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Abundance, diversity and development of thrips (Thysanoptera) on avocados and macadamias in the Levubu region of Limpopo Province, South Africa

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Abstract

Some thrips (Thysanoptera) species are presumed to injure avocado and macadamia trees and fruit when feeding as nymphs and adults. We investigated the abundance and species richness of thrips and monitored fruit and nut set and damage on four avocado (Fuerte, Hass, Maluma and Pinkerton) and macadamia (695, 814, 816 and A4) cultivars. Different stages of avocado fruit (1–3, 4–6 and 7–9 cm) or macadamia nut development (closed racemes, nut set, nut size 1–1.5 cm and nut size 3–4 cm) were sampled over two seasons in the Levubu region of Limpopo Province, South Africa. Thrips development on fruit, nuts and leaf flush was recorded to verify the thrips species causing damage. A total of 15 535 thrips were collected during August–January 2020–2021 and 2021–2022. Six thrips morphotypes were identified across macadamia and avocado orchards: *Scirtothrips aurantii* Faure (Thripidae), *Thrips tenellus* Trybom (Thripidae), *Haplothrips gowdeyi* Franklin (Phlaeothripidae), *Frankliniella occidentalis* Pergande (Thripidae), *Megalurothrips* sp. (Thripidae) and *Caliothrips* sp. (Thripidae). Thrips were less abundant in the 2020/2021 season compared to the 2021/2022 season and in avocados than in macadamias. Pinkerton (2020/2021: 4.9 ± 0.8 and 2021/2022: 13.1 ± 0.2) and Fuerte (2020/2021: 6.9 ± 1.3 and 2021/2022: 7.5 ± 0.1) had the highest damage and fruit set per inflorescence in both seasons. Fruit size 1–3 cm had a mean damage of 3.4 ± 0.8 in 2020/2021 and 4.0 ± 0.7 in 2021/2022, 4–6 cm had 5.3 ± 0.9 and 4.7 ± 0.7 in 2021/2022, and 7–9 cm had 5.2 ± 0.9 in 2020/2021 and 5.0 ± 0.8 in 2021/2022. Macadamia cultivars and developmental stages most affected by thrips were dependent on the season. Our results suggest that damage occurs earlier in fruit or nut development, and Fuerte avocados and Macadamia 695 were the least susceptible to thrips damage. *S. aurantii* larvae developed from all sampled avocado and macadamia tissues and were able to persist until the adult stage, confirming it as the main damaging thrips species of avocado and macadamia in the Levubu region.

KEYWORDS
abundance, cultivar, species richness, susceptibility, thrips development

INTRODUCTION

An increase in demand for healthier food products in middle- and high-income countries has led to an increased demand for avocado fruit and macadamia nuts. As a consequence, avocados and macadamias are currently the most widely consumed agricultural products globally (Stolp & Kodali 2022), and they are among the fastest growing agricultural industries in the world (Hardner et al. 2019; Huang et al. 2023). Avocados and macadamias are nutrient-rich and provide health benefits such as antioxidants, bioactive elements, and antimicrobial and anticancer properties (Alasalvar et al. 2020; Araújo et al. 2018). Their by-products are utilised in the cosmetic and personal care industries (Ferreira et al. 2022; Hanum et al. 2019). The avocado and macadamia industries also provide employment for millions of people around the world (Tesfaye et al. 2022).

In South Africa, the avocado industry is export-oriented, with 45% of its produce exported to Europe and the United Kingdom (South African Avocado Growers' Association [SAAGA] 2024; Zwane & Ferrer 2024). Kenya, Ethiopia and South Africa are the leading avocado producers in Africa, with an annual production of 322 556, 167 884 and 146 600 t, respectively (Mukhametzyanov et al. 2023). Even more impressive is that South Africa is currently the largest producer and exporter of macadamias globally, with 87 227 t of dry nut in shell produced at 1.5% moisture content during 2024 (Hardner et al. 2019; SAMAC 2025). Hass (44.1%) and Fuerte (15.55%) are widely grown avocado cultivars in South Africa, followed by Maluma (6.71%), Pinkerton (5.77%) and Ryan (3.87%) (SAAGA 2024; Vorster 2001). Macadamia 695 (Beaumont) is the most commonly grown cultivar, making up 48% of macadamia production, followed by the A4 (24%), 816 (16%), 814 (4%), Nelmak (2%) and 788 cultivars (2%) (Sibulali 2020).

The strong competitiveness of South African avocado and macadamia industries in international markets is challenged by insect pests. Among these, thrips (Thysanoptera) infestation and damage is a major concern to growers (Joubert et al. 2023). Thrips damage reduces crop yields and quality for avocado and macadamia exports (Bright 2018; Hoddle & Morse 2003). Globally, thrips found on avocados and macadamias include *Heliothrips haemorrhoidalis* Bouche (Thripidae) and the red-banded thrips, *Selenothrips rubrocinctus* Giard (Thripidae) (Steyn et al. 1993). *S. rubrocinctus* is found in Asia, Africa, Australasia and the Pacific Islands, North America and Central America (Taddei et al. 2021), while *H. haemorrhoidalis* has been documented in Africa, South America, Europe and the United States (Denmark & Fasulo 2010). They are both polyphagous and exploit unrelated vegetation, with *H. haemorrhoidalis* detected for the first time in greenhouses but was since reported from avocados and macadamias (Dupont 1993; Monteiro et al. 1999; Steyn et al. 1993). *S. rubrocinctus* was first found attacking cacao plants, but the species was confirmed to cause damage on avocados (Denmark & Wolfenbarger 2010). *Scirtothrips perseae* Nakahara (Thripidae) is also a pest of avocados found in Mexico, Guatemala and California, USA (Hoddle 2002; Hoddle & Morse 2003).

In South Africa's Mpumalanga Province, the assemblage of thrips on macadamias comprises species from the 'yellow', 'brown', 'black', 'leaf-feeding' and predatory groups of thrips (Hepburn 2015). The most common thrips species found on avocados in the KwaZulu-Natal Province of South Africa include the following: western flower thrips, *Frankliniella occidentalis* (Pergande); *Haplothrips bedfordi* Jacot-Guillarmod; *Haplothrips gowdeyi* Bagnall; *Megalurothrips sjostedti* Trybom; South African citrus thrips, *Scirtothrips aurantii* Faure; *Thrips gowdeyi* Franklin; *Thrips pusillus* Bagnall; and *Thrips tenellus* Trybom (Bara & Laing 2019). In the KwaZulu-Natal study, thrips were collected from avocados by using the beating method and later identified. Thereafter, rearing of plant tissues was done, and the results indicated *S. aurantii* Faure as the species damaging avocados in KwaZulu-Natal. Despite these reports, information on thrips infestation levels and damage at different avocado and macadamia developmental stages is limited. Thrips infestation and feeding damage by thrips, for example, scarring or other damage types, can be monitored in an integrated pest management system to detect problem areas early on and prevent further damage by intervention (Facun Sarmiento 2014).

In the Levubu region in the northern part of Limpopo Province, South Africa, avocado and macadamia trees are planted with other crops such as bananas, litchis and mangos to take advantage of the terrain as well as soil and agro-climatic conditions (Mpandeli 2014). This creates a situation where there may be shared thrips pests on multiple crops and movement between them. To begin to understand the potential for thrips movement between different crops, this study investigated the abundance and composition of thrips associated with avocados and macadamias in the Levubu region of Limpopo Province, South Africa. It also established the avocado and macadamia cultivars and developmental stages most susceptible to thrips damage and further determined the species of thrips causing damage by rearing them out of plant material. We hypothesised that young fruit, nuts and flush would be most susceptible to thrips damage and that different cultivars would exhibit different responses to thrips abundance and damage.

MATERIALS AND METHODS

Description of study sites

This study was done in the Levubu region, Limpopo Province, South Africa (Figure 1). The region is characterised by

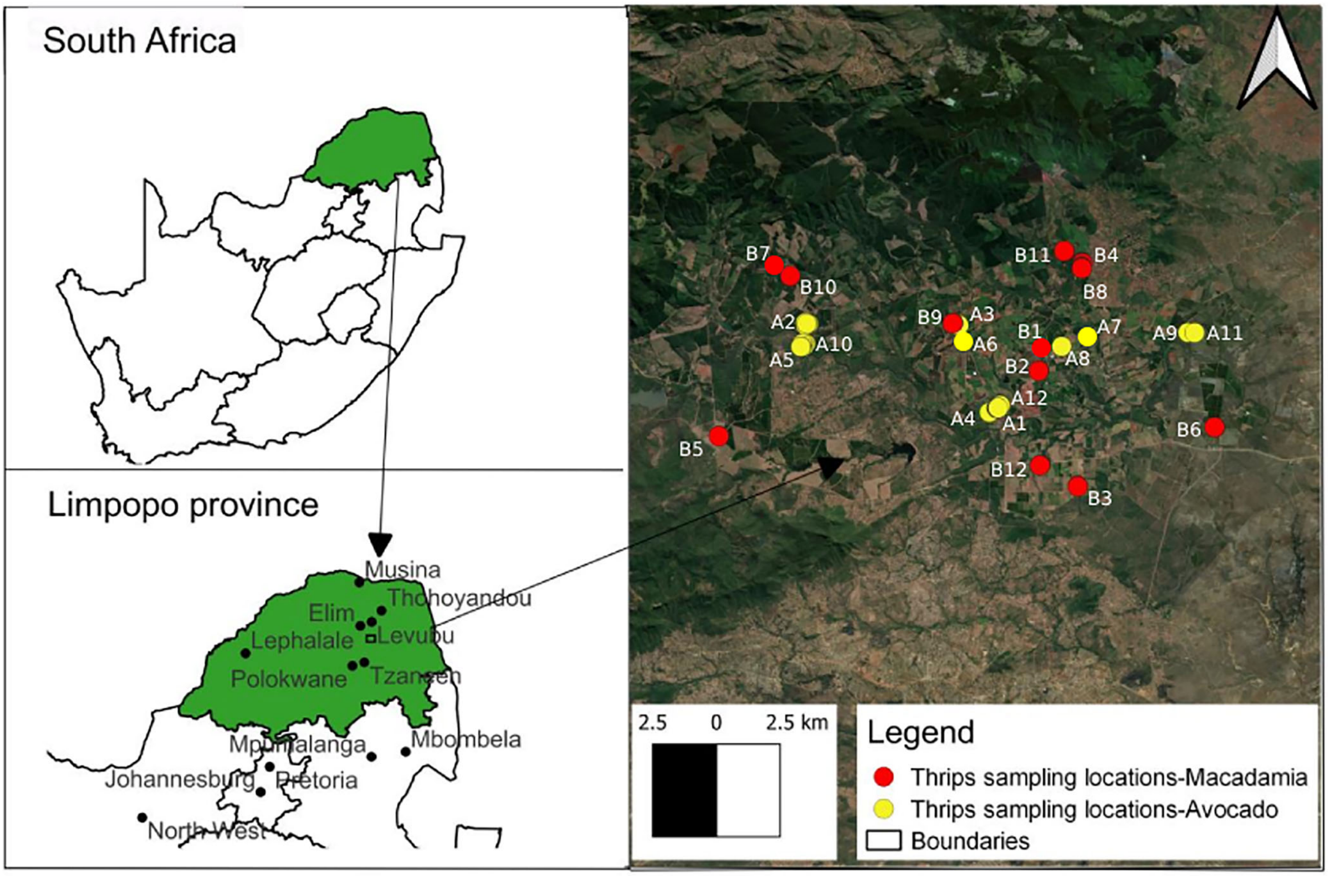

FIGURE 1 Location of sites used to sample thrips on avocados and macadamias in the Levubu region, Limpopo Province, South Africa. White lettering corresponds with the orchard codes given in Tables 1 and 2.

large variations in altitude (200–2100 m above sea level) and rainfall (200–1000 mm) due to its location on the southern side of the Soutpansberg mountain range. The climate of the region is characterised by warm, wet summers and dry winters, with rainfall occurring mostly in the summer period with little or no rainfall during winter (Nkuna & Odiyo 2016). During the period of our study, the region experienced a mean monthly daily temperature range of 14 ± 0.19°C to 24 ± 0.22°C, a maximum temperature of 41.44°C and a minimum temperature of 5.1°C. The area received an average annual total rainfall of 1100 ± 117 mm, an average monthly relative humidity range of 68 ± 0.90% to 91 ± 0.47% and an average monthly wind speed ranging from 1 ± 0.05 to 4 ± 0.08 km/h (Table S1). The Levubu region accounts for 8% (11 720 t) and 54% (79 110 t, Limpopo) of avocado production in South Africa, respectively (SAAGA 2024; Sibulali 2020). The region accounts for 11% (10 192 t) and 20% (17 506 t, Limpopo) of macadamia production in South Africa, respectively (SAMAC 2024; Sibulali 2020). For avocados and macadamias, 12 orchards of relatively similar age (10–15 years) were sampled to represent different eco-geographical conditions and cultivars. The orchards were between 2 and 400 ha and were located in a matrix of other avocado, macadamia and other fruit orchards, eucalyptus and pine plantations, and indigenous forest and savannah vegetation (Figure 1 and Tables 1, 2, S2 and S3).

