush for an historical discussion on *Phytophthora* in the Snowy Mountains. Thanks in particular to Keith McDougall for discussions about *Phytophthora*, coming into the field to collect root sample for analysis and commenting on the manuscript. Catherine Pickering also for commenting on the manuscript

References

Altieri, M.A. (1999) The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems & Environment* 74, 19–31.

Australian National Herbarium (2015) http://www.cpbr.gov.au/cpbr/herbarium

Billings, W.D. (1973) Arctic and alpine vegetations: similarities, differences and susceptibility to disturbance. *Bioscience* 23, 697-704.

BOM (Bureau of Meteorology) (2012) http://www.bom.gov.au/climate/enso/history/ln-2010-12/

BOM (Bureau of Meteorology) (2014) http://www.bom.gov.au/climate/updates/articles/a005-sep-2013-warmest-on-record.shtml.

BOM (Bureau of Meteorology) (2015) http://www.bom.gov.au/climate/data/stations/ accessed 12 July 2015

Bumbieris, M. & Wicks, T.J. (1980) *Phytophthora cambivora* associated with apple trees in South Australia *Australasian Plant Pathology* 9, 114.

Černý, K., Gregorová, B., Strnadová, V., Tomšovský, M., Holub, V. & Gabrielová, S. (2008) *Phytophthora cambivora* causing ink disease of sweet chestnut recorded in the Czech Republic *Czech Mycology* 60, 265–274.

Clarke, P.J., Keith, D.A., Vincent, B.E. & Letten, A.D. (2015) Post-grazing and post-fire vegetation dynamics: long-term changes in mountain bogs reveal community resilience. *Journal of Vegetation Science* 26. 278-290.

Costin, A.B. (1954) *A Study of the Ecosystems of the Monaro Region of New South Wales*. Government Printer, Sydney.

Costin, A.B. (1959) Vegetation of high mountains in Australia in relation to land use. In: *Biogeography and Ecology in Australia* (ed A. Keast), pp. 427-451 Dr. W. Junk, The Hague.

Costin, A.B, Gray, M., Totterdell, C.J. and Wimbush, D.J. (2000) *Kosciuszko Alpine Flora*. (2nd Edition). CSIRO, Melbourne.

Davies, P.W. & McLean C.R. (2002) Diversity of alpine root endophytes of Epacridaceae. In: *Biodiversity in the Snowy Mountains* (ed K. Green) pp 4-7. Australian Institute of Alpine Studies, Jindabyne.

Day, W.R. (1938) Root-rot of sweet chestnut and beech caused by species of Phytophthora: I. Cause and symptoms of disease: its relation to soil conditions. *Forestry* 12, 101-116.

Doherty, M.D., Wright, G. & McDougall, K.L. (2015) The flora of Kosciuszko National Park, New South Wales: Summary and overview. *Cunninghamia* 15, 13-68.

Donato, D.C. (2013) Limits to upward movement of subalpine forests in a warming climate. *Proceedings of the National Academy of Sciences* 110, 7971–7972.

Green, K. & Osborne W.S. (1994) *Wildlife of the Australian Snow Country*. Reed, Sydney.

Green, K. & Osborne, W.S. (2012) *Field Guide to Wildlife of the Australian Snow Country*. New Holland Publishers, Chatswood.

Green, K. & Stein, J.A. (2015) Modeling the thermal zones and biodiversity on the high mountains of Meganesia: the importance of local differences. *Arctic, Antarctic and Alpine Research* 47, 669–678.

Hardy, G.E.St.J., Barrett, S. & Shearer, B.L. (2001) The future of phosphite as a fungicide to control the soilborne plant pathogen *Phytophthora cinnamomi* in natural ecosystems. *Australasian Plant Pathology* 30, 133–139.

Hennessy, K.J., Whetton, P.H., Walsh, K., Smith, I.N., Bathols, J.M., Hutchinson, M. & Sharples, J. (2008) Climate change effects on snow conditions in mainland Australia and adaptation at ski resorts through snowmaking. *Climate Research* 35, 255-270.

Jung, T. (1998) Die Phytophthora-Erkrankung der europäischen Eichenarten – wurzelzerstörende Pilze als Ursache des Eichensterbens. Lincom Europe, München. (cited in Jung et al. 1999).

Jung, T., Blaschke, H. & Oßwald, W. (1999) Involvement of *Phytophthora* species in central and western European oak decline and the influence of site factors and nitrogen input on the disease. In: *Phytophthora Diseases of Forest Trees. Proceedings from the First International Meeting on Phytophthoras in Forest and Wildland Ecosystems,* (eds Everett, M. Hansen, E.M. & Sutton, W.) pp 28-33. Forest Research Laboratory, Oregon State University Corvallis, Oregon.

Körner, C. (2012) *Alpine Treelines—Functional Ecology of the Global High Elevation Tree Limits*. Springer, Basel.

Körner, C., & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31, 713–732.

Leigh, J.H., Wimbush, D.J., Wood, D.H., Holgate, M.D., Slee, A.V., Stanger, M.G. & Forrester, R.I. (1987) Effects of Rabbit Grazing and Fire on a Subalpine Environment. I. Herbaceous and Shrubby Vegetation. *Australian Journal of Botany* 35, 433-464.

