Journal of Agriculture and Food Research 12 (2023) 100569

Contents lists available at ScienceDirect

Journal of Agriculture and Food Research

journal homepage: www.sciencedirect.com/journal/journal-of-agriculture-and-food-research

Reduced macadamia nut quality is linked to wetter growing seasons but mitigated at higher elevations

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ARTICLE INFO

Keywords:
Agriculture
Climate change
Insect pests
Rainfall
Southern Africa
Subtropical

ABSTRACT

Climate and insect pests are vital variables that affect crop production. Climate change will alter the magnitude and timing of precipitation, but how rainfall and temperature interact to affect insect pest damage in agriculture is poorly understood. Here, we explore the interacting effects of elevation and contrasting weather conditions (a wet vs. dry year) on macadamia nut quality, which is strongly affected by insect pests. For two years, we sampled macadamia nuts at 40 plots, stratified across ten farms along an elevational gradient in subtropical Limpopo province of South Africa. As measures of nut quality, we related total kernel recovery, nut immaturity, and kernel insect damage to precipitation and elevation. Higher rainfall reduced nut quality in all three response variables, while colder temperatures at higher elevations mitigated this effect. Our findings suggest that future warmer temperatures, more intense and wetter rainy seasons could lead to lowered macadamia nut quality even at higher elevations and economic losses to the industry.

1. Introduction

Plant productivity depends on abiotic factors such as light, precipitation, temperature, and biotic factors such as herbivory and the biotic cycles that determine nutrient availability. Rainfall and temperature also limit herbivores and predators [1]. Global climate change scenarios predict alterations in these abiotic factors that will negatively impact the performance of crops and affect the animals (e.g., insects) associated with them [2]. In particular, ongoing climate change has resulted in alterations in rainfall quantities and timing [3]. Understanding the impact of these spatiotemporal trends is essential for mitigation and adaptation in agriculture. The inter-annual variability in precipitation will increase in response to a warmer climate [4], which will cause droughts, floods, and biodiversity loss and will severely impact crop and livestock production systems [5]. Global climate change affects productivity and alters the suitable areas of agricultural crop species worldwide, cascading effects on the economies and people.

Macadamia is one of the most profitable crop species in subtropical regions of the world [6]. Two species, *Macadamia integrifolia* Maiden and Betcher, and *Macadamia tetraphylla* L.A.S. Johnson, and their hybrids, are cultivated commercially [7]. *M. integrifolia,* or the smooth-shell macadamia, is a medium-sized evergreen nut tree native to the subtropical rainforests of the east coast of Australia [8,9]. Macadamias were introduced to South Africa in the 1960's, and the country has been the world's largest producer of macadamia nuts since 2014. Macadamia orchards in South Africa are located mainly in the three provinces of KwaZulu-Natal, Mpumalanga and Limpopo [10] and are one of the fastest expanding crops, with the annual production increasing from 3000 tons of DNIS (dry nuts-in-shell) and 7.3 million USD in 1996 to 68,840 tons of DNIS and more than 300 million USD in 2022 [11].

Macadamia flowering and nut set development occur on raceme inflorescences, and the nuts separate from the tree at about the time their seed is mature. The nut comprises a thick husk (pericarp) surrounding a thick and hard shell containing the edible kernel. Factors that affect nut set and kernel development can significantly impact the nut yield and kernel quality and thus have economic consequences for

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https://doi.org/10.1016/j.jafr.2023.100569
Received 20 August 2022; Received in revised form 15 March 2023; Accepted 25 March 2023

macadamia growers [9,12]. The South African macadamia industry loses 3–4% of kernels due to factors causing poor kernel quality. The macadamia industry defines unsound or defective kernels as immature, dark, mouldy, germinating, having shell marks, having brown centres, or showing signs of insect damage [11].

Insect pests are considered a significant threat and limiting factor to macadamia production worldwide. They damage the husk and kernel while the nut ripens on the tree [13,14]. In Australia, the world's second-largest macadamia producer, insect damage was the most important cause of factory kernel rejection between 2009 and 2020. In 2020, the estimated value of factory-level rejections due to insect damage was 240 USD/ha [15]. Annual losses from insect pest damage average at 15.2 million USD [11,16–18].