Thrips sampling

Thrips sampling was carried out from August to January 2020/2021 and 2021/2022 when avocados and macadamias started flowering until fruit or nuts were mature. Sampling was performed on Fuerte, Hass, Pinkerton and Maluma avocado cultivars and 695 (Beaumont), 814, 816 and A4 macadamia cultivars. Pinkerton and Fuerte avocados and macadamias A4, 816 and 814 are early- to mid-flowering and maturing cultivars, whereas Hass and Maluma avocados and Macadamia 695 are mid- to late-flowering and maturing cultivars (Allan 2006; Sippel et al. 1994; Van Rensburg 2021). The above cultivars were selected because they are the most commonly grown cultivars by farmers in the Levubu region and South Africa (SAAGA 2024). Furthermore, pre-existing data indicate the susceptibility of these cultivars to insect damage, including by thrips (Bara & Laing 2020; Jones 2002). Three orchards of each cultivar were used. Ten trees were selected from the four cardinal directions (north, east, south and west) of

TABLE 1 Summary information for avocado orchards sampled for thrips abundance in the Levubu region, Limpopo Province, South Africa.

Code	Cultivar	Farm name	Latitude	Longitude	Orchard age (years)	Orchard size (ha)
A1	Fuerte	Delaja	−23.1094	30.253958	10	5
A2	Fuerte	Neuholf	−23.0591	30.086824	15	10
A3	Fuerte	Springfield Farm	−23.0888	30.277123	15	20
A4	Hass	Delaja	−23.1106	30.252151	15	5
A5	Hass	Neuholf	−23.0707	30.082475	10	6
A6	Hass	Springfield Farm	−23.088	30.177751	15	15
A7	Maluma	Maluma	−23.0814	30.237428	10	5
A8	Maluma	Matari	−23.0817	30.237332	10	2
A9	Maluma	Ras	−23.0837	30.325268	10	5
A10	Pinkerton	Neuholf	−23.0591	30.086662	13	5
A11	Pinkerton	Ras	−23.084	30.325737	10	5
A12	Pinkerton	Delaja	−23.1121	30.249404	10	2

TABLE 2 Summary information for macadamia orchards sampled for thrips abundance in the Levubu region, Limpopo Province, South Africa.

Code	Cultivar	Farm name	Latitude	Longitude	Orchard age (years)	Orchard size (ha)
B1	A4	Matari	30.23534	−23.0804797	10	10
B2	A4	P43	30.08158	−23.0704764	15	7
B3	A4	Truter	30.28327	−23.1377983	10	2.5
B4	814	Lalani	30.28478	−23.0606746	15	10
B5	814	Welmac	30.14576	−23.1203066	10	10
B6	814	Vhavenda	30.33608	−23.1174327	15	5
B7	816	Koos	30.07022	−23.0580207	15	5
B8	816	Lalani	30.27831	−23.0553006	15	20
B9	816	Springfield Farm	30.17281	−23.0642357	15	25
B10	695	Koos	30.06983	−23.0586065	13	10
B11	695	Lalani	30.28478	−23.0588654	15	15
B12	695	Steff de Lange	30.26906	−23.1304875	10	10

the orchard. The trees were selected in a diagonal zigzag pattern from one corner of the orchard block. One tree to the next was selected in a simple random sampling way (Noor et al. 2022). The same 10 trees were sampled from each orchard block over 6 months, with the GPS coordinates of each tree recorded. Sampling was performed at different developmental stages for avocado fruits and macadamia nuts. For avocados, samples were collected at fruit sizes of 1–3, 4–6 and 7–9 cm, whereas macadamias were sampled at racemes (constituting flowers), nut set (first abscission period), nut size (1–1.5 cm) and hard shell (3–4 cm). At each tree, thrips were dislodged from closed racemes, nuts or fruit using a knock-down sampling method (Pizzol et al. 2010). Five racemes, fruits or nuts were selected for sampling from each of the four cardinal points (north, east, south and west; obtained by use of a compass) of each tree (i.e., 20 per tree). The numbers of nuts per raceme or fruit per inflorescence were recorded before each sampling.

Thrips were sampled by carefully holding the racemes, fruits or nuts in the centre of a plastic container (approx. 8 cm wide by 17 cm deep) in which 5 mL of 100% ethanol had been added. The container and plant tissues were firmly shaken to dislodge any attached insects, and sampled racemes, nuts or fruit were then marked with red flagging tape so they would be sampled repeatedly over time. A fine paintbrush was used to transfer the sample, including plant debris, from the plastic container into a pre-marked plastic vial containing a collection label with date, orchard identifier, cultivar, tree number and developmental stage.

Thrips damage assessment

Twenty randomly chosen racemes from branches, on the same trees, facing the four cardinal points (i.e., five racemes per direction) were evaluated for damage for macadamias. For avocados, 20 fruits were evaluated for damage on the same trees and developmental stages from branches facing the four cardinal directions (five fruits per direction). To categorise thrips damage, fruit or nuts with ≥10% of their surfaces with thrips scarring were considered damaged, whereas those with below 10% (1.25- to 2-cm scars in diameter) were considered healthy (Atakan et al. 2021; Phillips et al. 1995). Thrips damage was recorded as the presence (damaged) or absence (healthy) of fruit scarring out of the total fruit assessed per tree for avocados. For macadamia thrips damage, thrips damage was recorded as the presence or absence of nut scarring per raceme and nut set per raceme for macadamia. Fruit set or nut set was quantified as the number of fruits or nuts per inflorescence or raceme per tree. However, avocado fruit set per inflorescence was only recorded in the 2021/2022 season. In avocado orchards, thrips cause feeding damage on young avocado fruit; furthermore, the epidermal scarring during surface feeding results in noticeable aesthetic blemishes (Dennill & Erasmus 1992). On macadamias, thrips can cause direct and indirect damage. Direct damage to the flowers, fruit and leaves can reduce yields due to the lack of flowers, fruit abscission and reduced photosynthesis, respectively (Kawate & Tarutani 2004).

Thrips development

Direct sampling of selected tissues was performed to record thrips development from them. Sampling of avocados and macadamias was done on 10 trees per orchard. Ten avocado fruits at various sizes (1–3, 4–6 and 7–9 cm) were sampled. Ten racemes were chosen at each developmental stage (racemes, nut set, 1- to 1.5-cm diameter and shell hardening) for macadamias. During the 2022/2023 season, an additional 10 flushes per tree for avocados and macadamias were picked and placed in sealed, but ventilated, containers for eggs to develop into larvae and for larvae and pupae to develop into adults. These sample containers were transported to a room with a stable room temperature of 25°C. Wet cotton wool was placed on sample containers to prevent the avocado and macadamia tissues from drying. For the thrips development study, each raceme for macadamias and fruit for avocados represented a single replicate. On larval and adult development from plant tissue, thrips (larvae and adults) were transferred with a fine brush dipped in 100% ethanol to a pre-marked plastic vial containing a collection label and 100% ethanol. All thrips from each raceme were put into one vial labelled with the date, orchard identifier, cultivar, tree number and developmental stage. Thrips species development was quantified as the number of each larval and adult morphotype that developed from the tissues.

Thrips identification

Using a compound light microscope (Olympus BX41, Olympus, Tokyo, Japan) at 40×, 100× and 400× magnification, collected larval and adult thrips from knock-down sampling and reared from plant tissues were morphologically identified using taxonomic keys (Faure 1929; Mound & Stiller 2011). Verification of thrips specimens was done by genetic assessment and scanning electron microscopy (Kibor et al. unpublished data), which verified that compound light microscope observation was sufficient to correctly identify the thrips species encountered in this study.

Data analysis

Statistical analysis was performed with R software Version 4.1.1, running in RStudio Version 4.1.1 (R Core Team 2013). Analyses were performed separately for avocados and macadamias in each sampling season. This was due to there being considerable differences in the thrips assemblages and their patterns of abundance between seasons. Generalised linear mixed models (GLMMs) were used to evaluate the effects of cultivar and developmental stage on thrips abundance (i.e., number of individuals), species richness (i.e., number of species) and thrips species development from plant tissues (*S. aurantii*, *T. tenellus*, *H. gowdeyi* and *F. occidentalis*; juveniles and adults analysed separately). Tree and orchard were included in the models as random effects due to repeated measurements. Thrips abundance was assumed to fit a negative binomial distribution with a log link function due to many samples containing zero thrips. Gaussian distribution was used for species richness. Development of thrips from plant tissues was also assumed to follow a negative binomial distribution. GLMMs with the same predictors were also used for thrips damage probability (recorded as presence or absence). Presence and absence of damage were assumed to follow a binomial probability distribution with a logit function to predict variables.

The full models described above were simplified to the minimum adequate model based on the lowest Akaike information criterion (AIC) score. Models were built using the functions 'glm' or 'glmer' (from the 'lme4' package) (Bates et al. 2015). Type III analysis of variance by use of the function 'Anova' from the car package in R (Fox et al. 2007) was used to obtain the *p* value for the effects of each minimal adequate model. Significant main and interaction effects were tested using post hoc multiple comparisons by Tukey's honest significant difference (HSD) test using the 'emmeans' function from the emmeans package (Lenth 2023).

RESULTS

Thrips abundance and diversity

A total of 4499 thrips were collected from the different developmental stages of avocado cultivars and 11 036 from macadamia cultivars during the 2020/2021 and 2021/2022 seasons. A total of six morphotypes were found across avocado and macadamia during the sampling period in the Levubu region. Of these morphotypes were *Caliothrips* sp., *F. occidentalis*, *H. gowdeyi*, *Megalurothrips* sp., *S. aurantii* and *T. tenellus*. *S. aurantii* was the most abundant species across all cultivars and developmental stages of avocado and macadamia (Figures 2 and 3), followed by *T. tenellus*, *H. gowdeyi* and *F. occidentalis*. *H. gowdeyi*, *S. aurantii* and *T. tenellus* were associated with all sampled developmental stages of avocado and macadamia. *T. tenellus* were the most abundant on Macadamia 695 (Figure 3a). Rarer species caught were *Megalurothrips* sp. collected from Maluma avocados and Macadamia 695. *Caliothrips* sp. were caught from Maluma avocados and Macadamia A4.

