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RESEARCH ARTICLE

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Drier climatic conditions may lead to increased herbivorous insect pressure on a native tree, but not on an invasive competitor

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In this study we assessed how an invasive tree (*Acacia mearnsii*) and an ecologically equivalent native species (*Virgilia divaricata*) interact with their insect pests and fungal pathogens in sympatric populations along forest edges in the Cape Floristic region of South Africa. We determined how insect herbivore abundance and fungal disease development differ between the two species across a moisture gradient and whether observed differences can be explained by moisture availability and/or plant nutrient levels. The two host plants had similar foliar nutrient content, but measurements of δ12C / δ13C isotope ratios in leaves indicated that only the native plant experienced drought stress at drier sites. The degree of disease development after tree wounding was similar for both species and was not correlated with soil moisture content in either species. As predicted by the biotic release hypothesis, herbivore numbers were significantly higher on the native plant. Herbivore numbers on *A. mearnsii* were unaffected by moisture availability, but herbivore numbers on *V. divaricata* increased at drier sites. Consequently, under conditions of increased drought, *V. divaricata* may experience higher levels of drought stress than the invasive *A. mearnsii* and may suffer from increased insect herbivory, rendering it a weaker competitor. Herbivore abundance and disease development were significantly influenced by plant nutrient content for *A. mearnsii*, but not for *V. divaricata*. Relatively nutrient-poor *A. mearnsii* trees experienced higher herbivore loads but slower disease development than nutrient-rich trees. Therefore, the susceptibility of *A. mearnsii* seems to be determined by plant nutrient levels, a factor that varies independently from water availability.

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INTRODUCTION

In the natural environment, plants have many enemies that may influence their health and survival. The ability of a plant to defend against and overcome these threats depends on both its genotype and its interaction with the environment (Huber & Jones 2013; Potts & Hunter 2021). Understanding the interaction of enemies such as herbivores and pathogens with both the host plant and the environment is very important in the face of global climate change (IPCC 2001; Hogg et al. 2002; Raza & Bebber 2022) and increased globalisation (Ayres & Lombardero 2000; Wingfield et al. 2001; Guégan et al. 2023). The increased migration of non-native species causes an increase in encounters with new pests and pathogens for both native and non-native species and alters the competitive abilities of both (Ayres & Lombardero 2000).

The interaction of pests and pathogens with their host plants has been the focus of a large body of agricultural and forestry research aimed at securing crops (e.g., Murdock et al. 2013; Oliveira et al. 2014; Yang et al. 2014a,b; Martini & Stelinski 2025; Woodward et al. 2025). Based on such studies, Huber & Hanekleus (2007) proposed a disease triangle model that includes three main factors affecting pest and pathogen attacks on plants: the host plant itself, the pathogen/pest, and the environment. If any connections are broken between these factors, disease development and/or pest attack can be prevented (Huber & Hanekleus 2007), but these interactions are multi-dimensional and very complex (Huber & Jones 2013). Some studies have shown that plants that experience nutrient stress are less vigorous and more susceptible to disease and herbivory (Entry 1986; Huber & Hanekleus 2007; Martín-Cardoso & San Segundo 2025). Therefore, even though resistance to a specific infection is genetically controlled, to express this genetic ability, adequate resources are also required (Huber & Jones 2013; Martín-Cardoso & San Segundo 2025).

Plants with some level of resistance against pathogens and herbivores produce defence molecules when the defence system is activated (Agrios 2005; Paparu et al. 2007; Upadhyay et al. 2025). Nutrient shortage may reduce the production of these key anti-fungal or anti-herbivory compounds. Potatoes (*Solanum tuberosum* L.), for example, are more susceptible to the fungus causing early blight (*Alternaria solani* Sorauer) when they are deficient in nitrogen (N) (Barclay et al. 1973). Similarly, higher levels of N have been shown to reduce fungal endophyte content in *Lolium perenne* L. (Rasmussen et al. 2007). High N along with low phosphorous (P) levels may promote insect herbivory (Marschner 1995; Desaeger et al. 2004). Inversely, it has also been shown that when N levels are increased beyond levels for normal metabolic function, defence compound production may decrease (Ren et al. 2013). An increase in N may also promote morphological changes in the plant and delay plant maturation, both of which can favour insect damage and disease development (Agrios 2005).

As with nutrients, levels of water stress and attack by pests and pathogens are intimately linked (Schoeneweiss 1975; Ayres 1991; Agrios 2005). For example, water stress is known to enhance fungal infection, even though some fungal species are dependent on moisture for successful infection (Agrios 2005). Pest outbreaks are also commonly associated with water-stressed plants (Brodbeck & Strong 1987; Mattson & Haack 1987a, 1987b; Wang & Zhau 2025). The plant stress hypothesis (PSH) predicts that physiological changes in the plant due to water stress can make more N available to herbivorous insects/pathogens (White 1969). This can be due to the impairment of protein metabolism and amino acid synthesis (Brodbeck & Strong 1987). However, the PSH is challenged by Huberty & Denno (2004), who proposed that herbivorous insects may be negatively affected during continuous water-stress conditions. This is true in cases when a reduction in plant turgor and water content can interfere with accessing N (Huberty & Denno 2004). Furthermore, intermediate water-stress events, along with recovery periods, can make increased N available to herbivores, which is not the case under continued water-stress conditions. Intermediate water stress events, which are common in the natural environment and are likely to increase with predicted climate change models for Southern Africa (Ziervogel et al. 2014; DEA 2018), may therefore enhance herbivore pressure on their host plants (Herberty & Denno 2004).

