Title: Impact of *Phytophthora agathidicida* infection on canopy and forest floor nutrient concentrations and fluxes in a kauri-dominated forest

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Abstract

Kauri dieback, caused by *Phytophthora agathidicida*, is an ecosystem disturbance that poses a recent threat to the survival of kauri (*Agathis australis*) forests in New Zealand. Throughfall and stemflow play an important role in meeting the nutrient requirements of kauri forests. However, the effects of kauri dieback on canopy nutrient deposition remain unknown. Here we measured throughfall, stemflow and forest floor water yield and nutrient concentrations and fluxes (potassium, calcium, magnesium, manganese, silicon, sulphur, sodium, iron) of ten kauri trees differing in soil *P. agathidicida* DNA concentration and health status. We did not observe an effect of soil *P. agathidicida* DNA concentration on throughfall and stemflow water yield. Throughfall and forest floor nutrient concentrations and fluxes tended to decrease (up to 50%) with increasing soil *P. agathidicida* DNA concentration. Significant effects were found for potassium and manganese fluxes in throughfall, and calcium and silicon fluxes in forest floor leachate. The decline in nutrient input will have implications on plant nutrition, tree health and susceptibility to future pathogen infection in these ecologically unique kauri forests. Given our findings and the increasing spread of *Phytophthora* species worldwide, research on the underlying physiological mechanisms linking dieback and plant-soil nutrient fluxes is critical.

Keywords: forest floor leachate; macro-, micro- and beneficial nutrients; *Phytophthora*; plant pathogens; throughfall; stemflow

Introduction

Natural disturbances have the potential to substantially alter a variety of ecosystem processes and related functions, and consequently ecosystem services (Rouault *et al.,* 2006; Thom & Seidl, 2016; Schowalter *et al.,* 2018). Insects and pathogens are major and common natural biotic disturbance agents, and often an integral part of forest dynamics (Dale *et al.,* 2001; Wardle & Bardgett, 2008; Kautz *et al.,* 2017). Biotic disturbances can disrupt the structure, composition and function of ecosystems at the stand and landscape scale (Flower & Gonzalez-Meler, 2015; Seidl *et al.,* 2017; Burdon & Laine, 2019). Kauri dieback, caused by *Phytophthora agathidicida*, is one such recent threat that endangers the survival of the ecologically important conifer species *Agathis australis* (kauri) in New Zealand. *Phytophthora* species (*Oomycota, Stramenopila*) are soil-, water- or airborne plant pathogens that pose major challenges to global biosecurity, and some *Phytophthora* species are threats to forest ecosystems across the globe (Jung *et al.,* 2018). A changing climate may increase the pressure on forests, as changes in temperature and rainfall patterns may result in changes to the biogeographic range of plant pathogens (Shaw & Osborne, 2011) and may increase outbreaks (Jamieson *et al.,* 2012). *Phytophthora* species are responsible for the mortality of several tree species in Europe, North America, and Australia (Jung *et al.,* 2018). Several *Phythophtora* species (e.g., *Phytophthora cinnamoni, Phytophthora cryptogea, Phytophthora kernoviae*) are currently present in New Zealand native and plantation forests (Beever *et al.,* 2009; Scott & Williams, 2014). Studies have shown that *P. cinnamomi* results in fine root death and symptoms of chlorosis in New Zealand native tree species such as *Agathis australis* and *Phyllocladus trichomanoides,* affects regeneration, and thus may alter the long-term vegetation dynamic of these forests (Podger & Newhook, 1971; Horner, 1984; Johnston *et al.,* 2003).

Pathogen driven host mortality and subsequent changes in plant species composition are likely to affect biogeochemical fluxes. Given their rapid response to disturbance and environmental change, water-bound ecosystem fluxes function as an early marker of shifting ecosystem conditions (McClain *et al.,* 2003; Likens, 2013). Throughfall and stemflow are critical components of the hydrological and biogeochemical cycles of forested ecosystems, as they are main pathways for transferring precipitation, solutes, and microorganisms from the phyllosphere (aboveground surfaces of plants) to the pedosphere (Levia & Frost, 2003; Parker, 1983). Of particular importance is the transfer of plant nutrients which are essential or beneficial to fundamental physiological processes of plant metabolism, plant growth and

fitness, and forest nutrient cycling (Marschner, 2011; Schulze *et al.,* 2019). Precipitation passing through the canopy as throughfall and flowing along stems as stemflow becomes enriched in solutes, including micro- and macronutrients (Staelens *et al.,* 2007), trace metals (Avila & Rodrigo, 2004), and dissolved and particulate organic matter (Michalzik *et al.,* 2016; Van Stan & Stubbins, 2018). Solution collected underneath the forest floor (forest floor leachate) is often greatly enriched in nutrients compared to bulk precipitation and canopy water fluxes due to the leaching of elements from organic matter (Batjes, 1996).

The amount and quality of throughfall, stemflow and forest floor leachate are the result of the interaction of several variables, including meteorological conditions (Dunkerley, 2014), seasonality (Macinnis-Ng *et al.,* 2014), intra- and interspecies differences among tree species (Schroth *et al.,* 1999; Lilienfein & Wilcke, 2004) and canopy and tree structure (Crockford & Richardson, 2000; Levia & Herwitz, 2002). Plant health (e.g., plant nutrient status, mechanical injury, insect pest and pathogen-related damage) has also been shown to affect canopy water yields and nutrient fluxes. For example, annual throughfall fluxes of Ca, Mg and Fe were up to 100% higher beneath spruce trees affected by air pollutants, insects and microfungi in Sweden, while Mn and K fluxes decreased (up to 30%) compared to throughfall fluxes from healthy reference trees (Alenäs & Skärby, 1988). Bark beetle caused forest dieback in a Norway spruce dominated forest in the Czech Republic resulted in a decrease in K, Ca and Mg concentrations in throughfall (Kopáček *et al.,* 2017). Defoliation caused by the larvae of the pale tussock moth in a beech forest in southern Sweden resulted in an increase in K throughfall flux (Nilsson, 1978). Varying canopy nutrient flux responses to biotic disturbances may partly be driven by differences in the interaction of the pest and/or pathogen and host as well as the role of the host in the forest (Lovett *et al.,* 2002). However, the implications of plant pathogen caused forest dieback, especially through fungus-like organisms such as *Phytopththora* species, on canopy and forest floor nutrient fluxes remain largely unknown. A recent study has shown that dissolved carbon and nitrogen fluxes decreased with increasing *P. agathidicida* infection of kauri trees (Schwendenmann & Michalzik, 2019).