Thrips and their damage on avocado cultivars and developmental stages

In the 2020/2021 season, there was no difference in the abundance of thrips on Fuerte (3.3 ± 0.4) per inflorescence, Hass (5.1 ± 0.6), Maluma (4.0 ± 0.6) or Pinkerton (3.0 ± 0.5) avocados (Figure 4a). In the 2021/2022 season, cultivar had a significant effect on thrips abundance (Table 3). Maluma had the highest thrips abundance of 12.4 ± 1.7, followed by Pinkerton (9.8 ± 1.2), Fuerte (7.9 ± 1.0) and Hass (7.1 ± 0.8). In both seasons, the fruit developmental stage significantly affected thrips abundance, with the largest thrips abundance sampled from the fruit developmental stage of 1–3 cm (5.4 ± 0.6), followed by 4–6 cm (3.1 ± 0.3) and 7–9 cm (2.5 ± 0.3) in the 2020/2021 season (Table 3). In the 2021/2022 season, the fruit developmental stage of 4–6 cm (13.0 ± 1.3) had the highest thrips abundance, followed by 1–3 cm (8.5 ± 0.9) and 7–9 cm (5.8 ± 0.8), respectively. However, the abundance of thrips was also significantly affected by the interaction of cultivar and fruit developmental stage in the 2020/2021 and 2021/2022 seasons (Table 3). In the 2020/2021 season, at a fruit developmental stage of 1–3 cm, Fuerte had a higher abundance of thrips than Hass. By the next developmental stage of 4–6 cm, this had reversed, and Hass had higher thrips abundance than any other sampled avocado cultivar (Figure 4a). In the 2021/2022 season, at a fruit developmental stage of 1–3 cm, Pinkerton had a higher abundance of thrips than Maluma. When the developmental stage of 4–6 cm was

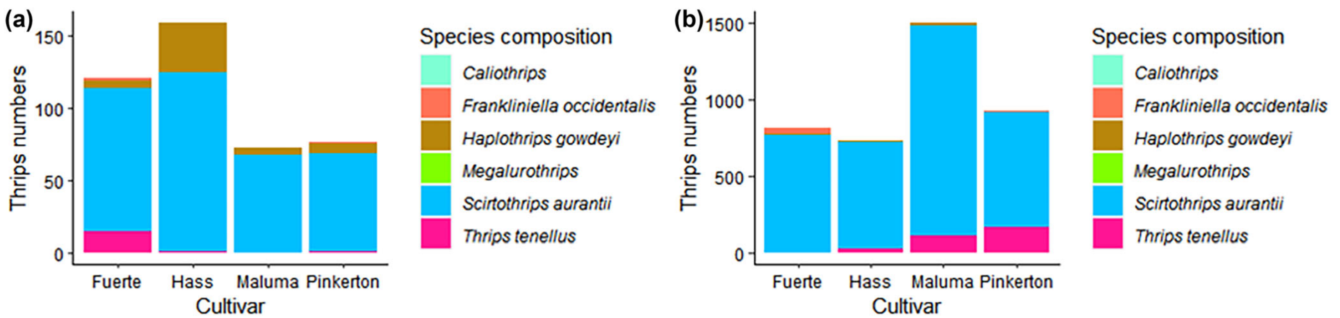

FIGURE 2 Abundance and species composition of thrips (adult or larval, female + male) (*Caliothrips* sp., *Frankliniella occidentalis*, *Haplothrips gowdeyi*, *Megalurothrips* sp., *Scirtothrips aurantii* and *Thrips tenellus*) in the Levubu region of Limpopo Province, South Africa, on four avocado cultivars in (a) the 2020/2021 season and (b) the 2021/2022 season. Values are the pooled number of each species across the months of August 2020–January 2021 and August 2021–January 2022.

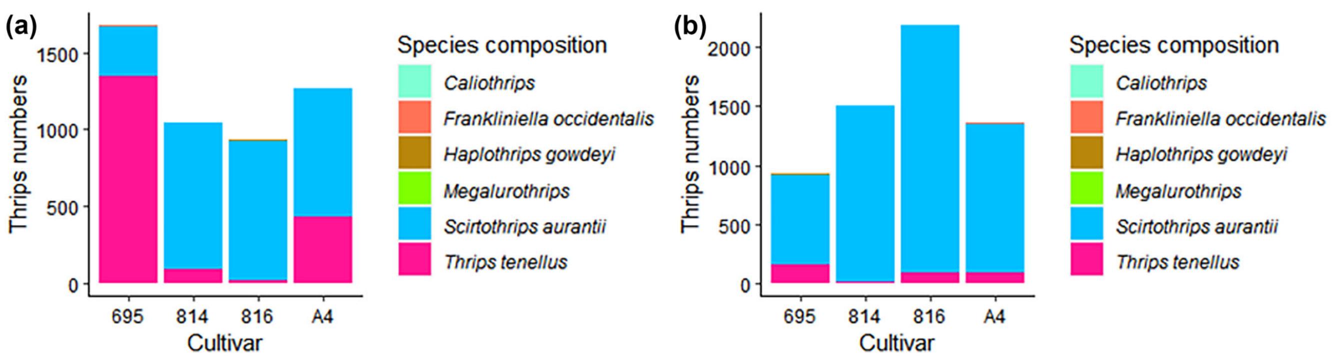

FIGURE 3 Abundance and species composition of thrips (adult or larval, female + male) (*Caliothrips* sp., *Frankliniella occidentalis*, *Haplothrips gowdeyi*, *Megalurothrips* sp., *Scirtothrips aurantii* and *Thrips tenellus*) in the Levubu region of Limpopo Province, South Africa, on four macadamia cultivars in (a) the 2020/2021 season and (b) the 2021/2022 season. Values are the pooled number of each species across the months of August 2020–January 2021 and August 2021–January 2022.

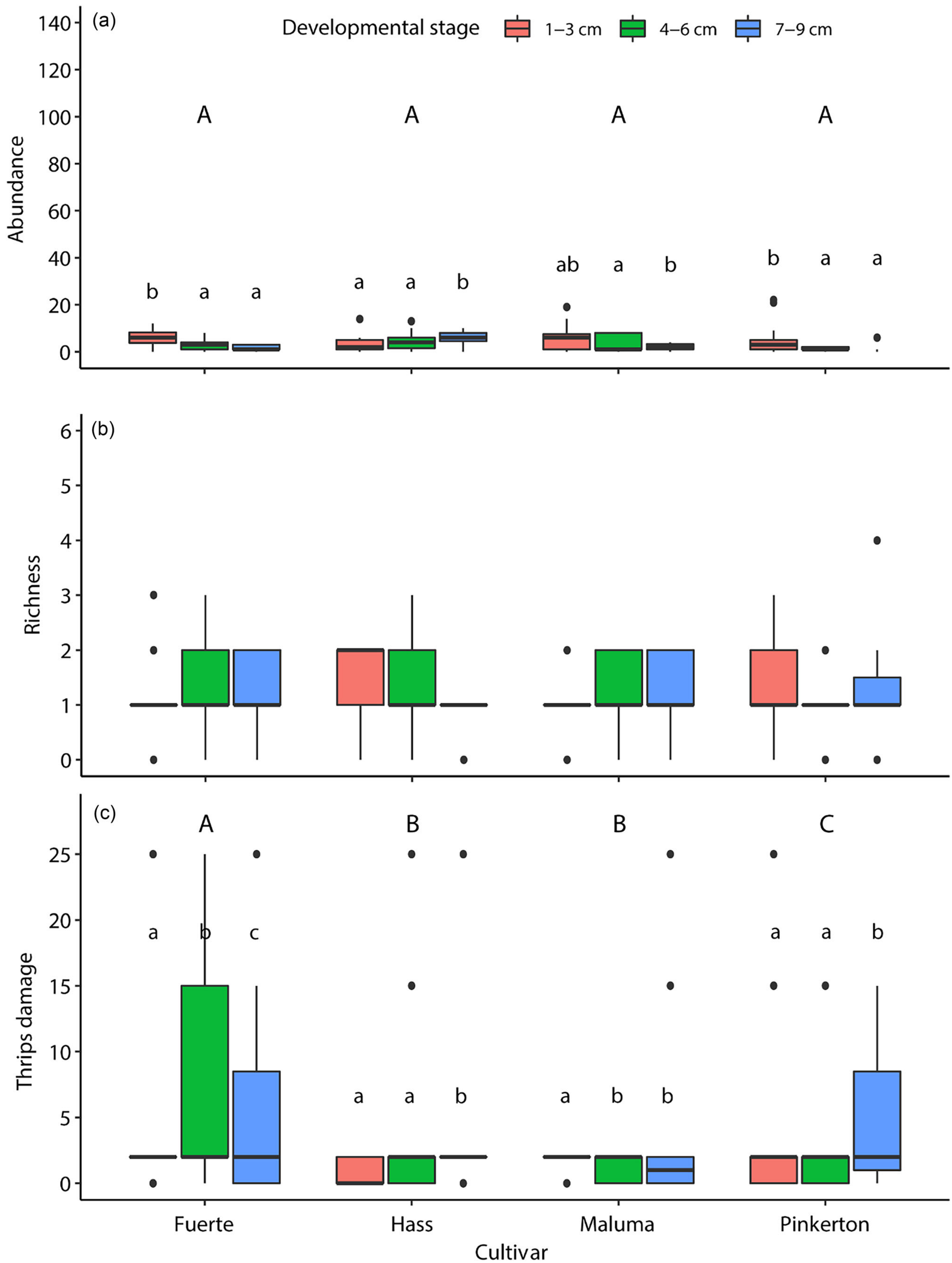

FIGURE 4 Legend on next page.

FIGURE 4 Boxplots of thrips (adult or larval, female + male) abundance (a), species richness (b) and damage (mean number of fruits) (c) on four avocado cultivars at three stages of fruit development in the Levubu region, Limpopo Province, South Africa, in the 2020/2021 season. Cultivars that are not significantly different from each other are labelled with the same capital letter. Developmental stages within a cultivar that are not significantly different from each other are labelled with the same lowercase letter ($\alpha = 0.05$). If no lettering is applied to a graph, there were no differences associated with cultivar or developmental stage.

TABLE 3 Summary statistics for generalised linear mixed models describing the effects of cultivar and developmental stage on thrips abundance, species richness, thrips damage and fruit set per inflorescence on avocados.

		2020/2021 season			2021/2022 season		
Response	Model predictors	Likelihood ratio χ^2	df	p	Likelihood ratio χ^2	df	p
Abundance	Cultivar	6.094	3	0.107	13.418	3	0.004
	Developmental stage	18.001	2	<0.001	7.606	2	0.022
	Cultivar × developmental stage	22.415	6	0.001	31.405	3	<0.001
Species richness	Cultivar	7.206	3	0.066	2.499	3	0.478
	Developmental stage	2.828	2	0.243	2.92	2	0.232
	Cultivar × developmental stage	15.056	6	0.019	2.806	6	0.833
Thrips damage	Cultivar	10.513	3	0.015	221.733	3	<0.001
	Developmental stage	2.945	2	0.229	19.944	2	<0.001
	Cultivar × developmental stage	13.588	6	0.035	5.965	6	0.427
Fruit set per inflorescence	Cultivar	_	_	_	158.362	3	<0.001
	Developmental stage	_	_	_	13.684	2	<0.001
	Cultivar × developmental stage	_	_	_	41.707	6 < 0	<0.001

Note: Effects presented are for minimal adequate models that were selected based on Akaike information criterion.

reached, Maluma had higher thrips abundance than any other sampled cultivar (Figure 5a).

Cultivar and fruit developmental stage did not significantly affect thrips species richness in the 2020/2021 season, but their interaction did (Table 3). Hass and Pinkerton avocados had the highest species richness in the earliest developmental stage of 1–3 cm (Figure 4b). At the developmental stage of 4–6 cm, Hass and Maluma had the highest species richness, but at the developmental stage of 7–9 cm, Fuerte had the highest species richness. In the 2021/2022 season, there was no significant effect on species richness of avocado cultivar and fruit developmental stage (Table 3). With no effect of cultivar or developmental stage (Table 3), the grand mean for thrips species richness in the 2020/2021 season was 1.5 ± 0.1 for Fuerte, 1.4 ± 0.1 for Hass, 1.3 ± 0.1 for Maluma and 1.6 ± 0.1 for Pinkerton (Figure 4b). The fruit developmental stage of 1–3 cm had a thrips species richness grand mean of 1.5 ± 0.1, 4–6 cm had 1.5 ± 0.1, while 7–9 cm had 1.6 ± 0.1. In the 2021/2022 season, Fuerte had a thrips species richness grand mean of 1.9 ± 0.1, Hass had 2.0 ± 0.2, Maluma had 2.0 ± 0.1, and Pinkerton had 1.9 ± 0.2. Regarding developmental stages, 1–3 cm had a grand mean of 2.2 ± 0.1, 4–6 cm had 1.9 ± 0.1, and 7–9 cm had 1.8 ± 0.1.