In South Africa, the Australian *Acacia mearnsii* De Wild (Fabaceae) is an important forestry tree (DAFF 2009), but has also become a notorious invasive weed (Dye & Jarmain 2004; Henderson 2007; Rodríguez-Echeverría et al. 2011, Richardson et al. 2023). In response, two herbivorous biocontrol agents have been released for its management in South Africa; a seed-feeding weevil, *Melanterius maculatus* Lea, and a flower-galling midge, *Dasineura rubiformis* Kolesik (Impson et al. 2011). Within the Knysna-Tsitsikamma forest complex, the largest forest complex in South Africa, it has invaded forest margins (Geldenhuys 2004) where it grows sympatrically with the native tree *Virgilia divaricata* Adamson (Fabaceae) (Goldblatt & Manning 2000). *Virgilia divaricata* is important as the most widespread forest margin tree in South Africa (Van der Bank et al. 1996; Mbambezeli & Notten 2003). Both species belong to the Fabaceae and they are ecologically similar (Van der Bank et al. 1996; Searle 1997; Mbambezeli & Notten 2003). They are fast-growing forest pioneer, woody perennial trees and both make use of biological nitrogen fixation through rhizobial associates (Sherry 1971; Joubert 2002). These similarities have led to extensive exchange in their associated organisms, especially insects (Van der Colff et al. 2015) and some pathogenic fungi (Van der Colff et al. 2017). For example, when excluding rare taxa (those with less than four individuals collected), over 75% of all arthropod species and 60% of all herbivore species collected in a previous study in the same region, were associated with both host trees (Van der Colff et al. 2015). These similarities probably lead to considerable competitive interactions, the effects of which can persist for many years even after alien tree removal (Maoela et al. 2016). However, how these two plant species interact with their pests and pathogens in their shared environment has not been studied. Understanding these interactions may provide insight into future reactions of forests to climate change and globalisation, both major future drivers of ecosystem dynamics (Ayres & Lombardero 2000).

We compared herbivorous insect numbers and fungal disease development on *A. mearnsii* and *V. divaricata* over a moisture gradient in populations where these trees grow sympatrically. We determined whether observed differences can be explained by differences in water availability and/or varying plant nutrient levels. We predicted that these tree species may be differentially influenced by environmental factors and that this may influence their susceptibility to pathogens and herbivorous arthropods. We hypothesised that trees with limited water availability would be more vulnerable to herbivorous insects and pathogen infection than trees with adequate water availability. Individual plants and species with high nutrient levels were further expected to be better protected against herbivores and pathogens. Such trees were thus hypothesised to have lower herbivore numbers and may be less affected by pathogens.

MATERIALS AND METHODS

Site selection

This study was conducted in the Knysna-Tsitsikamma forest complex in the Western and Eastern Cape Provinces of South Africa (Figure 1). These forests form part of the Afromontane forest belt situated along the African escarpment from the southern part of South Africa to Tanzania in the northeast (White 1978). The forests are fragmented across their distribution range and, in the experimental area, are interspersed with fynbos vegetation (Mucina & Rutherford 2006). Six localities were identified within the natural distribution of *V. divaricata* where *A. mearnsii* has invaded (Figure 1; and see also Table 1 in Van der Colff et al. (2015) for full site descriptions). These localities provided sites where these species occurred sympatrically from Gouna Pass, near Knysna in the west to Stormsriver in the east (Figure 1) following a moisture gradient (drier to wetter) (Goldblatt & Manning 2000) and where the two species were found in consistent densities (~ 1:2 ratio for *A. mearnsii* vs. *V. divariacata* as determined by estimated canopy cover in a 50 × 50 m plot at each locality). This area receives between 500 mm to 1 200 mm of precipitation annually, with peaks during autumn and early summer (Bond 1981).

Percentage soil water content and plant stress

Five soil samples (196 cm^3 each), 8–10 m apart, were collected at each site ($n = 6$) using a soil auger to a depth of 10 cm , avoiding leaf litter. These samples were collected during December 2012 in mid-summer when conditions were at their driest. Each sample ($n = 30$) was placed separately in moisture-proof bags and taken back to the laboratory, where they were weighed, dried for 24 h in an oven at 80°C and weighed again. The drying process was repeated until there was no change in soil weight between drying events. The final dry weight was recorded per sample, the percentage water content calculated following the methods of Hignett & Evett (2005) and the mean of the five samples per site was used for statistical analyses.