South African macadamia has more than 60 insect pest species, dominated by heteropterans and lepidopterans to a lesser degree [14, 19–21]. Stink bugs (Pentatomidae) dominate heteropteran species assemblages in macadamia orchards [22]. The two-spotted stink bug *Bathycoelia distincta* Distant, 1878 is the major pest in South Africa [23], representing 90% of insect damage [20]. Stink bugs feed on macadamia nuts at different stages, from the second-instar nymph to the adult stage, which damages mature kernels and can even cause premature nut drop [24,25]. The annual monetary loss caused by stink bugs went from 8.8 million USD in 2019 to 10.5 million USD in 2020 [11]. In South Africa, four lepidopteran species feed on macadamia nuts: three Tortricidae and one Pyralidae. However, the two main species causing nut damage are the Tortricidae: the macadamia nut borer *Thaumatotibia batrachopa* Meyrick, 1908 and the false codling moth *Thaumatotibia leucotreta* Meyrick, 1913 [16,26,27]. These two pests represent about 90% of the

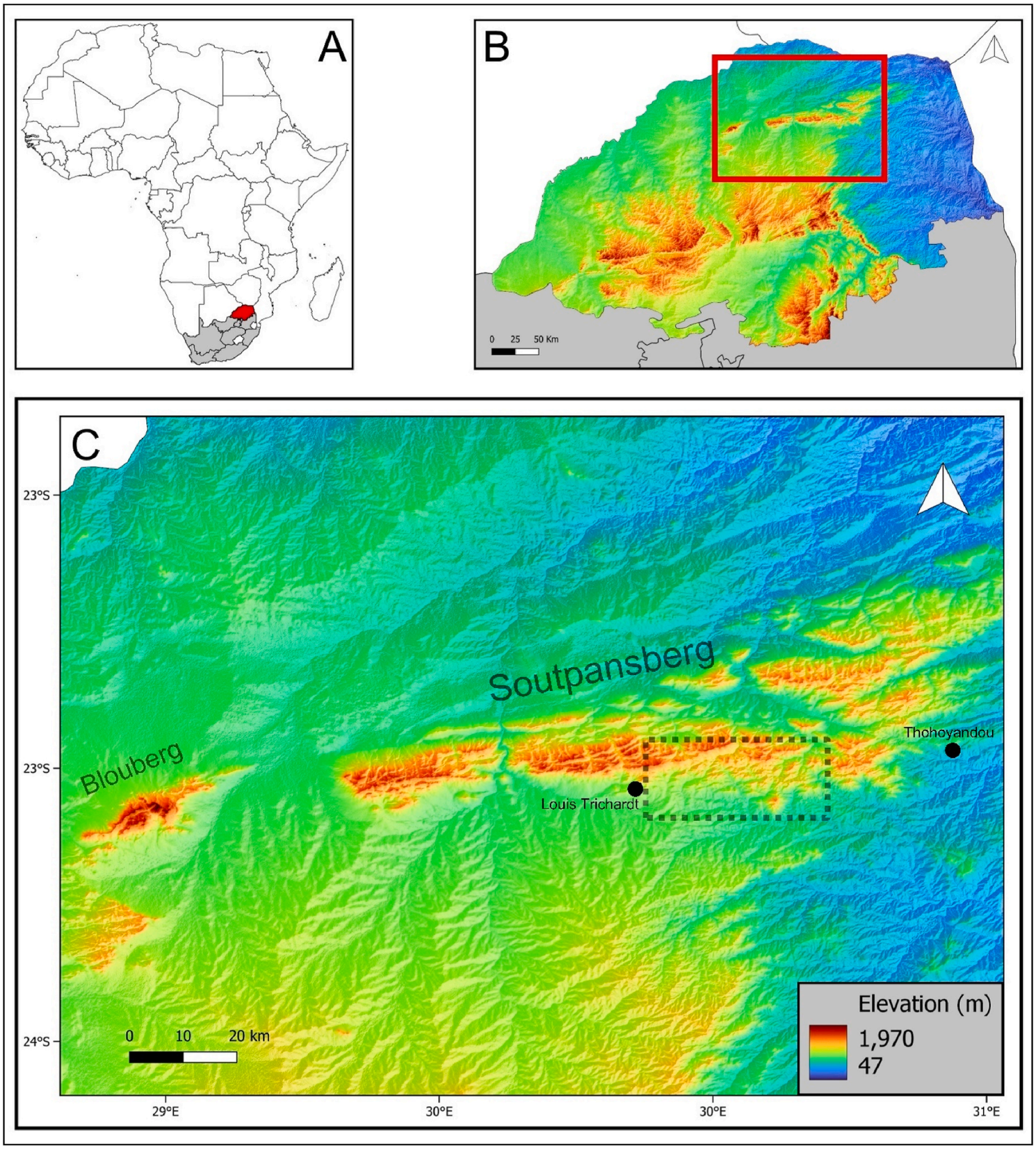

Fig. 1. Map of the study area. A) Limpopo province (marked in red) in South Africa (grey); B) Soutpansberg and Blouberg Mountains (red rectangle) located in the north of Limpopo province; C) Location of the sampled farms in Levubu region (dashed rectangle) between the towns of Louis Trichardt and Thohoyandou. The elevational gradient is indicated (m a.s.l.). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

tortricid moth damage found in macadamia orchards [16]. Recent studies found that the macadamia nut borer is the most significant tortricid pest of macadamias in South Africa, representing 95% of the larvae collected in damaged nuts across all growing regions (KwaZulu-Natal, Mpumalanga and Limpopo) [28]. Tortricid moths are particularly concerning for macadamia crops because their larvae feed on developing nuts [26].