Thrips damage on avocados during the 2020/2021 season was significantly affected by cultivar but not by developmental stage (Table 3). However, a significant interaction of cultivar and developmental stage was observed. In the 2020/2021 season, Fuerte and Pinkerton suffered the highest thrips damage with a mean number of 6.9 ± 1.3 and 4.9 ± 0.8 damaged fruits, respectively, with the former sustaining damage from the 4- to 6-cm stage, whereas the latter was affected in the 7- to 9-cm stage. In contrast, Hass (3.9 ± 1.3) and Maluma (2.2 ± 0.6) had a consistently low number of fruits damaged by thrips (Figure 4c). During the 2021/2022 season, avocado fruit damage by thrips was significantly affected by cultivar type and developmental stage, but there was no significant effect of their interaction (Table 3). In that season, thrips damage was highest across all developmental stages in Pinkerton (13.1 ± 0.2), which was significantly more than in Maluma (9.1 ± 0.2) and Hass (7.1 ± 0.2), with the latter having the lowest average thrips damage. Fuerte (7.5 ± 0.1) also had consistently low levels of thrips damage, which was significantly different from Maluma but not from other cultivars (Figure 5c). In the 2020/2021 season, there was a significant difference in thrips damage between developmental stages, with the 1- to 3-cm stage having thrips damage of 3.4 ± 0.8. This was significantly less than at the 4- to 6-cm (5.3 ± 0.9) and 7- to 9-cm (5.2 ± 0.9) stages, but the latter two stages did not differ in thrips damage (Figure 4c). In 2021/2022, damage intensity increased significantly with fruit developmental stages. Significant differences were observed on 1–3 and 4–6 cm ($p < 0.001$), 1–3 and 7–9 cm ($p < 0.001$), and 4–6 and 7–9 cm ($p = 0.005$) (Figure 5c). Fruit size 1–3 cm had a mean damage of 4.0 ± 0.7, 4–6 cm had 4.7 ± 0.7, and 7–9 cm had 5.0 ± 0.8.

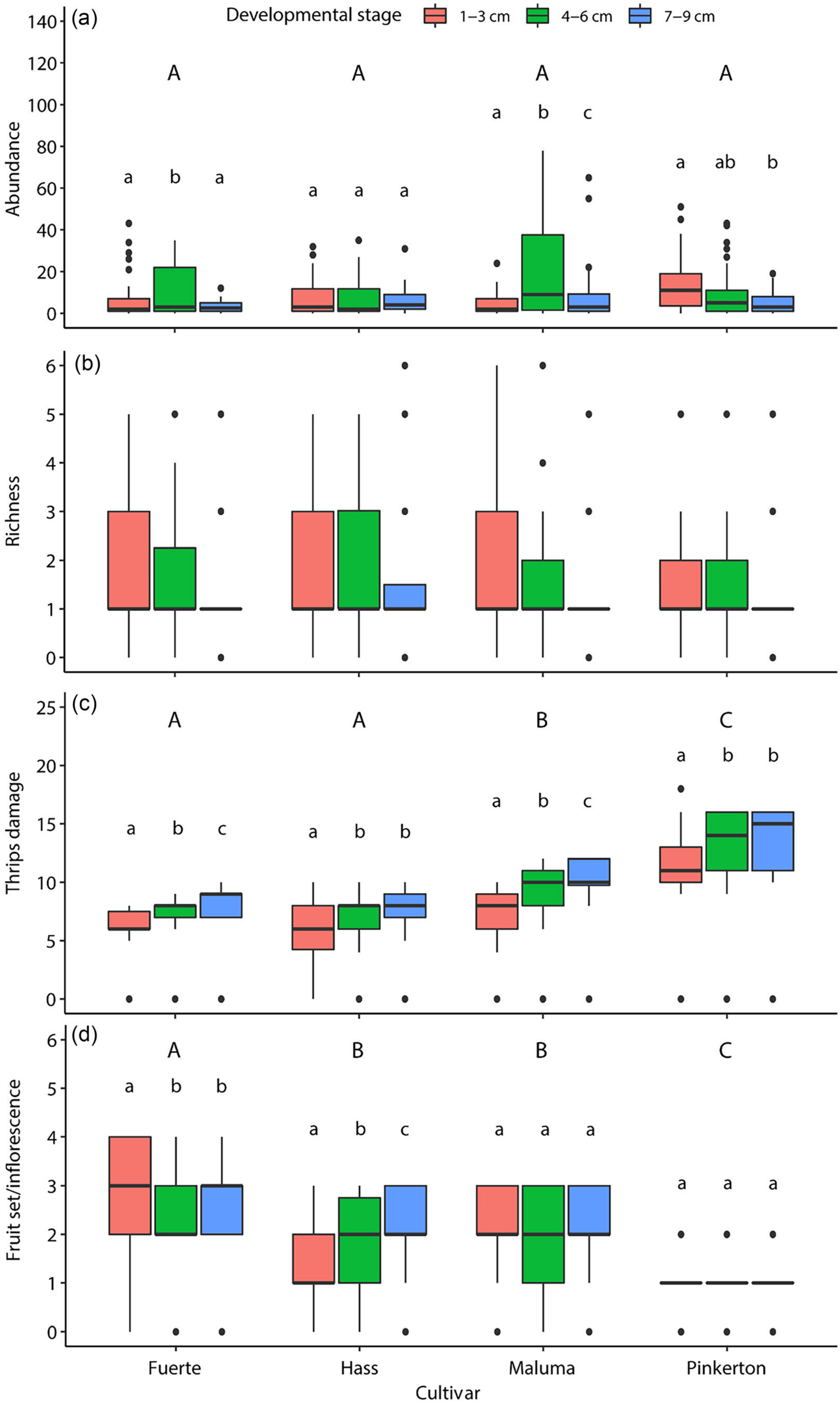

FIGURE 5 Legend on next page.

FIGURE 5 Boxplots of thrips (adult or larval, female + male) abundance (a), species richness (b) and damage (mean number of fruits) (c) as well as fruit set (d) on four avocado cultivars at three stages of fruit development in the Levubu region, Limpopo Province, South Africa in the 2021/2022 season. Cultivars that are not significantly different from each other are labelled with the same capital letter. Developmental stages within a cultivar that are not significantly different from each other are labelled with the same lowercase letter ($\alpha = 0.05$). If no lettering is applied to a graph, there were no differences associated with cultivar or developmental stage.

TABLE 4 Summary statistics for generalised linear mixed models describing the effects of cultivar and developmental stage on thrips abundance, species richness, thrips damage and nut set per raceme on macadamia.

		2020/2021 season			2021/2022 season		
Response	**Model predictors**	**Likelihood ratio χ^2**	**df**	***p***	**Likelihood ratio χ^2**	**df**	***p***
Abundance	Cultivar	1.618	3	0.655	23.905	3	<0.001
	Developmental stage	9.469	3	0.023	36.55	3	<0.001
	Cultivar × developmental stage	14.472	9	0.106	109.792	9	<0.001
Species richness	Cultivar	22.857	3	<0.001	29.211	3	<0.001
	Developmental stage	12.357	9	0.005	25.087	3	<0.001
	Cultivar × developmental stage	12.184	9	0.171	70.125	9	<0.001
Thrips damage	Cultivar	6.177	3	0.103	169.493	3	<0.001
	Developmental stage	0.46	3	0.928	86.388	3	<0.01
	Cultivar × developmental stage	2.729	9	0.974	23.451	9	<0.001
Nut set per raceme	Cultivar	8.467	3	0.037	198.709	3	<0.001
	Developmental stage	1.48	3	0.686	176.052	3	<0.001
	Cultivar × developmental stage	3.271	9	0.953	93.328	9	<0.001

Note: Effects presented are for minimal adequate models that were selected based on Akaike information criterion.

There was also a significant effect of cultivar type, fruit developmental stage and their interaction on fruit set per inflorescence during the 2021/2022 season (Table 3). The Fuerte cultivar had the greatest fruit set per inflorescence at the earliest developmental stages of 1–3 cm. However, this declined as fruit development progressed to levels equivalent to Hass and Maluma, at 4–6 and 7–9 cm, respectively. In comparison, Pinkerton had the lowest fruit set among the cultivars (Figure 5d). The overall mean fruit set per inflorescence for Fuerte was 2.8 ± 0.1, which was significantly higher than from any other cultivar. Maluma fruit set per inflorescence was 2.2 ± 0.1, which did not differ from Hass (2.0 ± 0.1), and both Maluma and Hass had significantly greater fruit set per inflorescence than Pinkerton (1.2 ± 0.0) (Figure 5d).

Thrips and their damage on macadamia cultivars and developmental stages

In the 2020/2021 season, there was no difference in thrips abundance between the cultivars (Table 4 and Figure 6a). Macadamia 695 registered a grand mean abundance of 17.1 ± 2.4 per raceme, Macadamia 816 registered 13.8 ± 1.4, Macadamia 814 registered 14.4 ± 2.0, and Macadamia A4 registered 10.2 ± 1.1. In the 2021/2022 season, there was a difference on thrips abundance between cultivars (Figure 7a). Macadamia 816 had the highest thrips abundance of 17.7 ± 1.5, followed by Macadamia 814 (12.0 ± 1.2), Macadamia A4 (9.7 ± 1.1) and then Macadamia 695 (7.2 ± 1.0). There were significant differences between thrips abundance on macadamias 695 and 814 ($p = 0.010$), 695 and 814 ($p < 0.001$), 814 and 816 ($p < 0.001$), and 816 and A4 in the 2021/2022 season ($p < 0.001$) (Figure 7a). During the 2020/2021 season, there was a significant difference in thrips abundance between developmental stages (Figure 6a). Raceme had the highest thrips abundance of 20.0 ± 0.7, followed by hard shell (17.1 ± 0.6), nut set (16.0 ± 0.8) and nut size 1–1.5 cm (15.6 ± 0.8). In the 2021/2022 season, a difference in thrips abundance between developmental stages was also observed (Figure 7a). Nut set had the highest thrips abundance of 15.8 ± 1.3, followed by nut size 1–1.5 cm (15.3 ± 1.4), racemes (9.1 ± 1.1) and hard shell (5.9 ± 0.9). In the 2020/2021 season, there was no interaction between cultivar type and fruit developmental stage (Table 4). However, in the 2021/2022 season, there was interaction of cultivar and developmental stages (Table 4). In the 2021/2022 season at raceme, 814 had the highest thrips abundance; at nut set and nut size 1–1.5 cm, 816 had the highest thrips abundance, and at hard shell, this had reversed; and 814 had the highest thrips abundance among all the cultivars (Figure 7a).