Phytophthora. agathidicida is a novel and significant threat to the survival of the endemic, ecologically unique and culturally important kauri forests in the northern part of New Zealand. Kauri is endemic to northern New Zealand (north of latitude 38°S) (Ecroyd, 1982) and is the largest and longest-living tree species in the country. A distinctive plant community is found underneath mature kauri trees (Wyse *et al.,* 2014) which has been

associated with the particular soil characteristics found in kauri dominated forests such as low pH and high ammonium concentrations (Verkaik *et al.,* 2007). Undisturbed kauri stands are characterised by thick forest floors (litter plus organic layer) with mean residence time of 9-78 years (Silvester & Orchard, 1999). Throughfall nutrient fluxes (sum of Na, Ca, K and Mg) were 2.5-times higher than litterfall nutrient fluxes (Reed, 1984), suggesting that the hydrologic pathways play an important role in meeting short-term nutrient requirements of kauri forests (Reed, 1984; Sangster, 1986). Similarly, throughfall has been found to be an important pathway for nutrient supply to the forest floor, particularly in systems with weathered soils (Parker, 1983; Forti & Moreira-Nordermann, 1991; Moslehi *et al.,* 2019).

In this study we use canopy and forest floor nutrient data collected over one year (1) to quantify tree water yield and nutrient fluxes in throughfall, stemflow and forest floor leachate and (2) to test whether canopy and forest floor nutrient fluxes change along a *P. agathidicida* infection gradient in a kauri dominated forest. We hypothesized that canopy and forest floor nutrient input would decline following *P. agathidicida* infection.

Material and Methods

Study area

This study was conducted in the Karamatura Valley (37°00'S, 174°33'E) near Huia. Huia is located ~ 30 km southwest of central Auckland, New Zealand, in the southern part of the Waitakere Ranges Regional Park. The study site (approximately 2500 m^2) is located along a northeast facing ridgeline between 125 and 140 m above mean sea level, with slopes ranging between 5º and 15º (Fig. 1).

Mean annual temperature in the area is 14 °C. Total annual rainfall measured at a nearby station (Arataki, 7.5 km northeast of the study area, 190 m above sea level) is approximately 1600 mm 1981-2010) (Environmental Monitoring, Auckland Council GeoMaps, https://geomapspublic.aucklandcouncil.govt.nz/viewer/index.html). Approximately 70% of annual rainfall occurs between June and August (austral winter).

The soils are loams/sandy loams and classified as Typic Haplohumult (US Soil Taxonomy; Soil Survey Staff, 2014), and developed from andesitic grit, sand and siltstone (Hayward, 1976). The parent material originates from volcanic conglomerate and lava flows caused by volcanic eruptions 12-25 million years ago (Searle, 1981). The area is characterised by a steep and rugged topography with elevation ranging from sea level to 475 m above sea level.

Regenerating native shrubland and forests, wetland, and dune ecosystems are the predominant vegetation types in the Waitakere Ranges. The area has been extensively logged in the mid-late 19th and early 20th centuries (Esler, 1983). Kauri is the dominant canopy and sub-canopy species covering over 70% of the study site. Other conifer tree species are *Phyllocladus trichomanoides* and *Dacrydium cupressinum*. Other common understory species are *Kunzea ericoides, Hedycarya arborea*, *Leionema nudum,* and *Cyathea dealbata*.

A change in the health status of kauri trees in the Waitakere Ranges Regional Park during the mid-2010s and subsequent investigations have shown that *P. agathidicida* is the underlying agent of kauri dieback (Waipara *et al.,* 2013; Weir *et al.,* 2015). Recent studies (Hill & Waipara, 2017) estimated that approximately 30% of the kauri-dominated forests in the Waitakere Ranges Regional Park exhibit symptoms of kauri dieback. Although kauri dieback in the area has been observed over the last 15 years, it is unknown for how long *P. agathidicida* has been present in this particular forest stand. It should also be noted that kauri dieback symptoms may be caused by other agents (e.g., other pests and/or pathogens) or environmental conditions (e.g., drought). Furthermore, kauri roots may already be infected but trees may not show any visual symptoms, as there may be a time lag between infection and the appearance of visual symptoms. Little is known about the incubation period, which may vary among kauri individuals and among environmental site conditions (Bradshaw *et al.,* 2020).

Tree characteristics

Ten kauri trees differing in their health status were selected for this study. Tree health status was visually evaluated by examining crown and trunk conditions, including leaf yellowing, canopy thinning, and occurrence of resin bleeding (Waipara *et al.,* 2013; Hill & Waipara, 2017).

The diameter of the selected kauri trees was measured at 1.3 m above the ground using a diameter tape (Table 1). Crown radii (= distance from the centre of the trunk to the perimeter of the crown) in eight cardinal directions were measured in the field. The crown projection area was estimated using the mean of the crown radii (Pretzsch *et al.,* 2015). The thickness of the forest floor (litter plus organic layer) was measured using a retractable tape.

Canopy density (also referred to as canopy closure) was determined from photographs taken at 1.5 m above the ground (next to the throughfall collectors) using a digital camera (OM-D

167 E-M5, Olympus, Olympus 12-50 mm lens set at 12 mm) and the computer software
168 CanopyDigi developed by Goodenough & Goodenough 2012).

169 To minimize the risks of spreading the pathogen, we followed the 'Hygiene procedures for
170 kauri dieback' (Kauri Dieback Management Programme, 2013) by cleaning and disinfecting
171 (using SteriGENE) footwear upon entering and leaving the study site, and all equipment was
172 sanitised between use on different trees.