To determine if plant individuals experienced drought stress at any of the sites, we determined the relationship between leaf $\delta^{12}C$ / $\delta^{13}C$ isotope ratio and percentage soil water content for *A. mearnsii* and *V. divaricata* across the sampling range. Water-use efficiency (WUE) can be estimated using carbon isotope discrimination and is therefore a good measure of drought stress. This methodology is based on a higher affinity of the carbon-fixing enzyme (Rubisco) for the more common $\delta^{12}C$ isotope over the less common $\delta^{13}C$ isotope. As the internal CO_2 concentration diminishes in a leaf, the $\delta^{12}C$ / $\delta^{13}C$ ratio decreases, which permits less discrimination in favour of $\delta^{12}C$. This lowered internal CO_2 concentration is normally associated with reduced stomatal conductance, which would increase WUE, assuming CO_2 fixation is not primarily limited by other factors (e.g., thermal deactivation of photosynthesis). A lower discrimination value would be associated with higher WUE (Richards 1996) and is indicative of drought, while a higher discrimination value would be indicative of normal plant functioning without drought stress (Farquhar & Richards 1984).

Leaf carbon stable isotope analyses were performed at the Archeometry Department at the University of Cape Town, South Africa. These values were expressed relative to a Pee-Dee Belemnite (PDB) standard for $\delta^{13}C$ and relative to atmospheric

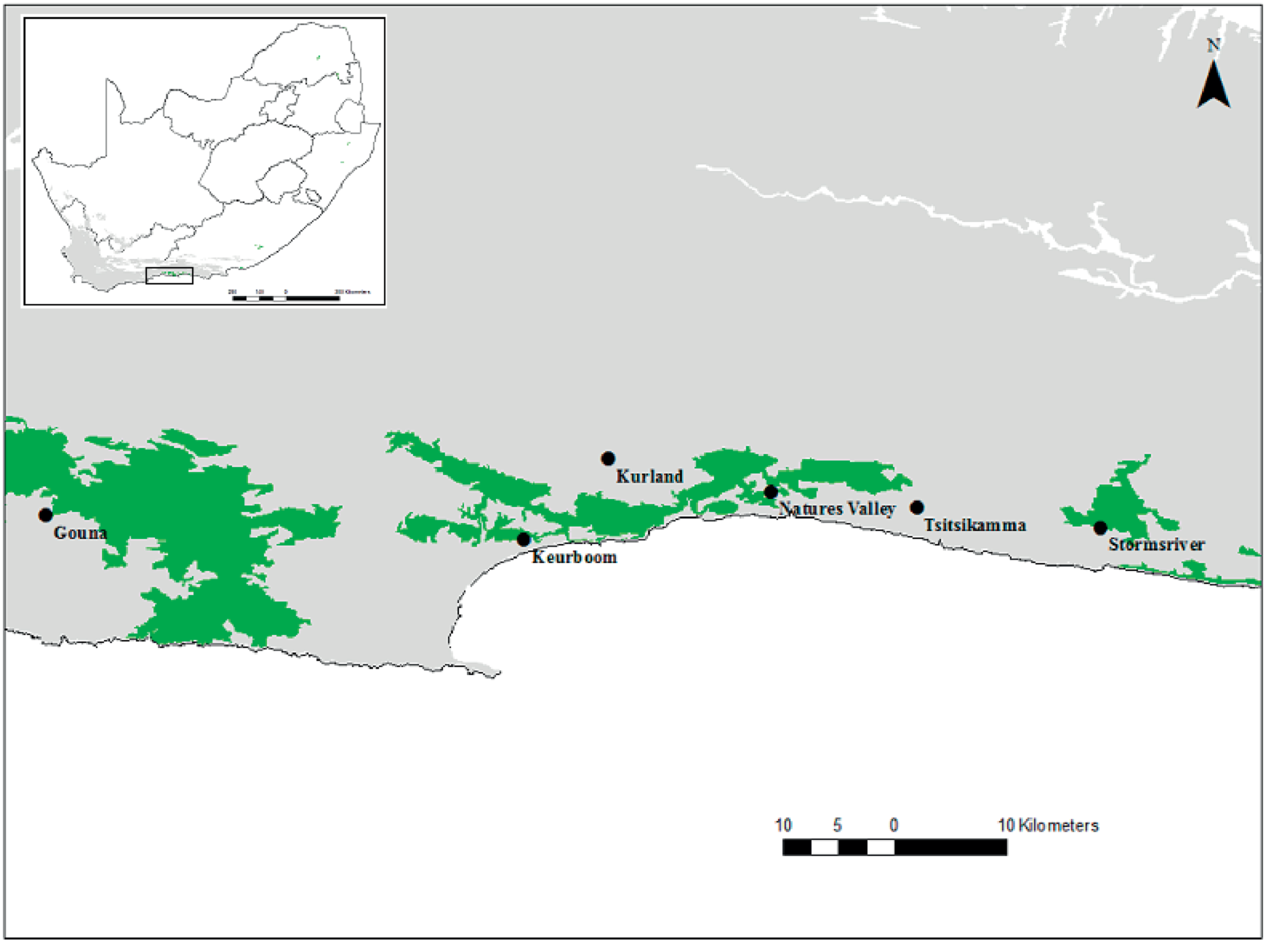

Figure 1: Map depicting the Fynbos Biome and Forest Biome (green) within the Cape Floristic Regions (grey) of South Africa. Sites sampled are indicated by dots.