Cultivar and developmental stage significantly affected thrips species richness in the 2020/2021 season; however, the interaction did not (Table 4). In the 2020/2021 season, Macadamia 695 had a higher species richness of 1.6 ± 0.1, followed by macadamias A4 and

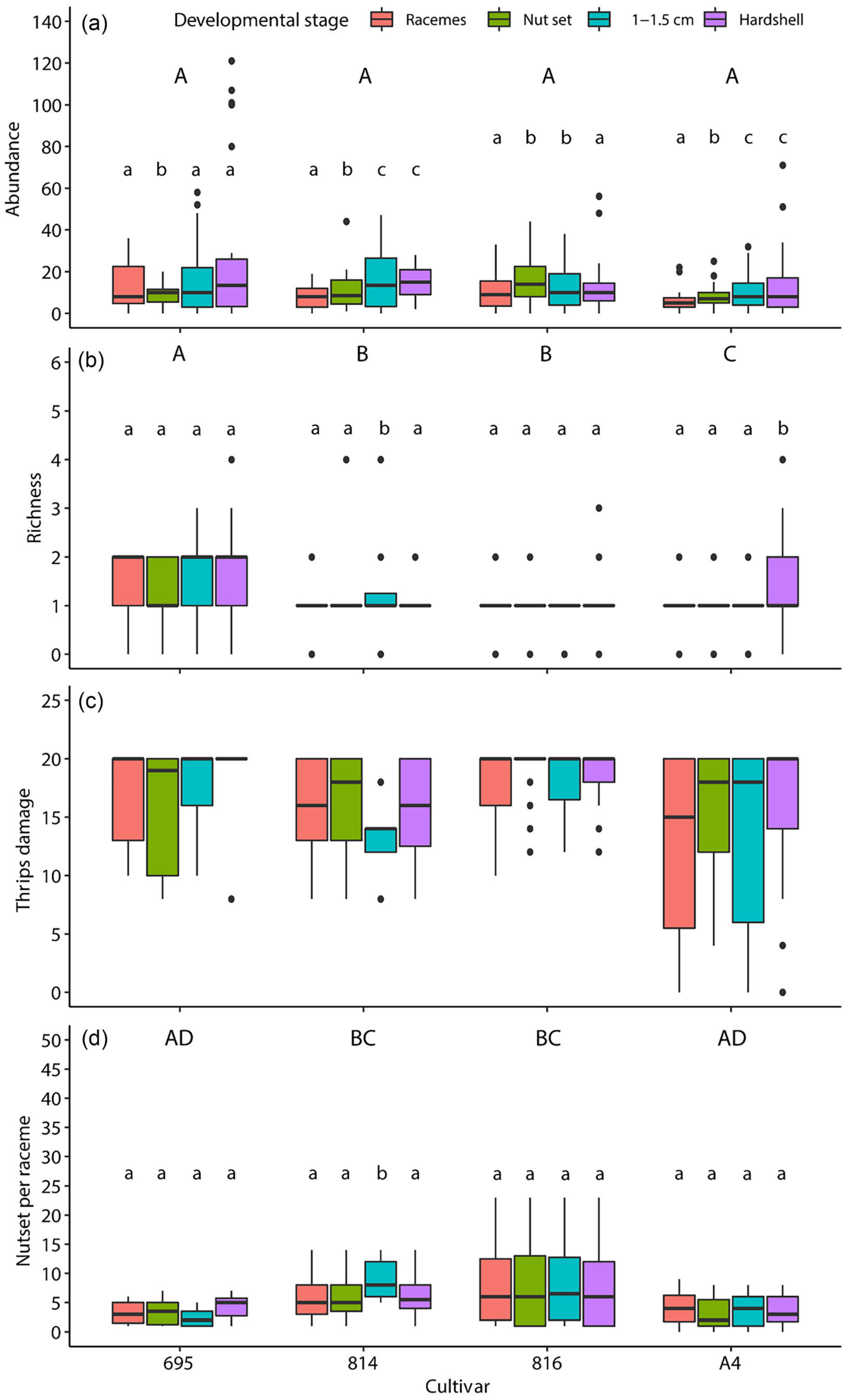

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FIGURE 6 Boxplots showing thrips abundance (adult or larval, female + male) during the 2020/2021 season (a), species richness (b) and damage (mean number of fruits) (c) as well as nut set (d) on four macadamia cultivars at three stages of fruit development in the Levubu region, Limpopo Province, South Africa. Cultivars that are not significantly different from each other are labelled with the same capital letter. Developmental stages within a cultivar that are not significantly different from each other are labelled with the same lowercase letter ($\alpha = 0.05$). If no lettering is applied to a graph, there were no differences associated with cultivar or developmental stage.

816 with a mean of 1.2 ± 0.1 and 1.1 ± 0.1, respectively, with the lowest being Macadamia 814 with a mean of 1.0 ± 0.0. Regarding developmental stages, nut set (1.52 ± 0.1) had the highest species richness followed by racemes (1.5 ± 0.1), nut size 1–1.5 cm (1.2 ± 0.1) and hard shell (1.1 ± 0.1). In the 2021/2022 season, cultivar, developmental stages and their interaction significantly affected thrips species richness (Table 4). During the 2021/2022 season, Macadamia 695 had a higher mean species richness of 2.4 ± 0.1, followed by macadamias A4 and 816 with a mean of 2.1 ± 0.1 and 1.9 ± 0.1 and lastly Macadamia 814 with a mean of 1.8 ± 0.1. Regarding developmental stages, hard shell had the highest species richness of 2.6 ± 0.2, followed by nut size 1–1.5 cm (2.2 ± 0.2), racemes (1.9 ± 0.1) and nut set (1.4 ± 0.1). In the 2021/2022 season at raceme, Macadamia A4 had the highest species richness; at nut set, macadamias 695 and 814 had the highest species richness; at nut size 1–1.5 cm, Macadamia 695 had the highest; and at hard shell, macadamias 695 and 816 had the highest species richness (Figure 7b).

Regarding thrips damage on macadamias, there was no main effect of cultivar type and developmental stage, as well as interaction during the 2020/2021 season (Table 4). During the 2020/2021 season, Macadamia 816 registered a grand mean number of 18.4 ± 0.3 damaged fruits, Macadamia 695 had 16.6 ± 0.8, Macadamia 814 had 15.6 ± 0.7, and Macadamia A4 had 14.1 ± 0.9 (Figure 6c). Regarding developmental stages, racemes had a grand mean of 17.0 ± 0.7, nut set had 15.9 ± 0.3, nut size 1–1.5 cm had 15.6 ± 0.8, and hard shell had 17.1 ± 0.6 (Figure 6c). In the 2021/2022 season, there were significant main effects of cultivar and developmental stage, as well as their interaction (Table 4). Macadamia 816 had the highest damage of 12.2 ± 0.3, followed by Macadamia 814 (9.6 ± 0.2), Macadamia A4 (8.8 ± 0.2) and Macadamia 695 (5.4 ± 0.2). Regarding developmental stages, nut size 1–1.5 cm had the highest damage of 9.8 ± 0.23, followed by nut size 1–1.5 cm (8.3 ± 0.3), racemes (7.2 ± 0.3) and hard shell (10.8 ± 0.3). At the raceme and nut set stages, macadamias 816 and 814 had the highest damage. At nut size 1–1.5 cm and hard shell, macadamias 816 and 814 still had the highest damage. Macadamias A4 and 695 had a consistently low number of raceme and nut damage by thrips (Figure 7c).

Cultivar type was associated with nut set per raceme, but developmental stage and interaction were not associated with nut set per raceme during the 2020/2021 season (Table 4). During the 2020/2021 season, the nut set per raceme by macadamias 816 (7.8 ± 0.8) and 814 (6.6 ± 0.7) was significantly higher than that by macadamias 695 (3.3 ± 0.3) and A4 (3.7 ± 0.3). During the 2021/2022 season, the nut set per raceme was significantly affected by cultivar, developmental stage and their interaction (Table 4). In that season, Macadamia 695 had the highest mean nut set per raceme of 12.9 ± 0.7, followed by Macadamia 816 (12.2 ± 0.3). Nut set of Macadamia 816 was significantly higher than that of Macadamia A4 (3.8 ± 0.1), with Macadamia 814 intermediate between the two (10.2 ± 0.2). However, in the 2021/2022 season, macadamias 814 and 816 had the highest nut set at the earliest developmental stages; at nut size 1–1.5 cm, Macadamia 695 had the highest nut set; and at hard shell, Macadamia 695 still had the highest nut set. Macadamia A4 consistently had the lowest nut set in all the developmental stages.

Thrips development from avocado and macadamia tissues

There were significant differences in *S. aurantii* larval development from avocado cultivars and development tissues (Figure 8a). The main effects of cultivar and developmental stage, as well as their interaction, significantly affected *S. aurantii* larval development from avocado tissues (Table 5). *S. aurantii* larval development was the highest from Pinkerton avocado flush and the lowest from Fuerte flush. At fruit size 1–3 cm, *S. aurantii* larval development was still high from Pinkerton and the lowest from Hass, but at fruit size 4–6 cm, the development was the highest from Maluma rather than Pinkerton, while development from Hass was the lowest. At fruit size 7–9 cm, *S. aurantii* larval development was the highest from Pinkerton, whereas Hass had the lowest (Figure 8a). There were significant differences in *S. aurantii* adult development from avocado cultivars and development tissues (Figure 8b). Adult development of *S. aurantii* was also affected by cultivar, developmental stage and their interaction (Table 5). Development on flush was the highest from Pinkerton, followed by Maluma and Hass, while Fuerte flush produced the fewest adult *S. aurantii*. At fruit size 1–3 cm, development was the highest from Pinkerton and the lowest from Hass. At fruit size 4–6 cm, development was the highest from Maluma and the lowest from Fuerte. At fruit size 7–9 cm, development was the highest from Pinkerton and the lowest from Hass (Figure 8b).

For *T. tenellus*, few larvae or adults developed from avocado tissues (Figure 8c,d). There was no significant effect of cultivar, developmental stage or their interaction on larval development of *T. tenellus* (Table 5). For adult