As small ectotherms, terrestrial insects are sensitive to variations in temperature and water availability [29], and their responses to climate change could impact crop losses to pests [2,30]. This impact by insect pests may exacerbate the losses caused by changing climatic conditions in highly profitable crops like macadamia, mainly due to factors driving immature nut drop (e.g., water stress, nutrient deficiencies, extreme temperature variation, insect damage) [16]. Climatic conditions influencing crops and pest insects vary greatly along elevational gradients, even over relatively short distances. Insect abundance and damage generally decrease at higher elevations due to colder ambient temperatures [31]. Unfortunately, few studies have focused on the effect of elevation and climatic factors on crop-pest insect interactions.

In the present study, we tested whether elevation (a proxy for temperature variation) and inter-annual variability of macadamia nut growing season precipitation, affect nut quality, while controlling for the effects of other major factors (landscape context and volant vertebrate insectivores). We addressed the impact of these issues on three macadamia nut quality metrics (total kernel recovery, nut immaturity, and kernel insect damage) by: i) quantifying variation between growing seasons with markedly different rainfall; ii) how they varied along an elevational transect; iii) and the interaction between these two factors.

2. Materials and methods

2.1. Study area

The study area is located between the towns of Thohoyandou and Louis Trichardt/Makhado in Limpopo province, the northernmost region of South Africa and the country's second-largest producer of macadamia nuts (Fig. 1). Levubu valley in Limpopo is South Africa's oldest macadamia growing area [17]. This valley lies on the southern foothills of the Soutpansberg Mountains (Fig. 2A), is a centre of biodiversity and endemism, and falls within UNESCO's Vhembe Biosphere Reserve [32]. The Levubu area has a subtropical climate with mean annual precipitation of 900 mm. The area receives most of its yearly rainfall between November and April in the summer, with peak rainfall from December to February. The dry winter season is between May and August. In the rainy summer (November to April), average monthly maximum and minimum temperatures range from 26 to 29 °C and from 16 to 19 °C, respectively. In the dry winter (May to August), average monthly maximum and minimum temperatures range from 23 to 25 °C and from 10 to 12 °C, respectively [33,34].