nitrogen for δ^{15}N, as (%), according to the following equation: $\delta Z = (R_{sample} / R_{standard} - 1) \times 1000$ where Z is the heavy isotope of either nitrogen or carbon, and R is the ratio of heavier to lighter isotope for the sample and standard (δ^{12}C / δ^{13}C or δ^{15}N / δ^{14}N). Oven-dried plant components were milled in a Wiley mill using a 0.5 mm mesh (Arthur H Thomas). Between 2.10 and 2.20 mg of each sample was weighed into 8 x 5 mm tin capsules (Elemental Microanalysis Ltd., Devon, UK) on a Sartorius microbalance (Goettingen, Germany). Samples were weighed to an accuracy of 1 microgram. The sample cups were then enclosed and combusted in a Flash 2000 organic elemental analyser and the gases were passed to a Delta V Plus isotope ratio mass spectrometer (IRMS) via a Conflo IV gas control unit. Three in-house standards (Merck Gel, Lentil, *Acacia saligna* (Labill.) H.L.Wendl) were used and calibrated against IAEA (International Atomic Energy Agency) standards. Leaf material used for this analysis was collected as outlined below. Leaf δ^{12}C / δ^{13}C ratio of ~ 2 g leaf material was measured per tree individual and the mean δ^{12}C / δ^{13}C per site ($n = 6$) was correlated with mean site percentage soil water content ($n = 6$) using Pearson product-moment correlation in the software program STATISTICA 11 (Statsoft, USA, 2012).

Leaf nutrient content

Fifteen fully expanded fresh leaves were collected from each of five randomly chosen trees of each species at each site and placed in brown paper bags (three branches per tree). These leaf samples were oven dried at 72°C for two days, whereafter they were milled and sealed into plastic tubes for later analysis of percentage P, N and C content. Phosphorous concentration was determined by an external laboratory (Elsenburg Laboratory services, Stellenbosch) using inductive coupled mass spectrometery (ICP-MS). The δ^{15}N and N concentration analyses were carried out at the Archeometry Department, University of Cape Town. The isotopic ratio of δ^{14}N / δ^{15}N was calculated as $\delta = 1000$ ‰ $(R_{sample} / R_{standard})$, where R is the molar ratio of the heavier to the lighter isotope of the samples and standards were as defined by Farquhar et al. (1989). Between 2.1 and 2.2 mg of each milled sample were weighed into 8 x 5 mm tin capsules (Elemental Micro-analysis Ltd., Devon, UK) on a Sartorius microbalance (Goettingen, Germany). The samples were then combusted in a Fisons NA 1500 (Series 2) CHN analyzer (Fisons instruments SpA, Milan, Italy). The δ^{15}N values for the nitrogen gas released were determined on a Finnigan Matt 252 mass spectrometer (Finnigan MAT GmbH, Bremen, Germany), which was connected to a CHN analyzer by a Finnigan MAT Conflo control unit. Three standards were used to correct the samples for machine drift – two in-house standards (Merck Gel and Nasturtium) and the IAEA (International Atomic Energy Agency) standard $(NH_4)_2SO4$. This analysis provided both δ^{15}N and N concentration values.

Mean leaf nutrient content for the two host plants was compared using a *t*-test following distribution testing (Shapiro–Wilk test) and testing for homogeneity of variance (Bartlett test of homogeneity of variances) for percentage P, N and C. These analyses were conducted using R statistical software (R Core Team, 2015).

Disease development

Wounds on trees are often colonised by insect-associated microbes such as the ophiostomatoid fungi (Wingfield et al. 1993). In the study area, fungi in insect-associated genera such as *Ceratocystis* Ellis and Halst. and *Sporothrix* Syd. commonly infect tree wounds, including those on *A. mearnsii* and *V. divaricata* (Machingambi et al. 2013; Van der Colff et al. 2013, 2017; Musvuugwa et al. 2020, 2024). Many of these are pathogenic to their hosts (e.g., Roux & Wingfield 1997; Chen et al. 2013; Machingambi et al. 2015; Musvuugwa et al. 2016).

To quantify disease development, trees of similar stem diameter (17–31 cm diameter) of each species were selected at random ($n = 10$) and wounded during November 2012, when temperatures were between 15 and 26°C. The same five individuals of each tree species used for determining leaf nutrient content and $\delta^{12}C$ / $\delta^{13}C$ isotope ratios were wounded. Wounds were created on the trunk of these trees at breast height following the methods of Kamgan et al. (2008). A hammer and flame-sterilised chisel were used to cut into the bark of trees to the depth of the cambium in a rectangular shape (4 × 7 cm) on all sides except for the uppermost side. The bark was lifted to a 20-degree angle with the tree trunk, with the undamaged uppermost side acting as a hinge. This wounding method creates a wound by lifting bark to expose the cambium of the tree and leaves a bark flap over the wound to retain moisture within the wound to enhance microbial infection by insect-associated tree pathogens (Kamgan et al. 2008). The wounds were left undisturbed for 9 months to enable natural colonisation by wound-infecting microbes and disease expression. After 9 months (during August 2013) we returned to the wounded trees, removed the bark from the diseased areas around the wound and measured the length of the lesions that resulted from microbial infection by measuring the length of the initial wound, the length of the lesion (dark stained wood) and calculating the difference in length (Matusick et al. 2010).