173

174 **Quantification of *P. agathidicida* DNA concentration in soil**

175 Quantitative PCR (qPCR) was employed to detect *P. agathidicida,* and to quantify the *P.*
176 *agathidicida* DNA concentration in the soil, using the TaqMan approach (Than *et al.,* 2013).
177 Mineral soil (0-10 cm) samples were taken at one meter distances to the trunk in four cardinal
178 directions and each sample was analysed separately (Singh *et al.,* 2017). The DNA was
179 extracted from the soil using the PowerSoil®DNA Isolation Kit (MO BIO Laboratories Inc.,
180 Solana Beach, CA, USA). The ITS (internal transcribed spacer) region was amplified using a
181 TaqMan probe and primers ITS_F2 and ITS_R3 (Than *et al.,* 2013). The qPCR was
182 performed on an ABI Prism 7900HT Sequence Detection System (Applied Biosystems) and
183 then analysed by the qPCR analysis software, SDSv2.4 (Applied Biosystems). The absolute
184 quantification method was used to infer the DNA concentration of *P. agathidicida* in each of
185 the samples. A standard curve was generated by plotting the log10 DNA concentration of
186 standards, against their mean Ct value, which was determined spectrophotometrically at the
187 exponential phase of the qPCR process. A linear regression model was applied to estimate the
188 *P. agathidicida* DNA concentration (ng/µg) in each soil sample. The values presented are the
189 median soil *P. agathidicida* DNA concentration of the samples taken in four cardinal
190 directions. Further details of the methodology are given in Singh *et al.,* 2017).

191

192 **Water sampling**

193 Bulk precipitation collectors (n = 3, spaced 10 m apart) were located in a pasture
194 (approximately 150 m from the study area, 50 m above sea level). The collectors consisted of
195 plastic funnels (area = 113 cm^2) mounted on top of 2 L polyethylene (PE) bottles. The same
196 type of collector was used for throughfall (Fig. 2a).

Throughfall collectors (n = 5 per tree) were positioned in a cross-shaped grid around each tree trunk. Four collectors were placed in the four cardinal directions at 1.5 m of the trunk, and one collector close to the trunk to capture the characteristics of the core crown area, following the approach described in Schroth *et al.,* 2001). To avoid contamination by animal and plant debris, a 2 mm PE mesh filter was placed at the bottom of the funnels. The PE bottles were washed frequently with HCl to reduce the growth of microorganisms. To minimize exposure to ultraviolet radiation and to prevent algae growth between sample collections, the collectors were wrapped in aluminium foil.

The stemflow collar consisted of a butyl inner tube and foam tube (4 cm in diameter, cut in half). The foam tube was wrapped around the trunk at approximately 1.3 m above the ground and fixed to the stem with the inner tube to create a watertight seal. The collars were sloped around the tree and connected to a PE tube fitted at the lowest point to drain off the stemflow into a 20 L PE bucket (Fig. 2b).

Free-draining lysimeters (n = 2 per tree) were used to collect forest floor leachate. One lysimeter was located at a 1.5 m distance from the trunk, and one was close to the trunk. The lysimeters (area = 298 cm^2) consisted of polypropylene (PP) plates covered with a 0.5 mm PE net, and were connected with a PE tube to 2 L PE bottles (Fig. 2c).

Bulk precipitation, throughfall, stemflow and forest floor leachate were collected over one year. From 5 July to 30 September 2015 the sampling interval was weekly to fortnightly. Due to logistical constrains, samples were collected on a monthly basis from 27 October 2015 to 20 June 2016. Throughfall from the individual collectors of a given tree was pooled to one volume-weighted sample per tree per collection date. The solution from each individual lysimeter was pooled to one volume-weighted sample per collection date. Water volume in each individual sampler on a given sampling date was measured with a graduated cylinder.

Chemical analysis

Water samples were filtered (GF 6, Whatman, GE Healthcare, Buckinghamshire, UK, pore size < 1 µm) on the day of collection and then frozen (-18°C). Potassium (K, 0.1 mg l^{-1}), calcium (Ca, 0.1 mg l^{-1}), magnesium (Mg, 0.02 mg l^{-1}), phosphorous (P, 0.1 mg l^{-1}), sulphur (S, 0.3 mg l^{-1}), sodium (Na, 0.1 mg l^{-1}), silicon (Si, 0.005 mg l^{-1}), iron (Fe, 0.01 mg l^{-1}), and manganese (Mn, 0.003 mg l^{-1}) concentrations were measured using an inductively-coupled plasma optical emission spectrometer (ICP-OES, Varian 725-ES, Agilent Technologies

Australia Pty Ltd, Mulgrave, Victoria, Australia). Values in brackets give the detection limit of a given element. Nutrient concentrations below the detection limit were arbitrarily set to half of that limit for further calculations. Phosphorous (P) concentrations were below the detection limit in most ecosystem components, and are not presented. Nutrient concentrations were not measured in samples taken on 21 July, 2 August, 26 August, and 9 September 2015.

Water yield and nutrient fluxes

Bulk precipitation, throughfall and forest floor leachate water yield were estimated in mm units as follows:

$$Bulk\ precipitation(BP), throughfall(TF), forest\ floor(FF)\ leachate(mm) = \frac{BP, TF, \wedge FF\ volume(BP,}{collector\ area(0.0113 m^2\ for\ BP \wedge T}$$

(1)

Stemflow yield was estimated by dividing the stemflow volume by the crown projection area of a given tree to obtain stemflow yield per tree (= stemflow depth) (Park & Cameron, 2008; van Stan & Stubbins, 2018).

$$Stemflow(mm) = \frac{stemflow\ volume(l)}{crown\ projection\ area(m^2)} \quad (2)$$

Frequent overflow of stemflow collectors was observed for trees 3, 4, and 13. Thus stemflow yield could not be calculated for these trees. In the case of missing stemflow values, or overflow of the remaining trees, gap filling was done. Regression analysis was applied to determine the relationship between bulk precipitation and stemflow, and throughfall and stemflow. These functions (linear or polynomial) were used to estimate stemflow volumes for collection dates with missing stemflow data or stemflow overflow.