McDougall, K.L., Summerell, B.A., Coburn, D. & Newton, M. (2003) *Phytophthora cinnamomi* causing disease in subalpine vegetation in New South Wales. *Australasian Plant Pathology* 32, 113–115.

McDougall, K.L., Walsh, N.G. & Wright, G.T. (2015) Recovery of treeless subalpine vegetation in Kosciuszko National Park after the landscape-scale fire of 2003. *Australian Journal of Botany* 63, 597-607.

Morgan, J.W. (2004) Drought-related dieback in four subalpine shrub species, Bogong High Plains, Victoria. *Cunninghamia* 8, 326-330.

NPWS (NSW National Parks & Wildlife Service) (2015) http://www.environment.nsw.gov.au/parkinfo/barringtontopsnpphytophthora.htm (accessed 20/7/2015)

National Herbarium of New South Wales (2015) PlantNet Online plant information. Royal Botanic Gardens Sydney http://plantnet.rbgsyd.nsw.gov.au

Office of Environment and Heritage (2015) NSW Office of Environment and Heritage, Department of Premier and Cabinet: OEH Atlas of NSW Wildlife.

Pickering, C.M. & Green, K. (2009) Vascular plant distribution in relation to topography, soils and micro-climate at five GLORIA sites in the Snowy Mountains, Australia. *Australian Journal of Botany* 57, 189-199.

Podger, F.D., Mummery, D.C., Palzer, C.R. & Brown, M.J. (1990) Bioclimatic analysis of the distribution of damage to native plants in Tasmania by *Phytophthora cinnamomi*. *Australian Journal of Ecology* 15, 281 – 289.

Raffa, K.F., Powell, E.N. & Townsend, P.A. (2012) Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proceedings of the National Academy of Sciences* 110, 2193-2198.

Ristaino, J.B. & Gumpertz, M.L. (2000) New frontiers in the study of dispersal and spatial analysis of epidemics caused by species in the genus *Phytophthora*. *Annual Review of Phytopathology* 38, 541-576.

Shearer, B.L. & Smith, J.W. (2000) Diseases of Eucalypts caused by soilborne species of *Phytophthora* and *Pythium*. In: *Diseases and Pathogens of Eucalypts* (eds Keane, P.J. Kile, G.A., Podger, F.D. & Brown, B.N.) pp 259-291. CSIRO Publishing, Collingwood.

USDA (United States Department of Agriculture) (2014) http://www.phytophthoradb.org/species.php?a=dv&id=124252 (accessed 13 June 2014)

Vannini, A., Breccia, M., Bruni, N., Tomassini, A. & Vettraino, A.M. (2012) Behaviour and survival of *Phytophthora cambivora* inoculum in soil-like substrate under different water regimes. *Forest Pathology* 42, 362–370.

Vettraino, A.M., Natili, G., Anselmi, N. & Vannini, A. (1999) Recent advances in studies on *Phytophthora* species associated with *Castanea sativa* and *Quercus cerris* in Italy. In: *Phytophthora Diseases of Forest Trees. Proceedings from the First International Meeting on Phytophthoras in Forest and Wildland Ecosystems,* (eds Everett, M. Hansen, E.M. & Sutton, W.) pp34-36. Forest Research Laboratory, Oregon State University Corvallis, Oregon.

Wahren, C.-H., Calmac, J.S., Jarrad, F.C., Williams, R.J., Papst, W.A. & Hoffmann, A.A. (2013) Experimental warming and long-term vegetation dynamics in an alpine heathland. *Australian Journal of Botany* 61, 36–51.

Whinam, J., Abdul-Rahman J.A., Visoiu, M., di Folco, M.-B.F. & Kirkpatrick, J.B. (2014) Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species. *Australian Journal of Botany* 62, 10-21.

Whetton, P.H. (1998) Climate change impacts on the spatial extent of snow-cover in the Australian Alps. In: *Snow: a Natural History; an Uncertain Future* (ed Green, K.) pp 195-206. Australian Alps Liaison Committee, Canberra.

Wicks, T. & Hall B. (1990) Evaluation of phosphonic (phosphorous) acid for the control of *Phytophthora cambivora* on almond and cherry in South Australia *Australasian Plant Pathology* 19, 132-133.

Williams, R.J. (1990) Growth of subalpine shrubs and snowgrass following a rare occurrence of frost and drought in south-eastern Australia. *Arctic and Alpine Research* 22, 412-422.

Williams, R.J. & Ashton, D.H. (1988) Cyclical patterns of regeneration in subalpine heathland communities on the Bogong High Plains, Victoria. *Australian Journal of Botany* 36, 605-619.

Wimbush, D.J. & Costin, A.B. (1979) Trends in vegetation at Kosciusko. III. Alpine range transects, 1959-1978. *Australian Journal of Botany* 27, 833-871.

Wimbush, D.J. & Forrester, R.I. (1988) Effects of rabbit grazing and fire on a subalpine environment. II. Tree vegetation. *Australian Journal of Botany* 36, 287-298.

Manuscript accepted 21 December 2015