To test for the possible effect of plant age on disease development (Heath et al. 2010), we determined the diameter of wounded individuals of each species ($n = 53$) and correlated this to the change in lesion length. Changes in lesion length using individual trees were also compared between the two tree species using a Wilcoxon rank sum test, following distribution fitting as mentioned before.

Herbivorous insect collection

The same trees that were used for the wounding experiment were used to sample foliage-associated arthropods using a vacuum sampler. The vacuum sampler was constructed from a Stihl SH 86 leaf blower/vacuum (Stihl, Germany) with a 15 cm diameter nozzle fitted with a collection net as described by Stewart & Wright (1995), and that is increasingly being used in arthropod biodiversity survey studies on woody vegetation (Van der Colff et al. 2015; Benadé et al. 2016; Maoela et al. 2016; Swart et al. 2017). Herbivore sampling was conducted during November prior to the wounding of the trees. Fifty branches on each tree were sampled by placing each branch within the vacuum nozzle for 3 s (Richmond & Graham 1969). The contents collected per tree was emptied into a re-sealable plastic bag and frozen until further analyses. Adult and larval herbivorous insects, identified based on their family identity and mouth parts (Labandeira 1997), were removed from these samples and their abundances were determined following the methods of Van der Colff et al. (2015).

To compare herbivorous insect abundance between the two host plants, we used Generalized Linear Models (GLZ) with Poisson distribution (with log-link functions) (O'Hara 2009; Zuur et al. 2010) in STATISTICA 11 (Statsoft, USA, 2012). The Wald x^2 (Z) statistic was calculated using the quasi-likelihood technique, given that the analysis showed no over-dispersion of variances compared to the models (Bolker et al. 2009).

Influence of nutrient levels and soil moisture content on herbivore abundance and lesion development

To test for the influence of percentage N, P, C and soil water content on herbivore abundance and change (Δ) in lesion length (i.e., vascular-staining disease development), respectively, GLZ analyses were performed in STATISTICA 11 (Statsoft, USA, 2012). Before analysis, all predictor variables (%N, %P, %C and soil water content) were assessed for any correlations. A strong correlation was found between %N and %P for *A. mearnsii*. Therefore %P was removed as a predictor variable and only %N and %C were used in the model (Bolker et al. 2009). Correlation analysis for nutrient levels in *V. divaricata* found a strong correlation between %P and %C, thus %C was removed from the analysis and only %P and %N were used in this model (Bolker et al. 2009). Removal of predictor variables was based on the strongest resultant fit of the data to the models for the remaining predictors.

Soil water content data (%) were only available as an average per site, while leaf nutrient, lesion length and herbivore abundance data were available for each tree. Therefore, a separate model was prepared for this predictor variable using mean herbivore abundance and mean lesion length data for each plant taxon at each site. Therefore six GLZs were built: 1) to assess the effect of leaf nutrient levels on changes in lesion length within each tree of *A. mearnsii* (Δ lesion length ~ %N + %C); 2) to assess the effect of % soil water content on changes in lesion length across sampled sites of *A. mearnsii* (Δ lesion length ~ % soil water content); 3) to assess the effect of nutrient levels on herbivore abundances within each tree of *A. mearnsii* (herbivore abundance ~ %N + %C); 4) to assess the effect of leaf nutrient levels on change in lesion lengths within each tree of *V. divaricata* (Δ lesion length ~ %N + %P + % N*%P); 5) to assess the effect of % soil water content on changes in lesion length across sampled sites of *V. divaricata* (Δ lesion length ~ % soil water content); and 6) to assess the effect nutrient levels on herbivore abundances within each tree of *V. divaricata* (herbivore abundance ~ %N + %P + %N*%P). The Wald statistic was used to model the data, and a p-value was calculated (McCulloch et al. 2008). Model selection was done based on the lowest Akaike's information criterion value (Bolker et al. 2009). All analyses were conducted in STATISTICA 11 (Statsoft, USA, 2012).

RESULTS

Percentage soil water content and plant water stress

The leaf $\delta^{12}C$ / $\delta^{13}C$ ratio of *A. mearnsii* was not significantly correlated with percentage soil water content across the sampling sites, while leaf $\delta^{12}C$ / $\delta^{13}C$ ratio of *V. divaricata* was significantly and positively correlated with percentage soil water content (Figure 2). Lower negative $\delta^{12}C$ / $\delta^{13}C$ ratio values were found in the leaves of plants growing at the drier sites indicating some drought stress at these sites. The drier sites included Gouna, Keurboom and Kurland to the west of the study area, confirming the existence of a general moisture gradient from west to east across the sampling range (Figure 1).

Leaf nutrients

Fewer samples were successfully analysed for %P content than for other nutrients, resulting in the sample size for %P determination being smaller than that of %N and %C. For analyses where %P was included, we therefore only used data from samples that had the full complement of nutrient data available. Subsequently, *A. mearnsii* had 15 full samples and *V. divaricata* 17 full samples that were used in statistical analyses. There was no significant difference in leaf %N (t-value = 1.3; df = 8.6, p-value = 0.2), %P (t-value = 0.95, df = 9.4, p-value = 0.36) and %C (t-value = 1.87, df = 9.8, p-value = 0.09) between the two tree species for the full dataset (Figure 3a–c). The subset of *A. mearnsii* (15) and *V. divaricata* (17) samples had similar results as the full set assessed for %N ($n = 15$, t-value = 1.03, df = 27.57, p-value = 0.31) and %P ($n = 15$, W = 95, p-value = 0.48) when comparing the two species.