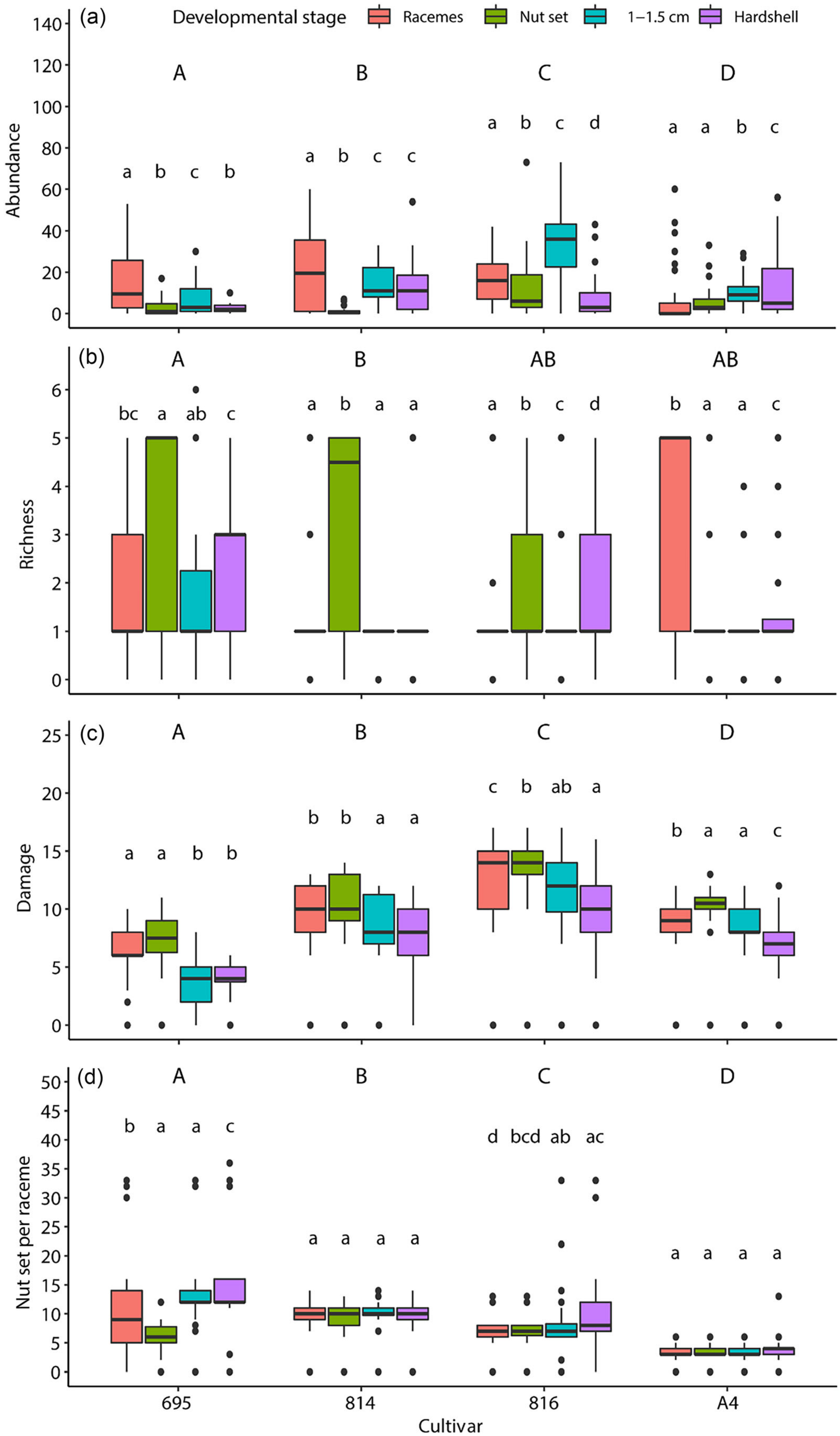

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FIGURE 7 Boxplots showing thrips abundance (adult or larval, female + male) during the 2021/2022 season (a), species richness (b) and damage (mean number of fruits) (c) as well as nut set (d) on four macadamia cultivars at three stages of fruit development in the Levubu region, Limpopo Province, South Africa. Cultivars that are not significantly different from each other are labelled with the same capital letter. Developmental stages within a cultivar that are not significantly different from each other are labelled with the same lowercase letter ($\alpha = 0.05$).

development of *T. tenellus*, the effects of cultivar, developmental stage and their interaction were similarly not significant (Table 5). *H. gowdeyi* larval development from avocado tissues was also negligible (Figure 8e). There were no significant effects of cultivar, developmental stage or their interaction on larval development of *H. gowdeyi* from avocados (Table 5). There was no development of adult *H. gowdeyi* (Figure 8f) or larval or adult *F. occidentalis* from avocado tissues (Figure 8g,h).

For macadamias, there was no significant difference in *S. aurantii* larval and adult development on cultivars and tissues (Figure 9a,b). Cultivar did not significantly affect *S. aurantii* larval development; however, developmental stage and their interaction significantly affected *S. aurantii* larvae (Table 6). *S. aurantii* larval development was the highest from the Macadamia A4 flush and the lowest from the Macadamia 814 flush. Larval development was the highest from Macadamia 814 racemes and the lowest from Macadamia A4 racemes. The larval development at nut set was the highest from Macadamia A4 and the lowest from Macadamia 814. At the developmental stage of 1–1.5 cm, *S. aurantii* larval development was still the highest from Macadamia A4, while the lowest was from Macadamia 816. At hard shell, larval development was the highest from Macadamia 814, while the lowest was from Macadamia A4 (Figure 9a). Regarding *S. aurantii* adults, cultivar and developmental stage had a significant effect on *S. aurantii* adult development, and so did the interaction between them (Table 6). *S. aurantii* adult development was the highest from the Macadamia 816 flush, followed by Macadamia 814, while the lowest development was from Macadamia 695. When considering racemes, development was the highest from Macadamia A4 and the lowest from Macadamia 816. Nut set saw the highest adult development from Macadamia A4 and the lowest from Macadamia 814. For nut size 1–1.5 cm, it was the highest on Macadamia 814 and the lowest on Macadamia 695. For hard shell, the development was the highest from Macadamia A4, whereas the lowest was from Macadamia 695 (Figure 9b).

For *T. tenellus*, there was no main significant effect of cultivar, developmental stage or the interaction on larval development (Table 6). *T. tenellus* larvae did not emerge from all the developmental stages of macadamia tissues, but a few adults emerged from the hard shell of macadamias A4 and 816 (Figure 9c,d). There was no main significant effect of cultivar and developmental stages on adults' development; however, the interaction between them did significantly affect the development (Table 6). *T. tenellus* adults were the highest from Macadamia A4, followed by macadamias 816 and 814, and then from Macadamia 695.

For *H. gowdeyi*, there was a significant difference of *H. gowdeyi* larval development on cultivars and tissues (Figure 9e). Cultivar, developmental stage and the interaction between them significantly affected larval development (Table 6). A few *H. gowdeyi* larvae developed from Macadamia 814 flush. However, the species was not sustained to adulthood (Figure 9e,f). *H. gowdeyi* larval development was the highest from Macadamia 695, followed by Macadamia 814, Macadamia 816 and finally Macadamia A4. Additionally, there was no *F. occidentalis* larval and adult development from macadamia tissues (Figure 9g,h) and thus no significant effect of cultivar, developmental stage or their interaction between the two on *F. occidentalis* development (Table 6).

DISCUSSION

Pinkerton and Fuerte avocados and macadamias 816 and 814 were the cultivars most prone to thrips damage in the Levubu region of South Africa, while Hass avocados and macadamias 695 and A4 were the cultivars least prone to thrips damage. Young fruit of size 1–3 cm on avocados and racemes and nut set on macadamias were the most prone developmental stages to thrips damage. *S. aurantii* was the most abundant species collected on avocados and macadamias, followed by *T. tenellus* Trybom, *H. gowdeyi* and *F. occidentalis*. *T. tenellus* was the most abundant on Macadamia 695 compared to *S. aurantii*, but this was driven by high abundance of the species in one season. The species reared most from both avocado and macadamia was *S. aurantii*, followed by *T. tenellus* but with far fewer individuals recovered. Consequently, *S. aurantii* is the species mainly responsible for damaging the fruits of the avocados and macadamias in the region.

Thrips damage on avocado fruits and macadamia nuts in most cases only became apparent as they developed. The damage on the avocado fruit or macadamia nut manifests itself as a scar or dead plant tissue that does not grow and leaves the fruit or leaves potentially misshapen. In most cases, the earliest developmental stage is when the thrips are the most abundant and hence might contribute to more damage. We recommend that control strategies be performed before the onset of flowering season and immediately after pollination before fruit set to effectively control thrips damage. Young fruits of size <1.5 cm and young flush of size 15–17 cm long on avocados have been found to be the most prone to damage by thrips (Yee et al. 2001). Other studies reveal that thrips

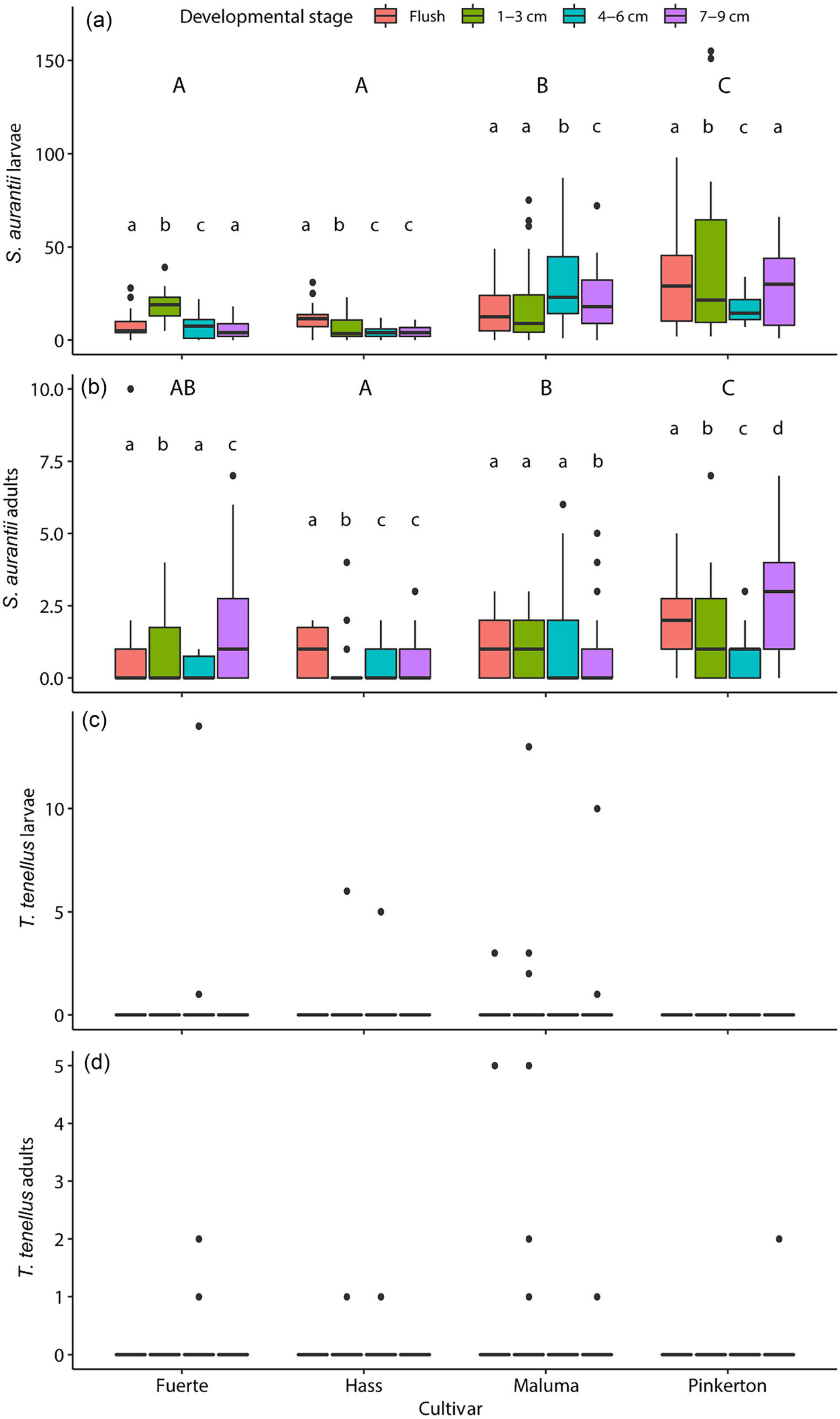

FIGURE 8 Boxplots of thrips (adult or larval, female + male) development from avocado tissues sampled from the Levubu region, Limpopo Province, South Africa. (a) *S. aurantii* larvae, (b) *S. aurantii* adults, (c) *T. tenellus* larvae, (d) *T. tenellus* adults, (e) *H. gowdeyi* larvae, (f) *H. gowdeyi* adults, (g) *F. occidentalis* larvae and (h) *F. occidentalis* adults. Cultivars that are not significantly different from each other are labelled with the same capital letter. Developmental stages within a cultivar that are not significantly different from each other are labelled with the same lowercase letter ($\alpha = 0.05$). If no lettering is applied to a graph, there were no differences associated with cultivar or developmental stage.

