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RESEARCH NOTE

Assessing susceptibility of *Metrosideros excelsa* (pōhutukawa) to the vascular wilt pathogen, *Ceratocystis lukuohia*, causing Rapid ʻŌhiʻa death

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Abstract
Metrosideros excelsa (pōhutukawa) is an important native tree species in Aotearoa-New Zealand. *Ceratocystis lukuohia* is an aggressive wilt pathogen of the Hawaiian forest tree *M. polymorpha* (ʻōhi ʻa) and could be a threat to pōhutukawa. A host response study was conducted to evaluate the susceptibility of *M. excelsa* seedlings to *C. lukuohia* infection. Forty-eight *M. excelsa* seedlings from six parent trees were inoculated with *C. lukuohia*. Disease symptoms and mortality were observed in *M. polymorpha* positive controls inoculated with *C. lukuohia*, but not in the *M. excelsa*. Dissections of the inoculated *M. excelsa* revealed significantly lower disease severity (mean range: 3.9%-9.0%) comparable to a mean of 1.7% for the *M. excelsa* negative control treatment. In comparison, the mean disease severity for the *M. polymorpha* positive control plants was 43.3 ± 6.1%. Aleurioconidia were present in the stem tissue of 86–100% of *C. lukuohia*-inoculated *M. excelsa* selections compared to 100% of *M. polymorpha* and 0% of *M. excelsa* inoculated with sterile water. These results suggest that *C. lukuohia* can infect *M. excelsa* if introduced to a wound, but the pathogen is not aggressive enough to cause wilt and mortality. There is potential for wild *M. excelsa* to become infected with *C. lukuohia* if a pathway allowed for the accidental introduction of the pathogen into Aotearoa-New Zealand. Differential susceptibility of other *M. excelsa* genotypes or *Metrosideros* species also needs to be considered. Therefore, measures should be taken to avoid the introduction of this pathogen into the country.

Keywords *Metrosideros* · *Ceratocystis* · Pathogenicity · ROD · Wilt

Aotearoa-New Zealand is one of the centers for *Metrosideros* (Myrtaceae) biodiversity with a total of 12 endemic species (Bylsma et al. 2014). In particular, pōhutukawa (*Metrosideros excelsa* Sol. ex Gaertn) has been described as one of the best-known and best-loved native trees in Aotearoa-New Zealand (Bergin and Hosking 2006). Pōhutukawa (also known as hutukawa, kahika, pohutukawa, and rātā), naturally occurs in a zone that lies between the Three King Islands and latitude 39°S of the North Island of Aotearoa-New Zealand (Wardle 1991). It is naturally a coastal species, although pōhutukawa forests also exist inland around the Central Volcanic Plateau of the central North Island (Bergin and Hosking 2006). For indigenous Māori, the tree is referred to as rākau rangatira (or chiefly tree) (Orbell 1985), one of the great trees of the forest (Hēnare 2014). The species has multiple uses including medicine, food, dyes, construction, ship building, and tool crafting (Anon 2021). Pōhutukawa are also valued for the production of honey and as landscape trees due to their vibrant red flowers (Anon 2021). Pōhutukawa also have an important role in ecosystem services, providing a valuable nectar source for a range of taxa including native avifauna, insects, geckos, and the short-tailed bat (*Mystacina tuberculata*) (Bylsma et al. 2014).

Due to harvesting of pōhutukawa following the arrival of Māori, a situation that accelerated significantly with the arrival of European settlers, approximately 90% of pōhutukawa have been lost in its native range (Forest Research Institute 1989). In addition, selective grazing by

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the introduced Australian common brushtail possum (*Trichosurus vulpecula*) has contributed to the death of thousands of trees (Hosking and Hutcheson 1993). This is in addition to grazing of the forest floor by feral and domestic stock that significantly impact the survival of seedlings (Hosking and Hutcheson 1993). Despite the decline of pōhutukawa, in 2012 the species was classified as "Not Threatened" under the New Zealand Threat Classification System (NZTCS) (de Lange et al. 2013). A reassessment was undertaken in 2017 with the arrival of myrtle rust (*Austropuccinia psidii*) (Ho et al. 2019) and the potential impact of two new plant pathogens, *Ceratocystis lukuohia* and *C. huliohia* affecting *Metrosideros* in Hawai'i (Keith et al. 2015; Barnes et al. 2018), should they reach Aotearoa-New Zealand. Consequently, and as a precautionary measure, the classification of pōhutukawa was elevated to 'Threatened' (de Lange et al. 2017, Pages 7–8).