Disease development and herbivore numbers

There was no significant relationship between tree diameter and lesion length in either *A. mearnsii* ($r = -0.21$, $r^2 = 0.04$; p-value = 0.13) or *V. divaricata* ($r = 0.144$, $r^2 = 0.02$; p-value = 0.34). We also found no significant difference in lesion lengths between *A. mearnsii* and *V. divaricata* for individual trees (W = 435.5, p-value = 0.81) (Figure 3d). In contrast, a significant difference in herbivore abundance was found between the two host plants (z-value = 15.86, df = 59, p-value < 0.0001). Higher numbers of herbivores were present on *V. divaricata* ($n = 30$) than on the invasive *A. mearnsii* ($n = 30$) (Figure 3e).

Influence of water stress and nutrient content on herbivore loads and lesion length

There was no correlation between any of the leaf %P ($r = -0.49$, $p = 0.32$), %N ($r = -0.37$, $p = 0.46$) or %C ($r = 0.69$, $p = 0.12$) and percentage water content in *A. mearsnii* or *V. divaricata* (%P ($r = -0.41$, $p = 0.41$), %N ($r = 0.2$, $p = 0.69$) and %C ($r = 0.45$, $p = 0.37$)). Thus, these response variables operate independently. Changes in lesion length were unaffected by soil water content in both tree species. *Acacia mearnsii* trees had larger changes in lesion length at high nutrient levels, with a strong positive correlation with %C and %N (Table 1). In contrast, herbivore abundance was significantly negatively related to %N and %C content of leaves in this species (Table 1). No significant effect of leaf nutrient levels on herbivore abundance or lesion length formation was detected for *V. divaricata*. There was, however, a significant negative correlation between herbivore numbers and soil water content in *V. divaricata* (Table 1).

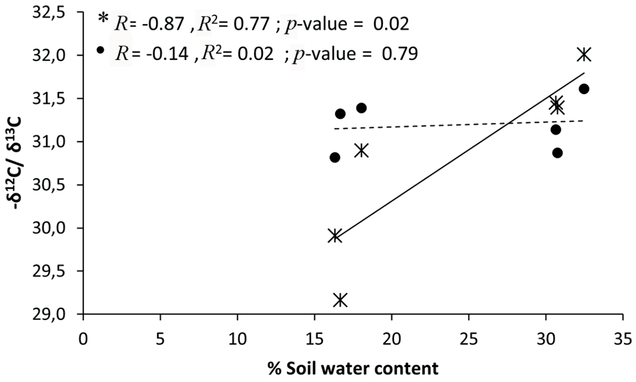

Figure 2: The relationship between δ12C / δ13C isotope ratio and percentage soil water content for *Acacia mearnsii* (• and dotted line) and *Virgilia divaricata* (* and solid line) across the sampling range.

DISCUSSION

Results of this study indicate that the native *V. divaricata* experienced water stress at the drier sites, while the invasive species did not. *Acacia mearnsii* thus seems more drought-tolerant than the native species. This is not surprising, as this species is known to be well-adapted to drought conditions (Morris et al. 2011; Crous et al. 2012). However, both tree species appear to have strategies to alleviate drought symptoms. For example, many vascular-infecting fungi are particularly effective when infecting water-stressed plants (Pegg 1985; Desprez-Loustau et al. 2006), but in this case, both species at drier sites did not show greater symptomatic response. Drier conditions expected under current climate change models (IPCC 1996, 2001; Taylor & Kumar 2013; Engelbrecht et al. 2024) may therefore not influence the susceptibility of these plants to vascular-infecting fungi. However, the mere presence of *A. mearnsii* in habitats where it occurs in sympatry with native species may lead to an increase in pathogen loads. Although not the focus of the present study, it is, for example, known that invasion by *A. mearnsii* leads to increased loads of