The nutrient input (mg m^{-2} sampling $date^{-1}$) to the mineral soil through the various water pathways for a given sampling date was calculated by multiplying nutrient concentrations (mg l^{-1}) with the corresponding water volume (mm). The nutrient flux of all collection sampling dates were summed together to obtain the annual nutrient yield per tree (mg m^{-2} $year^{-1}$).

To estimate the nutrient flux for collection dates with missing nutrient concentrations we determined the relationship between water yield and nutrient fluxes for a given tree across the sampling period using regression analysis.

To assess the canopy effect on bulk precipitation chemistry, the net throughfall nutrient fluxes were calculated as follows (Parker, 1983):

$$Net\ throughfall\ flux_x = throughfall\ flux_x - bulk\ precipitation\ flux_x \quad (3)$$

Where x is a given macro-, micro-, or beneficial nutrient.

The contribution of seasalt-derived elements was estimated as follows (Keene *et al.,* 1986; Pierret *et al.,* 2019):

$$Enrichment\ factor(X) = \frac{\left(\frac{X}{Na \vee Mg}\right)_{BP,TF,SF,FF}}{\left(\frac{X}{Na \vee Mg}\right)_{seawater}} \quad (4)$$

Where X/Na or $Mg_{BP, TF, SF, FF}$ is the ratio between the element X and the concentration of Na or Mg in the corresponding sample of bulk precipitation, throughfall, stemflow and forest floor leachate. X/Na or $Mg_{seawater}$ is the ratio between the element X and the concentration of Na or Mg in seawater.

These calculations were based on the assumption that Na or Mg originated from sea spray, and had a conservative behaviour. Na and Mg concentrations were strongly correlated (rho = 0.860, $p < 0.001$) suggesting that Mg in this ecosystem is mainly seasalt-derived. An enrichment factor > 1 indicates a contribution of non-sea sources (Keene *et al.,* 1986, Mimura *et al.,* 2016, Pierret *et al.,* 2019).

Statistical analysis

In view of the non-normal distribution of water yields, nutrient concentrations and fluxes, nonparametric statistical tests (Kruskall-Wallis followed by post-hoc separation; significant at $p < 0.05$) were used to assess differences in median values between ecosystem components (bulk precipitation, throughfall, stemflow, and forest floor leachate). The relationships between soil *P. agathidicida* DNA concentration, tree characteristics (canopy density, forest floor depth), annual water yield and nutrient fluxes were tested using Spearman Rank correlation analysis.

Linear mixed-effect models were used to identify the effect of soil *P. agathidicida* DNA concentration and canopy density on response variables (water flux, nutrient concentrations and fluxes) in throughfall, stemflow and forest floor leachate. Visual tree health status (*rho* =

285 0.723, p = 0.018, n = 10) and tree diameter (*rho* = -0.650, p = 0.042, n = 10) were
286 significantly correlated with soil *P. agathidicida* DNA concentration and thus were not
287 included in the linear mixed-effect models. Soil *P. agathidicida* DNA concentration
288 (expressed as a z-score), canopy density (expressed as a z-score), water flux (when testing
289 nutrient concentrations), and forest floor depth (when testing nutrient concentration and
290 fluxes in forest floor leachate) were defined as fixed effects. Sampling date (expressed as
291 days since the start of sample collection) was included as a random factor to account for
292 repeated measures. Simple (simple effects) models included soil *P. agathidicida* DNA
293 concentration, canopy density, water flux (when testing nutrient concentrations), forest floor
294 depth and sampling date. Complex models contained all factors without interactions, and
295 maximal models contained all factors and interactions. In cases of non-homogeneity of
296 residuals, the response variables were transformed. The models were run using restricted
297 maximum likelihood estimation. The Akaike's information criterion (AIC) value was
298 calculated for each linear mixed-model. The difference in AIC between models was
299 calculated (AIC_i-AIC_{min}). The models with the highest explanatory power were identified
300 when the model with the lowest AIC value differed by more than three from other models
301 (Burnham & Anderson, 2002).

302 All statistical analyses were conducted using the software package IPM SPSS Statistics
303 Version 25 (IBM Corporation, Chicago, IL, USA).

Results

Nutrient concentrations in bulk precipitation, throughfall, stemflow and forest floor leachate

Median concentrations in bulk precipitation varied by several orders of magnitude (ppb to ppm) between elements in the order Na > S > Mg > K > Ca > Si > Mn > Fe (Table 2). For most elements, concentrations increased along the vertical ecosystem profile from bulk precipitation < throughfall ≤ stemflow < forest floor leachate (Table 2). Although bulk precipitation concentrations tended to increase as precipitation is traversing the canopy, significant differences for most elements were only found between bulk precipitation and stemflow, and between bulk precipitation and forest floor leachate (Table 2). Forest floor leachate K, Fe, Mg, S, Si, Ca concentrations were significantly higher compared to throughfall (Table 2).

We found a clear seasalt contribution for Na in throughfall, stemflow and forest floor solutions, and for S in all components with enrichment factors between 0.44-0.86. Magnesium originated partly from seasalt with enrichment factors between 0.69-0.89 for bulk precipitation, throughfall and stemflow.

Annual nutrient fluxes in bulk deposition, throughfall and forest floor leachate

Medians of annual water flux decreased as precipitation percolated through the canopy and forest floor: bulk precipitation (1693 mm) > throughfall (1125 mm) > forest floor leachate (793 mm) (Table 3). Compared to bulk precipitation, the canopy was a source for most nutrients, as the positive median values of the net throughfall fluxes demonstrate (Table 3). Normalized to the crown projection area, stemflow nutrient fluxes contributed less than 3% of annual bulk precipitation nutrient fluxes (macronutrients: 0.3-1.4%; micronutrients: 2.6-2.8%; beneficial nutrients: 0.3-0.4%). Forest floor leachate was enriched in all nutrients compared to bulk precipitation and stemflow, and forest floor leachate had significantly higher Ca, Fe, Si fluxes than throughfall (Table 3). Compared to bulk precipitation, a very strong enrichment was observed for Fe in forest floor leachate (260-fold increase). Compared to throughfall, nutrient fluxes in forest floor leachate were between 1.2 and 4.3 times higher, except for Fe (82-fold) (Table 3).