In Hawai'i, the native forest tree *Metrosideros polymorpha* ('ōhi'a) is threatened by Rapid 'Ōhi'a Death (ROD). Over 1 million trees in more than 180,000 acres of 'ōhi'a forest have been affected by ROD (ROD SRP 2020). The cause of this crown wilt are the pathogens *Ceratocysis lukuohia* and *C. huliohia* (Barnes et al. 2018). *C. lukuohia*, the more aggressive of the two pathogens, is associated with the vast majority of the \`ōhi\`a mortality across the islands (Barnes et al. 2018).

Ceratocystis lukuohia infects *M. polymorpha* trees through open wounds containing woody vascular tissue where the pathogen colonizes the xylem (Hughes et al. 2020). Typical symptoms of *C. lukuohia* infection are the presence of black lesions in the sapwood and rapid wilting of the canopy leading to mortality (Keith et al. 2015). Stand mortality of *M. polymorpha* is variable, but can be as high as 90%, while mean annual mortality rates of *M. polymorpha* forest plots is 10% (F. Hughes, unpublished). This rapid and widespread mortality is a significant threat to the ecological, cultural, and economic systems supported by the species. While the effects of *C. lukuohia* on *M. polymorpha* biology and ecology have been subject to extensive investigation, little is known about its effects on other *Metrosideros* species in Hawai'i and throughout the Pacific. Due to the potential threat that *C. lukuohia* poses to *Metrosideros* in Aotearoa-New Zealand, a pilot study to evaluate the pathogenicity of *C. lukuohia* to *M. excelsa* was undertaken in Hawai 'i.

Seeds were collected from six different *M. excelsa* trees growing in the greater Auckland region of New Zealand. Seeds were collected from a single tree located at Scandrett Regional Park (S36.4439, E174.7712°) (hereafter referred to as Scandrett), one at Shakespear Regional Park (S36.6067, E174.82462°) (Shakespear), and four trees from the Auckland Botanic Gardens (ABG) (S37.0085, E174.9057). Trees from the ABG were originally collected from Titirangi (S36.9383° E174.6540°, ABG reference number 20000146, Supplemental Fig. 1), Manurewa (S37.0183° E174.8987, 19,971,073) and Waimatuka (S36.7670° E174.4935°, 20,000,203, Supplemental Fig. 2), while 'Vibrance' is a commercially available cultivar (19,971,253, Supplemental Fig. 3). Groups of seedlings from the various mother trees are henceforth referred to as selections. Seeds were collected in 2017 and 2018, and sent with phytosanitary clearance to the USDA-ARS Daniel K. Inouye U.S. Pacific Basin Agricultural Research Center in Hilo, HI, USA. The genetic variation amongst these seed lines is unknown.

Seeds from each tree were bulk sown into separate 24.5 cm diameter round plastic containers filled with peat-based potting mix (Sunshine Mix #4®, Sun Grow, Agawam, MA). These containers were placed in a shade house under 73% shade and irrigated with mist for 15 s every 30 min. Once seedlings were approximately 2–3 cm tall, they were individually transplanted into 10.16×10.16 cm square plastic containers with the same potting mix used in the bulk sowing and fertilized at transplanting and every three months with a granular slow-release fertilizer (13 N—11 P—11 K, Nutricote® Total Type 100, Chisso-Asahi Fertilizer Co., Ltd., Tokyo, Japan). These plants were irrigated three times per day for 3 min and grown without shade. *Metrosideros polymorpha* cuttings from two highly susceptible mother trees were used as positive controls in the inoculation experiment. Cuttings of semi-hardwood branch segments (approximately 2–3 mm in diameter) were collected from the mother trees and cut into 5 cm segments. The proximal end of each cutting was dipped in a 1:5 dilution of rooting hormone (1% indole-3-butyric acid, 0.5% 1-napthaleneacetic acid, Dip 'N Grow, Clackamas, OR, USA) and placed in vermiculite under the same irrigation and shade conditions as the *M. excelsa* containers. Plants were suitable for inoculation once they reached a stem diameter of at least 6 mm.