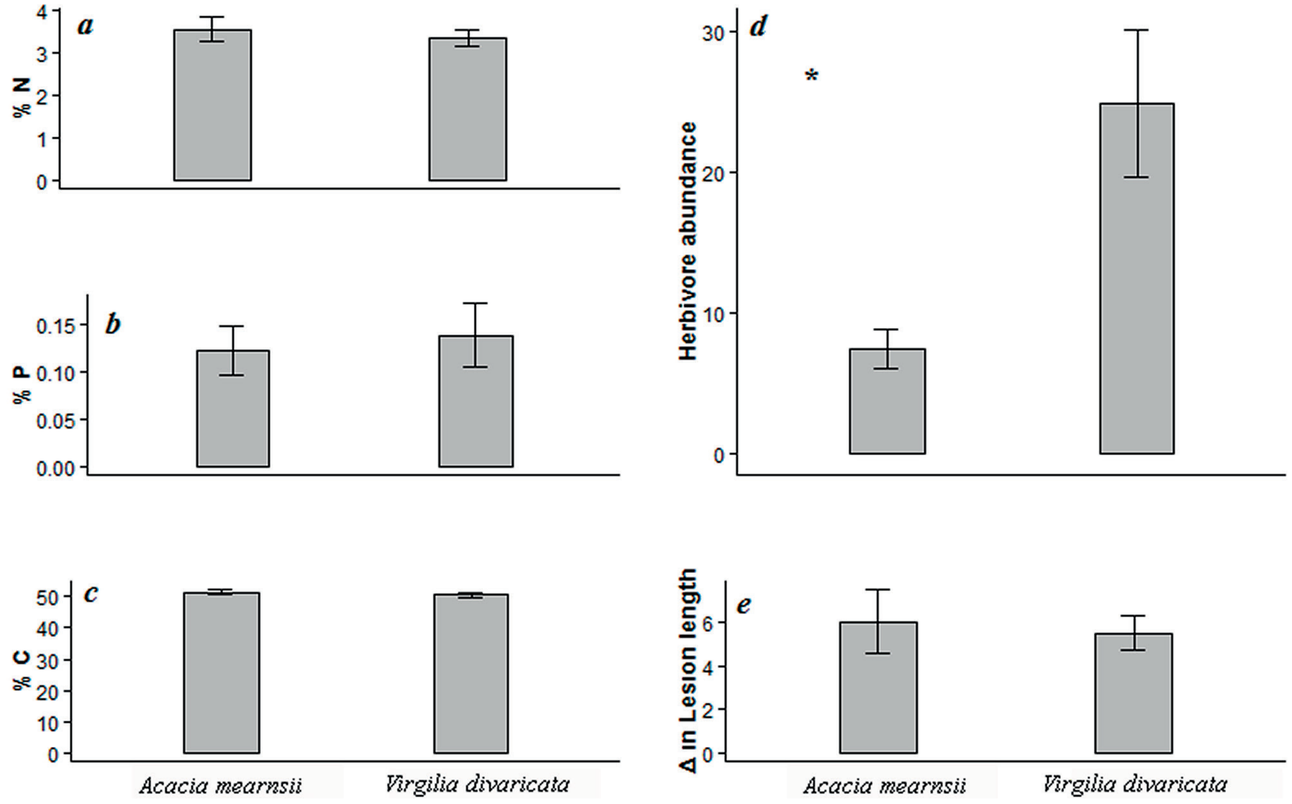

Figure 3: Differences in percentage (a) N, (b) P and (c) C content of leaves of *Virgilia divaricata* and *Acacia mearnsii*. (d) Foliage-associated herbivorous insect abundances were compared between the two host plants using a Generalized Linear Model (GLZ) using a Poisson distribution with a log link function. Means (SD) are plotted. (e) Change in lesion length after wounding of *Acacia mearnsii* and *Virgilia divaricata* ($n = 53$ per species) are compared using a Wilcoxon test, median (SE) are plotted. Asterisks (*) indicates significant differences.

Table 1: Results of Generalized Linear Models for the effect of leaf nutrient content (%N, %P and %C) and % soil water content on changes in herbivore abundance and change in lesion length for *Acacia mearnsii* and *Virgilia divaricata*.

Acacia mearnsii	df	Wald statistic	*p*-value	Direction
Change in lesion length				
%N (*n* = 29)	1	**5.41**	**0.02**	+
%C (*n* = 29)	1	**23.23**	**< 0.05**	+
Soil H_2O content (*n* = 6)	1	1.01	0.31	NA
Herbivore abundance				
%N (*n* = 29)	1	**7.66**	**0.01**	–
%C (*n* = 29)	1	2.44	0.12	–
Soil H_2O content (*n* = 6)	1	0.46	0.50	NA
Virgilia divaricata	**df**	**Wald statistic**	***p*-value**	**Direction**
Change in lesion length				
%N (*n* = 17)	1	0.39	0.53	NA
%P (*n* = 17)	1	0.00	0.95	NA
%N * %P (*n* = 17)	1	0.32	0.57	NA
Soil H_2O content (*n* = 6)	1	0.15	0.70	NA
Herbivore abundance				
%N (*n* = 15)	1	0.01	0.91	NA
%P (*n* = 15)	1	3.31	0.07	NA
%N * % P (*n* = 15)	1	1.71	0.19	NA
Soil H_2O content (*n* = 6)	1	**8.39**	**< 0.05**	–

phylopathogenic fungi on sympatrically occurring, distantly related native tree species, and these effects can persist for many years after removal of *A. mearnsii* (Maoela et al. 2016). In contrast to disease development, herbivore numbers on *V. divaricata* were significantly and negatively correlated with soil moisture content. Therefore, herbivores on this species seemed to prefer plants that experienced drought. We therefore find support for the plant stress hypothesis in *V. divaricata,* as herbivores were abundant where plants were stressed. This was not the case for *A. mearnsii,* which experienced similar herbivore pressure at all sites. This indicates that *V. divaricata* may become more vulnerable to herbivores than the invasive species if climatic conditions become drier.