335 **Effect of tree, soil and infection metrics on nutrient concentrations and fluxes**

336 We found significant negative correlations between *P. agathidicida* DNA concentrations and
337 throughfall Ca (*rho* = -0.723, *p* = 0.018), K (*rho* = -0.833, *p* = 0.003), Mg (*rho* = -0.717, *p* =
338 0.02) and S (*rho* = -0.857, *p* = 0.002) concentrations, but no correlation between throughfall
339 nutrient concentrations and canopy density. Stemflow nutrient concentrations were neither
340 significantly correlated with soil *P. agathidicida* DNA concentration nor with canopy
341 density. In contrast, forest floor leachate Mg (*rho* = -0.644, *p* = 0.044), Na (*rho* = -0.687, *p* =
342 0.028), S (*rho* = -0.657, *p* = 0.039) and Si (*rho* = -0.705, *p* = 0.023) concentrations were
343 negatively correlated with soil *P. agathidicida* DNA concentration, and forest floor leachate
344 Na (*rho* = 0.753, *p* = 0.012) and Si (*rho* = 0.833, p = 0.003) concentrations were positively
345 correlated with forest floor depth.

346 No significant correlation was found between throughfall, stemflow and forest floor leachate
347 water yield and soil *P. agathidicida* DNA concentration (Fig. 3a-c). Throughfall K and Mn
348 fluxes and forest floor Ca and Si fluxes were significantly negatively correlated with soil *P.*
349 *agathidicida* DNA concentrations (Fig. 4 a-d). A positive correlation was found between
350 forest floor depth and forest floor Mn (*rho* = 0.704, *p* = 0.023) and Si (*rho* = 0.642, *p* =
351 0.045) fluxes.

352 Linear mixed-effect models at tree level enabled separating the effects of canopy density,
353 forest floor depth and soil *P. agathidicida* DNA concentration on nutrient concentration and
354 fluxes. The results revealed that soil *P. agathidicida* DNA concentration significantly
355 affected throughfall S, K, Ca, Mg and Mn fluxes (Appendix Table A1b) and net throughfall
356 fluxes of Ca, K and Mg (Table A2). No effect of soil *P. agathidicida* DNA concentration was
357 found for stemflow nutrient concentrations and fluxes (Table A3a, b). Linear mixed-models
358 revealed a significant effect of soil *P. agathidicida* DNA concentration on K, Mg, Mn
359 concentration in forest floor leachate (Table A4a).

360

361 **Discussion**

362 **Solution chemistry and nutrient fluxes**

363 The nutrient concentration in bulk precipitation at Huia is similar to rainfall measured at
364 Huapai 1983-1985; Reed 1984; Sangster 1986), located 25 km north of Huia. The proximity
365 of Huia to the coast (Manukau Harbour and Tasman Sea) partly explains that a considerable
366 proportion of S and Mg in bulk precipitation originates from marine sources. A close

association between sulphur concentration in rainfall and the distance to the west and east coast of New Zealand has been reported by Ledgard & Upsdell 1991). Seasalt contributes most of the Na, Mg and K measured in bulk precipitation at stations located near the ocean, independent of longitude and latitude (Miller, 1963; Galloway *et al.,* 1982; Keene *et al.,* 1986; McDowell *et al.,* 1990; Nichol *et al.,* 1997; Mimura *et al.,* 2016; Pierret *et al.,* 2019).

Rainfall passing through the canopy, flowing along branches and stems, and percolating through forest floor becomes enriched in nutrients (Table 2). Throughfall and stemflow Na, K, Mg and Ca concentrations were similar to the range of concentrations measured in a kauri-dominated forest at Huapai (Reed, 1984; Sangster, 1986). Throughfall nutrient concentrations in these kauri broadleaf forests were 5 to 10 times higher than values measured in a beech-podocarp hardwood forest in New Zealand (Neary *et al.,* 1978). Higher throughfall nutrient concentrations at Huia (and Huapai) are partly explained by the seasalt-derived input of Na and Mg. Seasalt influencing throughfall chemistry has been observed across a range of conifer and broadleaf forests located near the ocean (Westman, 1978; Farrell *et al.,* 1998; Pierret *et al.,* 2019).

An increase in median nutrient concentrations from bulk precipitation < throughfall ≤ stemflow < forest floor leachate (Table 2) corroborates observations reported for many natural forest ecosystems and forest plantations across biomes (Parker, 1983; Bellot & Escarre, 1991; Lovett *et al.,* 1996; Staelens *et al.,* 2007). Higher nutrient concentrations in throughfall and stemflow compared to bulk precipitation are mainly attributable to the following processes: (1) the transfer of atmospheric and marine-derived nutrients (Parker, 1983), (2) wet and dry deposition of nutrients (Ulrich, 1983; Lovett & Lindberg, 1984; Staelens *et al.,* 2006), and (3) wash-off and leaching of nutrient from foliage, foliar microflora, twigs, branches and stems (Miller, 1963; Tukey, 1970; Potter, 1991; Staelens *et al.,* 2007).

However, to identify nutrient sinks and sources within an ecosystem, nutrient fluxes (amount per area and time), rather than concentrations, are required. Net throughfall fluxes highlighted the importance of throughfall as a pathway for nutrients in this kauri-dominated forest. Higher nutrient fluxes in throughfall compared to bulk precipitation has also been observed across deciduous and evergreen forests across biomes indicating the leaching of nutrients from the canopy (Carlisle *et al.,* 1966; Parker, 1983; Staelens *et al.,* 2007). Throughfall was a net nutrient source, independent of the element (Table 3). However, the importance of throughfall as a nutrient source varied between elements, and decreased in the order K (+

800%) > Mn (+ 660%) > Ca (+ 217%) ≈ Fe (+ 215%) > Mg (+ 136%) > S (+ 83%) ≈ Na (+ 82%) > Si (+ 17%). These differences are likely driven by element availability and leachability. Potassium is the most-required nutrient in plants (2–5% dry weight) (Schulze *et al.,* 2019). The cycling rate of K is fast, compared to other elements (Cole & Rapp, 1981). As a monovalent cation, K is the most mobile element in the canopy and is readily leached (Parker, 1983; Staelens *et al.,* 2003), while divalent cations (e.g. Ca, Mg) are more strongly bound (Cape, 1993; Pallardy, 2007). In contrast, Mn and Fe occur in plants in chelated form and are less easy to leach, although Mn exhibits the second-highest increase among the studied nutrients, which might point to pathogen-induced leaf tissue damages or early leaf senescence.