2.2. Data collection

The study included ten commercial macadamia farms stratified along an elevational transect (735–1330 m a.s.l., Appendix Fig. A.1), and the farms were all more than 5 km apart. Elevation was used as a proxy for ambient temperature changes (Appendix Fig. A.1). Sampling was done over two years (September 2019–May 2021). We extracted weather data (rainfall and temperature) for the two years, during the rainy summer season (i.e., macadamia nut growing season), from a weather station at the lowest part of the elevation transect (735 m a.s.l.). We also obtained annual rainfall data recorded at the highest part of the transect (1330 m

Fig. 2. Macadamia orchards studied. A) Levubu subtropical valley landscape on the southern slopes of the Soutpansberg mountains; B) One of the ten macadamia orchards from our study; C) Exclosure cage treatment containing two adjacent macadamia trees; D) Control for the cage treatment containing two adjacent macadamia trees.

a.s.l.) for the last eight years (October 2013–September 2021) (Appendix Fig. A.2). The two growing seasons in our study differed considerably in terms of rainfall quantity (Table 1, Appendix Fig. A.2): November 2019 to May 2020, is therefore referred to as the "dry growing season" and November 2020 to May 2021 as "wet growing season" (Table 1).

All the macadamia orchards in this study were in full production and of similar age (Fig. 2B). Macadamia cultivars varied across the farms, with Pahala (788) being the most common in our sampling units. Sampling units consisted of two adjacent trees; each farm had four sampling units (4 sampling units × 10 farms = 40 samples). Sampling units were paired, two at the orchard's edge, adjacent to natural or semi-natural vegetation, and two 50 m from the natural edge. One of the paired units (one sampling unit at the edge and one at 50 m from the edge) received a treatment that excluded volant vertebrate predators (insectivorous bats and birds) but allowed access to arthropods. The cage was composed of a wooden frame (dimensions 5 × 10 × 5 m) and a nylon mesh net (net eye size 2 × 2 cm) (Fig. 2C). The control plots were within 20 m of the treatment plots (Fig. 2D). None of the sampling units received pesticide treatments.

Once the macadamia nuts have reached their full size, their shell hardens (between December and February). After shell hardening, oil accumulates in the kernel. This process continues for around two months between January and May [8,35]. Once matured, the nuts drop to the ground from February to June. We collected the nuts weekly or biweekly from each sampling unit over two consecutive macadamia growing seasons (Fig. 3A). A total of 36,012 DNIS (dry nuts-in-shell) weighing 194.2 kg were collected. Husks were manually removed (de-husking). The nuts-in-shell were stored in well-ventilated paper bags for a few days until dry. After drying, we weighed the dry nuts-in-shell. We cracked the shell to extract the kernel (Fig. 3B). Kernels were weighed, examined and classified using standardized protocols to identify the major categories of unsound kernels: immature kernels and kernels with insect damage (Fig. 3C and D). The other types of defective kernels are much less common and include kernels that are mouldy, germinating, dark, and have shell marks or brown centres [11,15].

The first response metric calculated was total kernel recovery (TKR). TKR is the proportion of whole kernel weight per weight of DNIS (dry nuts-in-shell) (Fig. 3B). TKR is an essential measure of the economic profit of macadamias, along with the tree yield and nut quality, and can be directly dependent on kernel immaturity [16,36,37]. Next, we calculated immaturity, which is the weight of immature kernels as a proportion of the total weight of kernels. We classified kernels as immature based on their very small size, abnormal shape, and rubbery texture due to the premature drop before reaching full size or the completion of the oil accumulation stage [16]. Mature macadamia kernels contain the highest oil content of any edible nut, reaching up to 75% oil by weight. This oil content is the most significant factor determining its quality [38]. The amount of oil each kernel contains can be used to separate mature kernels from immatures by floating the kernels in a saline bath. We used this technique as an additional method of identifying immature kernels by floating them in a saline bath (1300 g salt on 20 L water), and those that sank were regarded as immature (according to practices used within the South African macadamia processing industry) [39].

Table 1
Weather data (rainfall and temperature) for the two years in our study (wet vs. dry year), recorded at a weather station located at the lowest part of the elevation transect (735 m a.s.l.) in Levubu region (Limpopo, South Africa).

Macadamia nut growing season (i.e., rainy summer season)	Total rain (mm)	Average daily rain (mm)	Average temperature (°C)
"dry" (November 2019 to May 2020)	801.9	4.36	20.7
"wet" (November 2020 to May 2021)	1119.3	6.12	20.5

We identified three types of insect damage on the kernels: "early stink bug damage" resulting from stink bugs feeding on young nuts; "late stink bug damage" resulting from stink bugs feeding on more mature nuts that have higher oil content (Fig. 3C); and "nut borer damage" caused by species of Tortricid moths (Fig. 3D). We calculated insect damage as the proportion (in weight) of kernels with at least one type of insect damage per total weight of kernels.