The two host trees were remarkably similar in terms of leaf nutrient levels and their response to infection by vascular-staining microbes. These plants are also known to share up to 60% of their herbivorous arthropod taxa (Van der Colff et al. 2015, Maoela et al. 2016) and have similar wound-associated fungal communities (Machingambi et al. 2013; Van der Colff et al. 2017; Musvuugwa et al. 2016, 2020, 2024). Therefore, the ecological similarities between these two plant species are striking. If *V. divaricata* experiences more stress from drought and increased herbivore pressure than *A. mearnsii* under drier conditions, it may give the invasive species a greater competitive advantage over the ecologically similar native species, which would aid its invasive success. Increased invasions by *A. mearnsii* will have great ecological consequences, as, for example, seedlings of native trees cannot establish in *A. mearnsii* stands like they do in *V. divaricata* stands (Stinson et al. 2006; Van der Waal 2009; Richardson & Rejmánek 2011; Coetsee & Wigley 2013). This contrasts with invasive *A. melonoxylon* in these forests, as no differences were recorded in native sapling richness, diversity and density underneath *A. melanoxylon* trees versus underneath indigenous trees (Kraaij et al. 2023). Future studies should, however, test for the effect of climatic shifts on pest and pathogen pressures on this invasive species as compared to its native counterparts.

Herbivore abundance and disease development were significantly influenced by plant nutrient content in *A. mearnsii* and not in *V. divaricata*. The pests and pathogens on *V. divaricata* seem well-adapted to it as their presence and usage of this tree lie beyond nutritional value and may rather be related to historical associations (Keane & Crawley 2002). The differences in the response of pests and pathogens between the two hosts in terms of changes in nutrient levels may be linked to the origins of the organisms involved. Most of the herbivores and pathogens associated with these hosts are native and therefore have a long co-evolutionary history with the native *V. divaricata* (Van der Colff et al. 2015; Musvuugwa et al. 2016, 2020, 2024). The plants may therefore have evolved mechanisms to deal with these native pests and pathogens under various nutritional states. In contrast, most pests and pathogens of *A. mearnsii* are likely foreign to this less-preferred host and find this host more attractive under specific nutritional states.

For *A. mearnsii*, nutrient-poor trees experienced higher herbivore loads and slower disease development than nutrient-rich trees. Therefore, the susceptibility of *A. mearnsii* seems to be determined by plant nutrient levels. The opposite was found for herbivores associated with this tree species in riparian systems in South Africa. Here, herbivore numbers showed a positive response to increasing N levels in leaves (Maoela et al. 2016). However, in that case, the effect of plant density was the main factor driving the observed pattern of increased herbivory (denser plant communities also had greater average N levels). In our study, the density of both tree taxa was relatively constant at all sites, negating these effects. The negative association between arthropod abundance and plant nutrient contents found in *A. mearnsii* in the present study may be linked to weakened herbivore defences. Nutrient content was not correlated with water availability and is therefore determined by other factors such as differences in soil nutrient levels, differences in microclimatic conditions and/or plant genotypic variation not determined here.

The positive relationship between lesion length and plant nutrient content in *A. mearnsii* agrees with the results of previous studies showing that some fungal taxa prefer hosts with higher nutrient content, as they receive higher quality nutrition (Desaeger et al. 2004). Within the xylem and phloem of their host plants, these fungi have access to nutrient-rich sap, enabling them to spread through the plant (Pegg 1985). An excess of N in plant tissue has been shown to cause imbalances in other nutrients, decreasing the ability of the plant to produce defence molecules (McMahon 2012). However, increased nutrient levels in *A. mearnsii* plants did not lead to increased damage by phylopathogens in a study by Maoela et al. (2016). Here again, the effect that nutrients may have had on the susceptibility of *A. mearnsii* to phylopathogens was likely overshadowed by the effect of host density (Maoela et al. 2016). It is also possible that vascular-staining pathogens react differently towards changes in host nutrient levels than pathogens associated with the leaves, a possibility that should be tested in future studies.

CONCLUSION

The effect that the environment has on disease development and pest attack is important, since many environments are predicted to become drier and soil nutrient levels may change with the influx of new sources of nutrients from organisms such as invasive legumes. How native and invasive species respond to these changes influences their interaction with their pests and pathogens and ultimately their competitive abilities. *Virgilia divaricata* was affected by drought conditions, and, with drier climatic conditions predicted, this may render it a much weaker competitor against *A. mearnsii* invasion. While *V. divaricata* is well-adapted to fungal infection during stressed conditions, *A. mearnsii* is affected by nutrient content in both disease development and herbivore attack. However, when invasive stands become very dense, these trees could become much more vulnerable to herbivore attack (Maoela et al. 2016). Where *A. mearnsii* occurs in dense stands at sites with limited nutrients, and is exposed to pests and pathogens, they could potentially serve as sources of natural biological control organisms for use in invasive control strategies. Alternatively, these areas could act as sources for the acquisition of pests and pathogens that could negatively impact timber production in the future.

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AUTHOR CONTRIBUTIONS

DvdC: conceptualisation, data curation, methodology, writing – original draft, writing – review & editing. LLD: conceptualiaation, funding acquisition, methodology, resources, supervision, writing – review & editing. AV: conceptualisation, funding acquisition, methodology, resources, supervision, writing – review & editing. FR: conceptualisation, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, writing – review & editing.

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