While median nutrient concentrations in stemflow tended to be slightly higher than throughfall, the contribution of stemflow to ecosystem nutrient fluxes was small (< 3 % of annual nutrient fluxes in bulk precipitation) due to low annual stemflow water yield (1.43 mm yr^{-1}; 0.8% of bulk precipitation) (Table 3). Stemflow normalized to the crown projection area accounted for 1.0-4.7% of bulk precipitation in a kauri-dominated catchment at Huia (Sangster, 1986) and ~4% a kauri forest in Northland, New Zealand (Fowler, 2015). Kauri stemflow water yield is highly variable depending on the size of rainfall events, tree size and morphology, and bark coarseness (Sangster, 1986). A global review showed that stemflow in two-thirds of the studies was less than 2% of bulk precipitation (van Stan & Gordon, 2018). However, stemflow can be enriched in nutrients (10-100 times higher than bulk precipitation and throughfall) and thus be an important spatially localized nutrient source to the soil near tree stems (Enright, 1987; van Stan & Gordon, 2018).

The forest floor in this kauri-dominated forest was an additional nutrient source, especially for Fe (+ 8082%) >> Si (+ 326%) > Ca (+ 205%) > Mn (+ 64%) > K (+ 38%) > S (+ 24%) > Mg (+ 19%) and was also a minor sink for Na (-10%). The high Fe flux was astonishing, given that Fe content in leaves and plant biomass is low (< 100 µg g^{-1} DW) (Schulze *et al.,* 2019). We suggest that Fe might be derived from the dissolution of ferric oxides by water-soluble organic compounds (carboxylic acids, polyphenols) leached from kauri leaves and organic matter (Bloomfield, 1955). We assume that the net release of the other nutrients from the forest floor is due to leaf litter decomposition and leaching. The nutrient concentrations in dead kauri leaves decline in the order Ca > K >> Na = Mg (Enright & Ogden, 1987), which roughly aligns with the sequence given above.

To assess throughfall and forest floor-derived nutrient inputs in relation to litterfall derived nutrient input, we compared nutrient fluxes in throughfall and forest floor leachate at Huia (Table 3) with annual litterfall-derived nutrient fluxes measured in a nearby Huapai kauri-dominated forest (Enright, 2001). Forest structure, basal area and litterfall at Huia (van der Westhuizen, 2014) and Huapai (Enright, 2001) are similar. The amount of K and Mg returned to the forest floor via throughfall was 2 and 2.5 times higher, respectively, than via litterfall. The leaching of K and Mg from the forest floor was up to three times larger than K and Mg input via litterfall. This is in line with results from a study conducted at Huapai where nutrient input via throughfall and stemflow was three times that from litterfall (Reed 1984). Large build-up of organic matter (up to 2 m close to tree trunks) with resident times of up to 78 years (Silvester & Orchard, 1999) partly explains the lower nutrient return through litterfall. Similar findings have been reported from exotic conifer stands in New Zealand where throughfall reaching the soil under Douglas fir contained twice as much K as litterfall (Will, 1959), while atmospheric deposition plus canopy leaching delivered three times more K to the soil than the internal nutrient recycling via litterfall (van Langenhove *et al.,* 2020). These studies highlight that canopy leaching is an important nutrient source, particularly of K. Canopy-derived nutrient fluxes may be critical in sustaining the productivity of forests, in particular in soils characterised by low soil nutrient availability, such as soils under kauri forests (Verkaik *et al.,* 2006; Steward & Beveridge, 2010).

Effect of *P. agathidicida* infection on nutrient concentrations and fluxes

Throughfall:

With increasing soil *P. agathidicida* DNA concentration, throughfall nutrient concentration and fluxes decreased (Fig. 4a-d), supporting our hypothesis. The same pattern has been found for dissolved N and C concentration and fluxes (Schwendenmann & Michalzik, 2019). High variability in water yield (700-1350 mm; Fig. 3a) may partly explain the lack of a relationship between soil *P. agathidicida* DNA concentration and water yield (Schwendenmann & Michalzik, 2019). Further, differences in canopy density between trees (Table 1) did not seem to be large enough to affect throughfall water yield.

The following processes may explain the observed decline in nutrient concentration and fluxes in throughfall:

(1) Decline in leaf nutrient concentration, which reduced the amount of nutrients leached from foliage. Like many other Phytophthora species, *P. agathidicida* infects the roots. Fine roots become necrotised, then the pathogen may progress up the root and into the root crown, or invade xylem vessels (Jung *et al.,* 2018). Root dieback and/or the obstruction of nutrient and water transport via the xylem limits the uptake of nutrients. The visible symptoms are often chlorosis and wilting of leaves, a thinning of the crown, and eventually the death of the infected tree (Oßwald *et al.,* 2014). Studies reported lower leaf N concentrations in infected *Quercus robur* (Jönsson *et al.,* 2003; Jönsson, 2004) and *Fagus sylvatica* seedlings (Fleischmann *et al.,* 2004), which suggests a reduction in nutrient uptake, and/or translocation of nutrients from the leaves to the roots to sustain root production and/or produce defensive compounds (Jönsson, 2006). A ~ 30% reduction in Mg leaf content was observed in *Fagus sylvatica* seedlings infected with *Phytophthora citricola* (Wang *et al.,* 2003). In contrast, substantial root dieback of *Quercus robur* seedlings following *Phytophthora quercina* and *Phytophthora cactorum* infection did not have a significant effect on leaf nutrient concentrations (Ca, Mg, K, Mn, Fe, S) (Jönsson, 2004).