Sterile 6 mm filter paper disks were soaked for approximately 30 s in a 1×10^6 spores/ml suspension or sterile water as a negative control. The spore suspension was produced from 7-day-old cultures of *C. lukuohia* isolate P14-1–1 grown on 10% V8 agar following recommendations from Luiz and Keith (2021). The disks subjected to both treatments were then placed on sterile 10% V8 agar, allowed to dry, and incubated at 28 °C for two days. Eight plants per selection were inoculated with either *C. lukuohia*-treated or sterile water-treated filter paper disks (negative control) for each trial via a tangential stem wound made with a sterile scalpel (Keith et al. 2015; Luiz et al. 2021). *Metrosideros polymorpha* plants served as the positive control. Stem wounds were wrapped in laboratory film (Parafilm®, Bemis Company, Inc., Neenah, WI, USA) and all plants were placed in a growth chamber (Controlled Environments Ltd., Manitoba, Canada) set at 28 °C with 12-h light and ~ 70% relative humidity. Plants were observed for disease symptoms and watered by hand every 2–3 days for

60 days. After this period, the plants were relocated to a shade house and observed under ambient conditions for a further 123–150 days. Plants in the shadehouse were irrigated twice a day for 5 min. Upon completion of the shade house observation period, surviving plants were dissected by scraping away the bark to reveal the vascular tissue and any black internal staining caused by *C. lukuohia*. Plant height and lesion length were recorded, and disease severity (percentage of plant sapwood discolored by the pathogen) was calculated using these measurements following Oliveira et al. (2016). In addition, shavings approximately 2 mm in length were excised from the main stem at the highest point of a lesion and examined under 400 × magnification on a compound microscope (Leica DMi8, Leica Microsystems, Wetzlar, Germany) to observe whether aleurioconidia were present in the wood tissue. Shavings taken from the same location were used to confirm infection by the pathogen via re-isolation using carrot slices (Moller and DeVay 1968) or qPCR (Heller and Keith 2018). Each selection was subjected to two trials of testing. To compare disease severity among the *M. excelsa* groups, a Welch's ANOVA and Games-Howell post-hoc test was conducted using the "rstatix" package version 0.7.0 (Kassambara 2021) in the R statistical environment version 4.0.3 (R Core Team 2020).

In addition, one inoculated seedling each of Titirangi, Manurewa, Waimatuka, and 'Vibrance' was not dissected to allow for long-term observation. Seedlings remained in the shadehouse under the same conditions described above.

Wilt symptoms and mortality were not observed on any *M. excelsa* whether they were treated with *C. lukuohia* or the sterile water disk (Table 1). In comparison, 75% of the *M. polymorpha* inoculated with *C. lukuohia* died. Aleurioconidia presence in discolored *M. excelsa* wood tissue was commonly observed, ranging from 86 to 100% of inoculated plants in each selection (Supplemental Fig. 4). Mean disease severity was statistically insignificant between trials for each group, thus the data were combined for further analysis. Mean disease severity of all six *M. excelsa* selections ranged from 3.9% to 9.0% and were significantly less than that of the *M. polymorpha* positive control (Table 1, Supplemental Fig. 5). Symptom development in *M. polymorpha* and aleurioconidia in the stem tissue of both species were caused by *C. lukuohia*.

In total, 43 of 44 wood shaving samples from plants inoculated with *C. lukuohia* produced mycelium and perithecia on carrot baits. For the single plant that *C. lukuohia* was not detected via carrot slices, the pathogen was detected by qPCR using wood shavings from the stem lesion. Carrot slices were not used to reisolate the pathogen from plants in the second trial of Titirangi, Manurewa, Waimatuka, and 'Vibrance', as perithecia grew directly on the stems of dissected plants inoculated with *C. lukuohia* one week after dissection. Perithecia from three stems were confirmed to be *C. lukuohia* by qPCR. Carrot slices were negative for all sterile water control plants.

A visual assessment of the four seedlings not destructively sampled, one year and seven months post-inoculation (December 2021), indicated that the plants were healthy with no wilt symptoms.