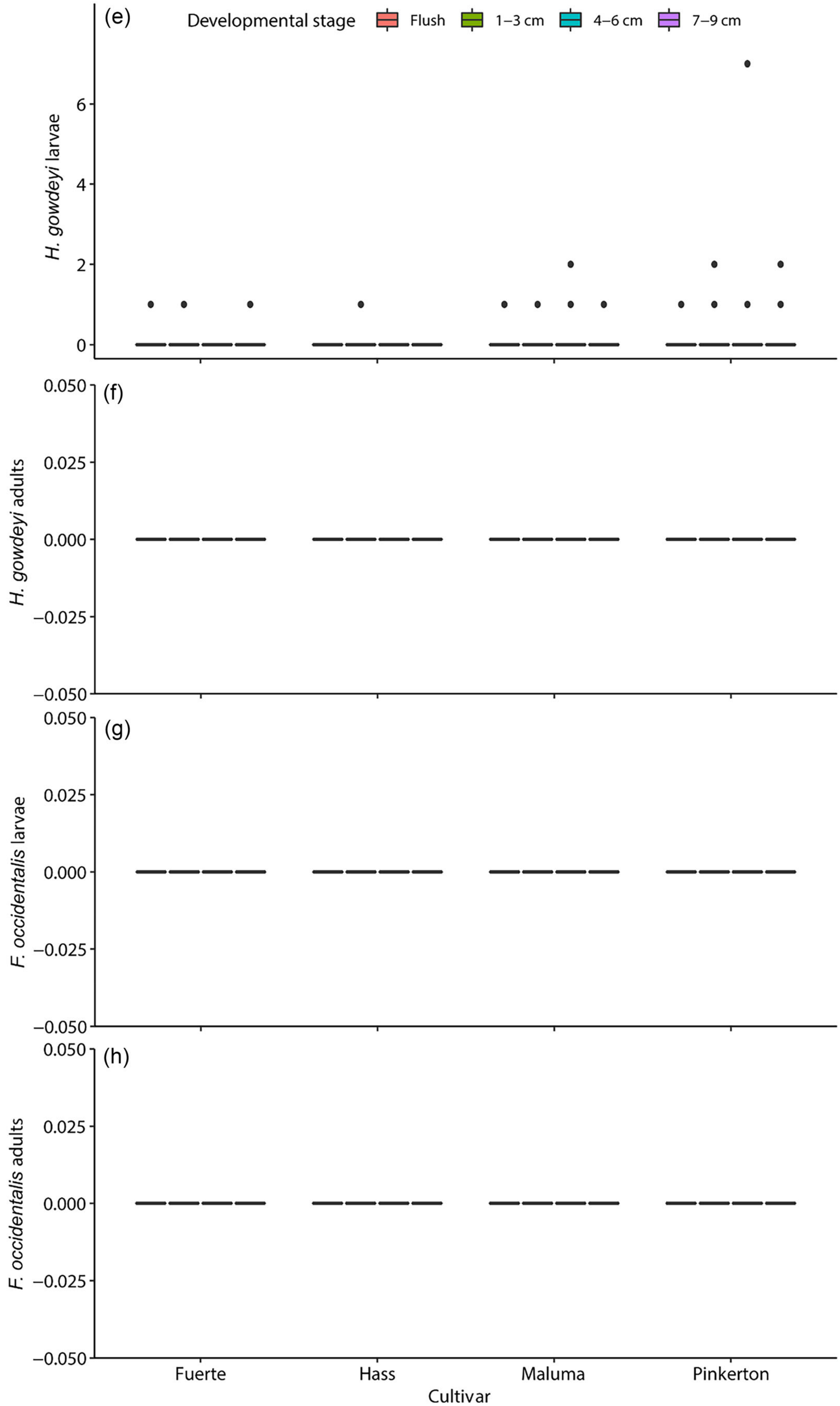

FIGURE 8 (Continued)

TABLE 5 Summary statistics for generalised linear mixed models describing the effects of cultivar and developmental stages on the number of thrips larvae and adults reared from avocado plant tissues.

Model predictors	Likelihood ratio χ^2	df	p	Likelihood ratio χ^2	df	p
	S. aurantii larvae			*S. aurantii* adults		
Cultivar	42.695	3	<0.001	13.889	3	0
Developmental stage	23.068	3	0.001	15.791	3	0
Cultivar × developmental stage	61.34	9	<0.001	22.854	9	0.01
	T. tenellus larvae			*T. tenellus* adults		
Cultivar	0.627	3	0.89	2.578	3	0.46
Developmental stage	4.699	3	0.195	3.006	3	0.39
Cultivar × developmental stage	12.145	9	0.205	14.295	9	0.11
	H. gowdeyi larvae			*H. gowdeyi* adults		
Cultivar	1.073	3	0.783	_	_	_
Developmental stage	0.85	3	0.837	_	_	_
Cultivar × developmental stage	12.461	9	0.188	_	_	_
	F. occidentalis larvae			*F. occidentalis* adults		
Cultivar	_	_	_	_	_	_
Developmental stage	_	_	_	_	_	_
Cultivar × developmental stage	_	_	_	_	_	_

Note: Effects presented are for minimal adequate models that were selected based on Akaike information criterion. Blank cells indicate no effects of cultivar or developmental stage on thrips larvae and adults reared from avocado plant tissues.

damage occurs at flowering and young fruits and becomes visible as scars on the fruit surface and calyx (Thongier et al. 2014). The damage on young fruits and nuts on avocados and macadamias in the Levubu region could be associated with the thrips abundance and palatability of young fruits as well as the feeding preference of thrips, although this was only strongly evident in Macadamia 816 with high abundance and damage in both seasons. Thrips prefer to feed on young avocado fruit within the first 2 weeks of fruit set (Yaseen et al. 2021).

While there were effects of avocado fruit and macadamia nut development on the abundance of thrips and the damage they caused, there were cultivar-specific differences. In the Levubu region, the most widely planted avocado cultivars are Fuerte and Hass, with 695 being the most widely planted macadamia cultivar, so some host plant resistance may already be available to many farmers. Identification of the mechanisms underpinning the differences in susceptibility of avocado and macadamia cultivars as well as their developmental stages would be valuable for plant breeding initiatives to increase host plant resistance to thrips. Cultivar differences could also be associated with differences in skin thickness or smoothness, husk architecture, and fruit and nut properties in the avocado and macadamia cultivars surveyed. Rough- and thick-skinned avocado and thick-shelled macadamia fruits are less prone to insect damage and injury, while thin-skinned and smooth-surfaced fruits and nuts are more prone to insect damage (Bright 2021; Knoche & Lang 2017). Hass avocados, which were less prone to thrips damage in the Levubu region, have a rough and highly lignified thick skin, whereas Fuerte avocados have thin skin, and Pinkerton avocados have a rough skin similar to Hass but thinner (Arpaia et al. 1987). In KwaZulu-Natal, Pinkerton avocados were more prone to *S. aurantii* damage than any other cultivars assessed (Bara & Laing 2020). In our study, Pinkerton had the highest abundance of thrips in the 2021/2022 season. In Hawaii, macadamias 816 and A4 were recorded to have the highest tropical nut borer damage among the cultivars assessed, due to their soft and thin skin (Jones 2002). The physical properties of each variety, such as the colour of flowers, fruit and flush, as well as reproductive cycles (i.e., flowering period and fruit or nut set period), could also contribute to differences in abundance and damage of thrips on avocado and macadamia cultivars. High abundance of *T. tenellus* on Macadamia 695 could be associated with high production of racemes by the cultivar. Macadamia 695 has been linked to high raceme production (Wilkie et al. 2009). *T. tenellus* has been associated with flowers in mangoes (Grove et al. 2001). Crop phenology can influence the life cycles of pests including their habitat suitability, behaviour and distributions (Kennedy & Storer 2000). The difference in time of flowering, fruit set and leaf flush among avocado cultivars determines thrips infestation levels due to the availability or lack of food resources for thrips to exploit (Yee et al. 2003). Cultivars such as the thrips-susceptible Pinkerton bear a purple flush that is attractive to thrips (Sippel et al. 1992). Furthermore, Pinkerton avocados flower early and have a long flowering period and an extended fruiting period, which exposes the fruit to thrips damage (Sippel et al. 1994). This phenomenon might also

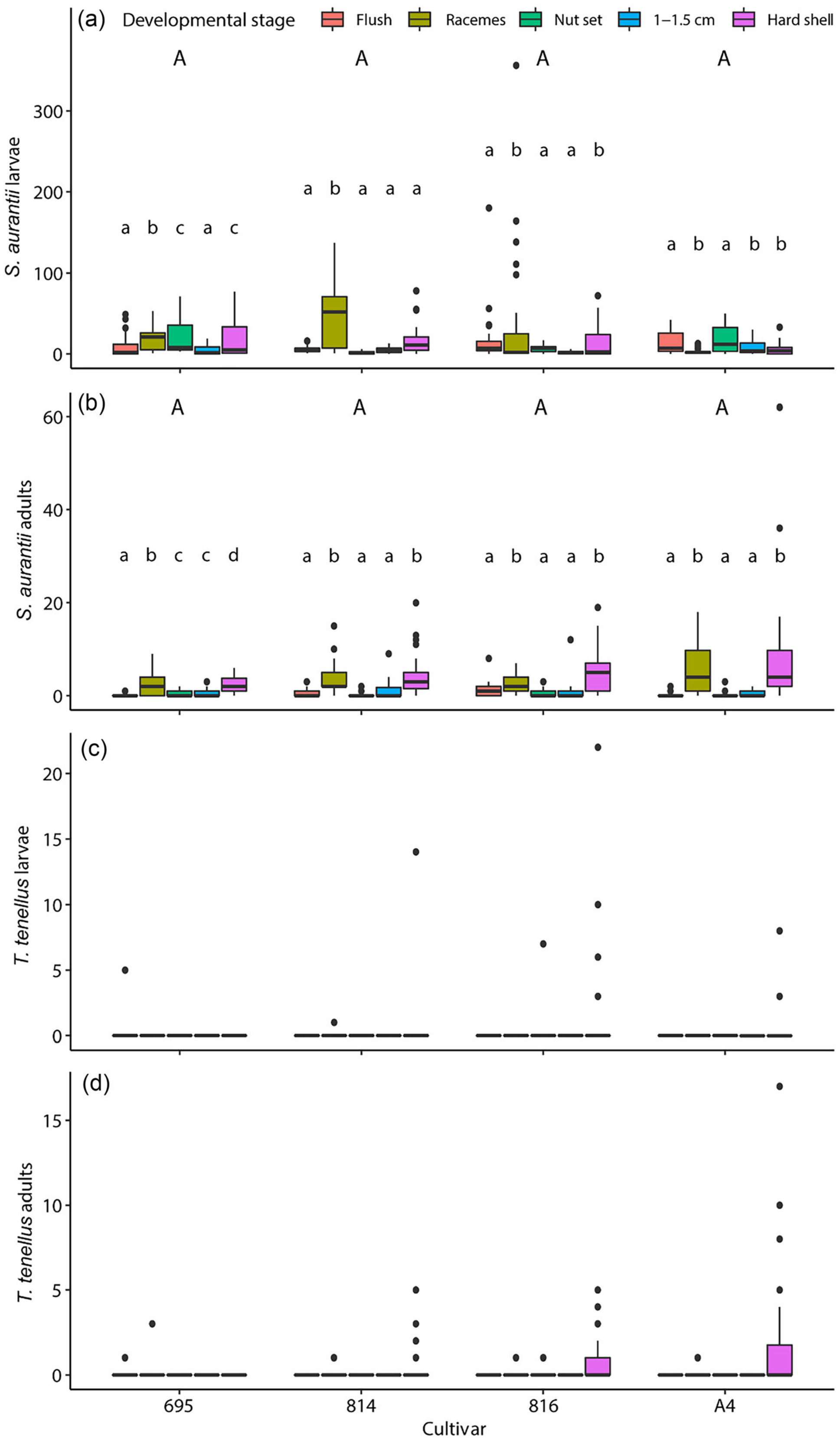

FIGURE 9 Boxplots of thrips (adult or larval, female + male) species development on macadamia tissues in Levubu region, Limpopo Province, South Africa: (a) *S. aurantii* larvae, (b) *S. aurantii* adults, (c) *T. tenellus* larvae, (d) *T. tenellus* adults, (e) *H. gowdeyi* larvae, (f) *H. gowdeyi* adults, (g) *F. occidentalis* larvae and (h) *F. occidentalis* adults. Cultivars that are not significantly different from each other are labelled with the same capital letter. Developmental stages within a cultivar that are not significantly different from each other are labelled with the same lowercase letter ($\alpha = 0.05$). If no lettering is applied to a graph, there were no differences associated with cultivar or developmental stage.