(2) Loss of foliage due to pathogen infection diminished the interaction of water with foliar surfaces, thus decreasing throughfall nutrient concentrations (Parker, 1983). Trees with higher soil *P. agathidicida* DNA concentration showed considerable canopy thinning (Fig. 5), reducing washoff (McDowell & Likens, 1988; Parker, 1990), and foliar leaching (of potentially nutrient-depleted foliage) (Tukey, 1970; Czech & Kappen, 1997).

(3) Foliicolous lichens were found on some leaves shed by kauri trees characterised by higher soil *P. agathidicida* DNA concentrations. In a blue oak woodland in California trees with epiphytic lichens had higher N, Ca, Mg, Na and Cl depositions under their canopy than trees were lichens were removed (Knops *et al.,* 1996). Based on this finding, we speculate that the loss of foliicolous lichens may partly contribute to the decrease in nutrient deposition.

Stemflow:

Soil *P. agathidicida* DNA concentration had no significant effect on stemflow nutrient concentrations and fluxes. This may partly be explained by the high variability in stemflow nutrient concentrations and water yield between trees masking the effect of *P. agathidicida* infection. Given that stems of highly-infected trees showed a higher cover of vines, bryophytes (moss) and lichens (Appendix Fig. A1), we were expecting a change in stemflow

nutrient concentrations and fluxes. Previous studies have shown that epiphytic lichens and bryophytes affect stemflow chemistry by selective uptake or release of nutrients (Lang *et al.,* 1976; Jordan *et al.,* 1980). For example, the depletion of stemflow N, P and Ca fluxes in a subtropical montane forest has been attributed to nutrient uptake by the epiphytic bryophytes (Liu *et al.,* 2002).

Forest floor leachate:

Forest floor leachate concentrations (Mg, Na, S and Si) and fluxes (Ca, Si; Fig. 4c,d) decreased significantly with increasing soil *P. agathidicida* DNA concentration as hypothesised.

The observed decrease in nutrients can partly be explained by the following processes:

(1) Higher plant nutrient uptake due to changes in density and composition of understory plant communities. Understory plant density was higher underneath kauri trees characterised by high soil *P. agathidicida* DNA concentrations and severe canopy dieback. Studies have shown that dieback or removal of dominant trees can lead to greater productivity of the remaining species (Klein & Perkins, 1978) and higher plant nutrient uptake. Understory plant species did not show any signs of dieback and are functionally different to kauri and kauri-associated plant species (van der Westhuizen, 2014; Wyse *et al.,* 2014). Several kauri-associated species belong to the family of *Ericaceae* (Wyse *et al.,* 2014). The replacement of these often slow-growing 'stress tolerant' plant species (Grime, 1977) by species with higher nutrient requirements may have resulted in an enhanced uptake of nutrients from the forest floor.

(2) Lower forest floor nutrient reservoirs due to lower leaf litter nutrient concentrations, decrease in litter fall and decline in forest floor depth. Lower fine root N, P, Ca, Mg, Fe content have been found in European beech seedlings with *P. citricola* (Wang *et al.,* 2003). Differences in microbial and fungal communities between asymptomatic and symptomatic mature kauri trees (Byers *et al.,* 2020) and changes in microclimatic conditions (van der Westhuizen, 2014) are likely to affect nutrient cycling.

Long term implications of a decline in canopy- and forest floor-derived nutrient input

Given that throughfall and forest floor leachate are an important source of plant available nutrients in this kauri-dominated stand, the significant reduction in throughfall K, Mn and in forest floor Ca and Si fluxes may have long term implications on ecosystem processes, tree health, and host pathogen interactions (Olivia *et al.,* 2014). Potassium plays a critical role in biochemical and physiological processes such as enzyme activation, amino acid synthesis, and carbohydrate metabolism, influencing plant growth and susceptibility of host plants to pathogens and insects (Amtman *et al.,* 2007; Dordas, 2008; Marschner, 2012). Manganese is critical for overall plant vigor and an important regulator of plant responses to stress and disease resistance (Dordas, 2008). Manganese inhibits (1) aminopeptidase production, reducing the supply of essential amino acids for fungal growth and (2) pectin methylesterase, a fungal enzyme that degrades host cell walls (Dordas, 2008; Marschner, 2012). Some studies have shown that Si can restrict fungal hyphae penetration by creating a physical barrier, or by producing antifungal compounds (Dordas, 2008). Further, Si has been identified as a beneficial nutrient for many vascular plant species, in particular under stress conditions (Pontigo *et al.,* 2015). Calcium ions preserve the structural integrity and functionality of membranes and cell walls, increase host resistance to invasion, and inhibit mycelial growth and zoospore release (Sugimoto *et al.,* 2010). Calcium applications have been shown to reduce Phytophthora root rot in citrus, avocado and oak (Messenger *et al*., 2000; Campanella *et al.,* 2002; Serrano *et al.,* 2013).

Root or bark infection by Phytophthora species results in root dieback, which affects nutrient and water uptake (Oßwald *et al.,* 2014). Root dieback hampering nutrient uptake, plus the lack of plant-available nutrients in the soil may accelerate the decline in tree health. Further, repairing infected tissues and/or building up plant defences increases the carbon and nutrient requirement of the host (Olivia *et al.,* 2014). Leaf nutrient deficiency and leaf-loss induced weakening of plant defences may facilitate the build-up of pathogen inoculum and produce further damages (Olivia *et al.,* 2014). In summary, a long-term reduction in plant available K, Mn, Si and Ca may accelerate the decline in tree health and increase the susceptibility of kauri to *P. agathidicida* infection.

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Author Contribution

L.S. and B.M. contributed equally to: design of the research, field and lab work, data analysis and interpretation, and writing the manuscript.

Data Availability

The data that support the findings of this study will be openly available in figshare.