Trees infected by the vascular wilt pathogen, *C. lukuohia*, generally show rapid crown wilt (Hughes et al. 2020). Little is known about the genetic resistance of Hawaiian *Metrosideros* spp. to *C. lukuohia*; however, a preliminary study by Luiz et al. (2021) demonstrated that *M. polymorpha* varieties differ in susceptibility. The timeframe of symptom onset for *C. lukuohia*-inoculated *M. polymorpha* averaged ~ 14 days post-inoculation. In contrast, all *C. lukuohia*-inoculated *M. excelsa* remained visually healthy throughout the duration of the experiment. However, aleurioconidia presence and wood discoloration of

Table 1 Number of replicates, mortality, mean disease severity (± SEM), and intratissue presence of aleurioconidia (percentage of plants with aleurioconidia observed within host tissues) among the *M. polymorpha* positive control and six *M. excelsa* selections. Letters represent significantly different groups according to a Welch's ANOVA and Games-Howell post-hoc test ($p < 0.05$)

Species	Selection	Number of plants		Mortality (%)	Mean disease severity (%)	Intratissue aleurioconidia presence (%)
		Total	Dead			
M. polymorpha	-	12	9	75	43.3 ± 6.1 a	100
M. excelsa	Shakespear	8	0	0	3.9 ± 0.8 bc	88
M. excelsa	Scandrett	8	0	0	5.8 ± 1.2 bc	100
M. excelsa	Titirangi	8	0	0	5.5 ± 0.8 b	86
M. excelsa	Manurewa	8	0	0	5.5 ± 0.9 b	100
M. excelsa	'Vibrance'	8	0	0	4.3 ± 0.3 b	100
M. excelsa	Waimatuka	8	0	0	9.0 ± 3.3 bc	100
M. excelsa	Negative controls	48	0	0	1.7 ± 0.4 c	0

C. lukuohia-inoculated *M. excelsa* demonstrates that *M. excelsa* can be infected by *C. lukuohia*, although extensive discoloration and mortality was not observed on this host. The results suggest that at a minimum, tolerance exists in the *M. excelsa* seedlings evaluated in this study.

The initial results from a limited number of *M. excelsa* mother trees indicate that, under the experimental conditions described here, the species is resistant to *C. lukuohia*, since symptom development did not occur. The variability in disease severity observed in this study suggests that there may be varying levels of resistance amongst the *M. excelsa* genotypes found in Aotearoa-New Zealand (Young et al. 2001; Broadhurst et al. 2008), as has been indicated for *M. polymorpha* in Hawai ‘i (Luiz et al. 2021). Similarly, levels of resistance to *C. lukuohia* may vary amongst *Metrosideros* species. There are 12 *Metrosideros* species endemic to Aotearoa-New Zealand, some of which are classified as endangered or nationally critical (e.g. *Metrosideros bartlettii* J.W. Dawson, also known as Bartlett's rātā), or have a limited distribution (e.g. *Metrosideros kermadecensis* W.R.B. Oliver, also known as Kermadec pōhutukawa, a species restricted to the Kermadec Islands). Understanding the potential impact of *C. lukuohia* on these species, along with *Metrosideros umbellata* Cav. (Southern rātā), the most widespread of the New Zealand tree rata species, would seem to be an important step.

While the potential pathways for ROD (both *C. lukuohia* and *C. huliohia*) to reach Aotearoa-New Zealand, as well as vectors for the pathogens within the country, have not been elucidated, a precautionary approach needs to be considered. Anthropogenic dispersal of contaminated biological material through other Pacific Islands where *Metrosideros* species occur naturally, could aid spread. A more aggressive lineage of *C. lukuohia* could arise over time (Pariaud et al. 2009) and, along with the risk of host range shifts (Slippers et al. 2005; Giraud et al. 2010), impacts are potentially significant. This is particularly so for other Myrtaceae classified as taonga or threatened because of habitat loss or limited numbers (de Lange et al. 2018). *Ceratocystis* species host shifts have been observed, for example *C. manginecans* infection of bullet wood (*Mimusops elengi* L.) (Pratama et al. 2021) and *C. albifundus* infection of king protea (*Protea cynaroides* L.) (Lee et al. 2016). The potential for plant death arising from infection with *C. lukuohia* could potentially be exacerbated by the presence of myrtle rust, which infects a wide range of Myrtaceae including *Metrosideros* species (Toome-Heller et al. 2020).

In conclusion, the results show that *C. lukuohia* can infect *M. excelsa* if artificially inoculated at high concentrations into the stem of seedlings, but the pathogen did not cause wilt and mortality. Further research is needed to understand pathogenicity under more temperate climatic conditions and to related *Metrosideros* found in Aotearoa-New Zealand to better understand potential landscape-scale impacts.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13313-022-00858-9.

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Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

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