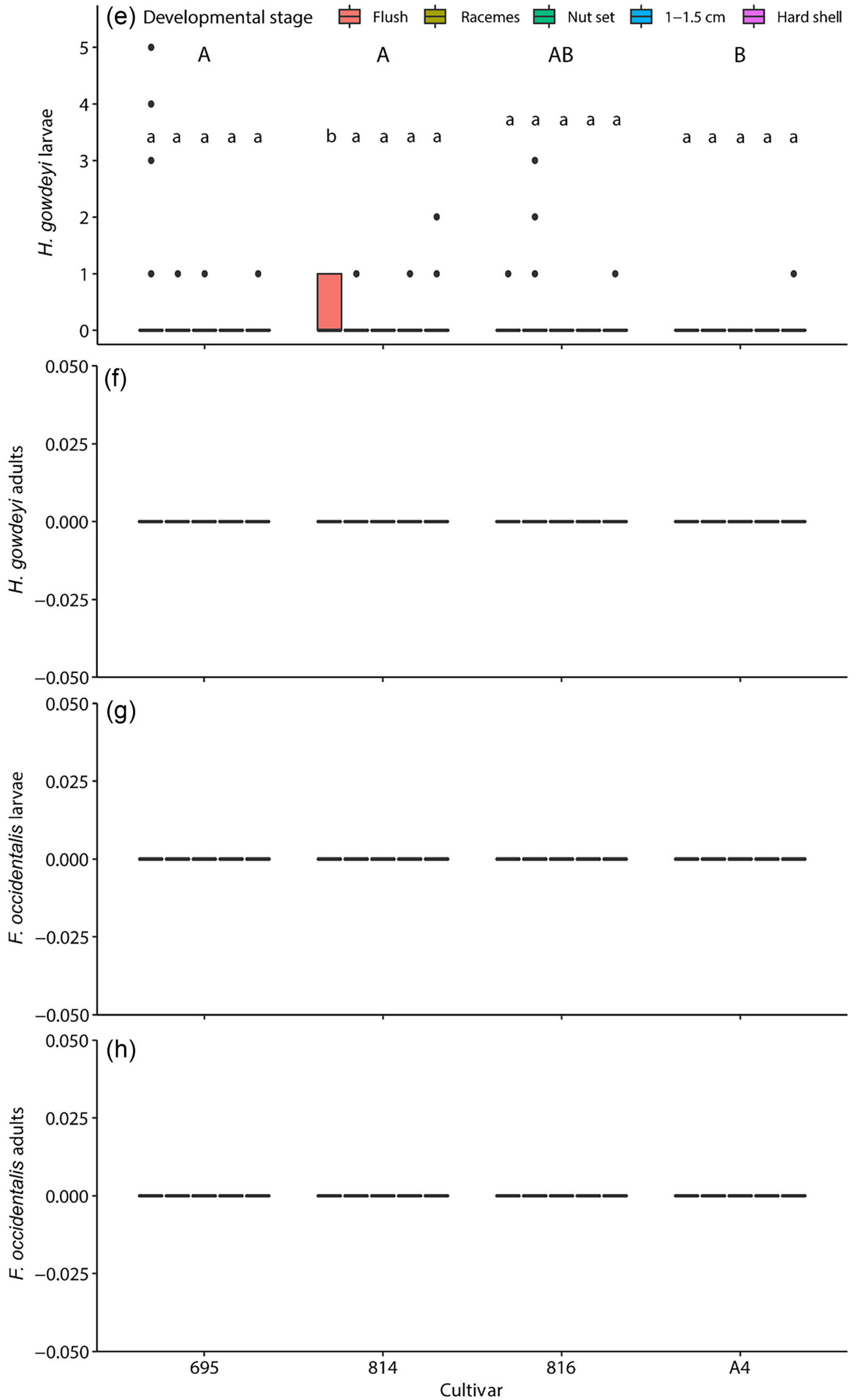

FIGURE 9 (Continued)

TABLE 6 Summary statistics for generalised linear mixed models describing the effects of cultivar and developmental stages on the number of thrips larvae and adults reared from macadamia plant tissues.

Model predictors	Likelihood ratio χ^2	df	p	Likelihood ratio χ^2	df	p
	S. aurantii larvae			*S. aurantii* adults		
Cultivar	7.404	3	0.06	9.804	3	0.0203
Developmental stage	29.3	3	<0.01	38.523	4	<0.001
Cultivar × developmental stage	131.663	12	<0.001	43.433	12	<0.001
	T. tenellus larvae			*T. tenellus* adults		
Cultivar	0.988	3	0.804	0.19	3	0.979
Developmental stage	1.054	4	0. 0.901	0.634	4	0.959
Cultivar × developmental stage	18.642	12	0.097	48.648	12	<0.001
	H. gowdeyi larvae			*H. gowdeyi* adults		
Cultivar	36.535	3	<0.001	_	_	_
Developmental stage	32.302	3	<0.001	_	_	_
Cultivar × developmental stage	34.037	12	<0.001	_	_	_

Note: Effects presented are for minimal adequate models that were selected based on Akaike information criterion. Blank cells indicate no effects of cultivar or developmental stage on thrips larvae and adults reared from macadamia plant tissues.

be similar to macadamias such as 816 and 814, which had high thrips abundance and were prone to thrips damage.

Other plant traits such as plant defence compounds might contribute to differences in thrips abundance and damage on the four avocados and macadamias that were surveyed in the Levubu region. Plant defence mechanisms have been linked to the response of plants against insects and plant enemies. Examples of plant defence mechanisms include the release of chemicals such as plant secondary metabolites, which repel insect enemies (Abebe 2021). Inducible plant defence in avocados and macadamias linked to jasmonic acid signalling has been associated with physiological responses against insects and infections such as *Phytophthora cinnamomi* (Ab Rahman et al. 2018; Reeksting et al. 2014). Hass avocados have chemotypes linked to response to insects and plant enemies (Espinosa-García et al. 2021). The nutritional qualities of avocados and macadamia cultivars such as differences in macronutrients and micronutrients may also be an important factor influencing the differences in thrips abundance and damage on the four avocado and macadamia varieties. Plant species including avocado and macadamia trees have macronutrients such as soluble carbohydrates and proteins (sucrose, raffinose, glucose and fructose) and micronutrients such as vitamins and minerals responsible for the growth, physiology and development of the plant (Toor et al. 2021). Nutritional status of different plant species can modulate the infestation and damage levels of thrips. For instance, leaves at the top of the *Peumus boldus* Molina (Monimiaceae) tree with high protein and carbohydrate levels are prone to *H. haemorrhoidalis* Bouche (Thysanoptera: Thripidae) thrips damage compared to leaves on the lower canopy levels (Scott Brown et al. 2002). Minerals such as calcium, magnesium and zinc are also positively correlated with *Thrips tabaci* (Lind.) (Thysanoptera: Thripidae) populations in cotton (Saleem et al. 2013). This might also be the case for *S. aurantii* on avocados and macadamias in the Levubu region.

In addition, environmental conditions may have had an influence on the difference in thrips composition, abundance and damage on the four avocado and macadamia cultivars studied. For instance, *T. tenellus* was more abundant on macadamia than other thrips species collected in the 2020/2021 season. The Levubu region exhibits varied temperatures, rainfall, relative humidity and sunshine, which change from year to year (Nkuna & Odiyo 2016). Weather conditions have been documented to influence the abundance and distribution of thrips, such as *Frankliniella schultzei* (Trybom), *H. gowdeyi*, *M. sjostedti* (Trybom) and *Thrips australis* (Bagnall) (Thysanoptera: Thripidae) in banana orchards in Kenya (Ireri 2015). Changes in climatic conditions have been recorded to have an influence on the biology and ecology of *H. haemorrhoidalis* on avocados (Odanga 2017). Management practices such as fertiliser application and irrigation could also contribute to thrips abundance and damage that we documented on avocados and macadamias. In the Levubu region, farmers apply irrigation during the summer period and also nitrogen-based fertilisers (calcium ammonium nitrate and urea), phosphate fertilisers (triple superphosphate) and compound fertilisers (di-ammonium phosphate) to supplement nutrients such as nitrogen, calcium, phosphorous and potassium required for avocado and macadamia flower and fruit development (Blakey & Wolstenholme 2014). Fertiliser application and irrigation have been documented to modulate abundance and distribution of *F. occidentalis* in chrysanthemum and *T. tabaci* in onions (Chau et al. 2005; Embarak 2022). In addition, most farmers in the Levubu region use chemical insecticides such as spinetoram (spinosyn), formetanate (carbamates), tartar-emetic and abamectin to control thrips, more so on macadamias, the overuse of which may lead to insecticide resistance among thrips (Melin et al. 2020). As a consequence of overuse of chemical insecticides, an elevation in thrips (*Sericothrips variabilis* Beach (Thysanoptera: Thripidae) and *F. occidentalis*) populations has been reported in soybean crops (Regan et al. 2017).

S. aurantii was overall the most abundant thrips species collected by knock-down sampling from avocados and macadamias in the Levubu region. Its hosts are abundant in the Levubu area, and this might contribute to their relative abundance, with potential movement between patches of vegetation with suitable host tissue available throughout the year. The species has been documented on 70–100 species of plants ranging from indigenous vegetation such as acacia to fruit trees such as citrus and mangoes (Rafter & Walter 2012). Thrips of the genus *Scirtothrips* have been documented to damage most crops around the world; for example, *S. perseae* was associated with damage of avocados in California (Yee et al. 2003). *S. aurantii* was the most abundant species collected on avocados in KwaZulu-Natal Province (Bara & Laing 2019) and macadamias in Mpumalanga Province (Hepburn 2015). The results of our thrips rearing experiment align with those from our knock-down sampling, where *S. aurantii* was the most abundant species, followed by *T. tenellus*. *S. aurantii* being the dominant thrips species being reared from plant tissues confirms that it is responsible for causing damage. This species was also reared from tissues and was sustained to adulthood on avocados collected in KwaZulu-Natal, confirming its role in causing damage (Bara & Laing 2019). No published data exist on the status of *T. tenellus* on avocados and macadamias, although the species was the most abundant on Macadamia 695 and particularly on flowers. The species was also among the thrips that developed from avocado and macadamia tissues, supporting the development of both larvae and adults. High abundance of *T. tenellus* on Macadamia 695 could be associated with cultivar and flower feeding preference by this species. *H. gowdeyi* larvae also developed from macadamia tissues. Feeding preferences among thrips could be a driving factor behind the development of larval stages of *H. gowdeyi* from macadamia, which is regarded as fungivorous (Ananthakrishnan 2017). *F. occidentalis* is regarded as pestiferous (Allsopp et al. 2019; Facun Sarmiento et al. 2014), although there was no development of this species from avocado and macadamia tissue. This species infests the flowers and fruit of other host plants such as pepper, citrus and apples (Reitz 2009).

In conclusion, the results suggest that Pinkerton and Fuerte avocados and Macadamia 816 are the most susceptible to thrips damage. Hass avocados, Macadamia 695 and Macadamia A4 are the least susceptible to thrips damage. In the Levubu region, the most widely planted avocado cultivars are Fuerte and Hass, with 695 being the most widely planted macadamia cultivar, so some host plant resistance may already be available to many farmers. Identification of mechanisms underpinning the differences in susceptibility of avocado and macadamia cultivars as well as their developmental stages would be valuable for plant breeding initiatives to increase host plant resistance to thrips. Thrips infest at the earliest developmental stages, and young fruits and flush are the most prone to thrips damage. We recommend that control strategies be introduced before the onset of flowering season and immediately after pollination before fruit set to effectively control thrips damage. *S. aurantii* was the most dominant, confirming that it is the species responsible for the main damage and therefore should be a species of concern to the avocado and macadamia industries. Thrips abundance and damage were more dependent on seasons; there is a need to investigate environmental variables driving *S. aurantii* species to cause damage on avocados and macadamias.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The experimental data in support of the findings of this study are publicly available. They can be found here: https://doi.org/10.25403/UPresearchdata.29041577

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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