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900 **Figure Captions**

901 Fig. 1. Map of study area and location of investigated kauri trees, Huia, Waitakere Ranges
902 Regional Park, Auckland, New Zealand

903 Fig. 2. Canopy and forest floor leachate collectors: (A) throughfall, (B) stemflow, and (C)
904 free draining lysimeter

905 Fig. 3. Soil *P. agathidicida* DNA concentration versus annual water yield of (A) throughfall,
906 (B) stemflow, and (C) forest floor leachate.

907 Fig. 4. Soil *P. agathidicida* DNA concentration versus annual throughfall (A) potassium and
908 (B) manganese fluxes and annual forest floor (C) calcium and (D) silicon fluxes.

909 Fig. 5. Effect of increasing soil *P. agathidicida* DNA concentration and decreasing foliage
910 cover on water yield and nutrient fluxes.

911 Table 1. Tree characteristics, health status and soil *P. agathidicida* DNA concentration
912

Tree number	Tree health status[1] (2015)	Basal area (2015)	Crown projection area (2013)	Canopy density (2013)	Median soil *P. agathidicida* DNA concentration (2015)	Forest floor (2015)
		m^2	m^2	%	ng l^{-1}	cm
2	10	0.155	17.1	82.9	56.4	2.0
3	9	0.256	42.1	69.4	56.6	3.0
4	8	0.276	100.7	74.2	48.8	3.0
6	7	0.311	79.3	72.6	27.9	3.0
8	4	0.658	102.3	79.6	25.4	12.0
9	3	0.243	31.9	83.7	42.0	4.0
10	5	0.353	80.7	75.6	21.3	6.5
11	1	0.435	40.5	81.8	23.1	15.0
12	2	0.177	30.7	86.7	25.4	4.0
13	6	0.290	83.5	83.9	35.5	6.5

913 [1]Visual assessment: Scale from 1-10 with 1 indicating "minimal visual signs of dieback" and 10 as
914 "dead".
915

Table 2. Macro- (K, Ca, Mg, S), micro- (Fe, Mn), and beneficial (Na, Si) nutrient concentrations in bulk precipitation, throughfall, stemflow and forest floor leachate, Huia, New Zealand. Values are median, minimum (min) and maximum (max) concentrations across all trees (n=10) and sampling dates (n=17). Different letters indicate significant differences between water pathways for a given element.

	K	Ca	Mg	S	Fe	Mn	Na	Si
					mg l^{-1}			
Bulk precipitation								
median	0.591[a]	0.491[a]	0.841[a]	1.137[a]	0.0005[a]	0.0015[a]	5.558[a]	0.017[a]
min.-max.	0.050-0.681	0.075-0.824	0.164-1.554	0.150-1.876	0.0005-0.0005	0.0015-0.007	1.461-10.110	0.008-0.281
Throughfall								
median	6.715[a,b]	1.896[a]	2.900[a,b]	3.006[a,b]	0.0005[a]	0.024[a,b]	13.480[a,b]	0.035[a,b]
min.-max.	0.218-23.840	0.178-6.658	0.257-13.160	0.150-11.580	0.0005-0.035	0.0015-0.245	1.461-62.930	0.005-0.112
Stemflow								
median	10.040[b]	2.190[a]	3.221[b]	3.452[b]	0.012[b]	0.074[b]	15.840[b]	0.053[b]
min.-max.	0.391-44.900	0.209-17.120	0.194-19.930	0.472-13.790	0.0005-0.078	0.002-0.316	1.767-66.230	0.008-0.197
Forest floor leachate								
median	14.590[b,c]	8.478[b]	5.289[b,c]	4.993[b,c]	0.240[b]	0.046[b]	20.035[b]	0.161[b,c]
min.-max.	2.465-51.940	1.517-27.940	0.782-15.620	0.385-12.460	0.089-0.809	0.002-0.780	1.645-65.090	0.039-0.683

Table 3. Annual macro- (K, Ca, Mg, S), micro- (Fe, Mn), and beneficial (Na, Si) nutrient fluxes in bulk precipitation, throughfall, stemflow and forest floor leachate, Huia, New Zealand. Values are median, minimum (min) and maximum (max) fluxes across all trees (n=10 for throughfall, n=10 for forest floor leachate, n=7 for stemflow). Different letters indicate significant differences between water pathways for a given element.

	Water yield mm yr^{-1}	**K**	**Ca**	**Mg**	**S**	**Fe**	**Mn**	**Na**	**Si**
					mg m^{-2} $year^{-1}$				
Bulk precipitation									
median	1693	1000.56[a]	717.83[a]	1692.15[a]	1924.94[a]	0.85[a]	4.23[a]	9409.69[a]	28.49[a]
Throughfall									
median	1125	9135.17[b]	2277.7[b]	3988.40[b]	3521.08[b]	2.67[b]	32.24[b]	17091.16[b]	33.23[a]
min	719	5830.03	1508.78	1959.32	1844.03	1.98	20.18	8759.80	27.23
max	1319	12947.64	3140.06	5387.15	5071.22	6.11	61.77	22542.41	45.62
Stemflow									
median	1.433	14.37[c]	4.93[c]	4.66[c]	5.26[c]	0.02[c]	0.11[c]	27.86[c]	0.10[b]
min	0.424	4.24	0.85	1.12	1.23	0.01	0.03	6.06	0.02
max	2.537	34.12	6.60	11.33	10.41	0.03	0.26	51.78	0.12
Forest floor leachate									
median	793	12876.50[b]	6966.98[d]	4737.33[b]	4361.42[b]	220.04[d]	53.16[b]	15464.25[b]	141.99[c]
min	709	9910.17	4567.42	3378.62	3045.18	137.13	30.49	11531.06	108.22
max	962	21407.08	8201.97	7718.33	6740.08	320.66	82.15	23476.63	249.14
Net throughfall flux									
median		8134.61	1559.87	2296.25	1596.14	1.82	28.01	7681.47	4.75
min		4829.47	790.94	267.16	-80.91	1.13	15.95	-649.89	-1.25
max		11947.07	2422.91	3694.99	3146.28	5.26	57.54	13132.72	17.13