2.3. Statistical analyses

The statistical analyses were done using R version 4.2.2 [40]. We used Generalized Linear Mixed Effect models (GLMM) with binomial error structure and a log link function [41] to explore to what extent rainfall, elevation, and their interaction explain variation in the three macadamia kernel quality metrics (TKR, immaturity and insect damage). The "dry" and "wet" macadamia growing seasons represent inter-annual variability in rainfall (Table 1), while elevation is highly negatively correlated with temperature (Appendix Fig. A.1). We included the treatment (excluding volant vertebrate predators) and the context of landscape (presence or absence of natural or semi-natural vegetation adjacent to the sampling units) nested within each farm as random factors. Elevation was scaled to zero mean and unit standard deviation. The model with the lowest AIC (Akaike Information Criterion) value and all additional models within 2 ΔAIC of the best model were included in the results. Model residuals were tested for normality and homoscedasticity. Additionally, we calculated a pseudo-R^2 of the best GLMM model comprising conditional (R^2c) and marginal (R^2m) values. R^2m accounts for the proportion of the variance explained by the fixed factors. In contrast, R^2c accounts for the proportion of the variance explained by the whole model (i.e., fixed plus random factors) [42].

3. Results

Rainfall quantities during the macadamia nut growing season contrasted between the two consecutive years at the lowest part of the elevation transect (Table 1). Total rainfall and average daily rain were 39.6% and 40.4% higher, respectively, in the wet growing season (2020–2021) than in the dry growing season (2019–2020) (Table 1). This contrast between a dry and a wet year was also found when comparing total annual rainfall between these two consecutive years at the highest part of the elevation transect, with 58.2% higher total annual rainfall (Appendix Fig. A.2). Additionally, the wet year in our study (2020–2021) saw the highest annual rainfall (1041 mm) in the recorded eight years (Appendix Fig. A.2). Average temperatures did not vary between the two growing seasons (Table 1). Maximum temperature decreased by 6 °C from the lowest to the highest site along the elevational gradient (Appendix Fig. A.1).

Rainfall variability between the two years significantly affected total kernel recovery (TKR) (Table 2). TKR was lower (28% vs. 32%) in the wet growing season (Fig. 4A). Elevation (as a proxy for temperature variation) had no significant effect on TKR. Still, elevation interacted with rainfall, as higher elevation mitigated the negative impact of the wet year (Fig. 4A). The overall model for TKR explained less than 1% of the variance ($R^2c = 0.006$ and $R^2m = 0.003$).

The incidence of immature nuts was also significantly higher (Table 2) in the wet growing season (31% vs. 16%) (Fig. 4B). This incidence of immaturity decreased at higher elevations, and the negative impact of the wet growing season was less at higher elevations. The overall model for nut immaturity explained 15% of the variance ($R^2c = 0.150$), while the fixed factors explain nearly 11% of the variance ($R^2m = 0.106$).

The incidence of insect damage was also higher in the wet growing season (7.2% vs. 4.9%) (Fig. 4C), with early stink bug damage on 3.4% of the kernels, 2.3% damaged by late stink bug and 1.6% by nut borers; while in the dry growing season, 2.1% kernels had early stink bug damage, 0.5% had late stink bug and 2.3% nut borers. Elevation did not

Fig. 3. Macadamia nuts sampled in our study. A) Nuts still in their husk; B) Kernel extracted from the shell; C) Kernels with early or late stink bug damage; D) Kernels with nut borer damage.

Table 2
GLMM binomial model outcomes for the analyses of total kernel recovery, kernel immaturity and kernel insect damage.

Total kernel recovery **Fixed effects**	**Estimate**	**Std. error**	**z-value**	**p-value**
Intercept	−0.76	0.03	−22.81	<0.001
Elevation	−0.06	0.03	−1.95	0.050
Season	−0.19	0.01	−15.01	<0.001
Elevation:Season	0.06	0.01	4.80	<0.001
Kernel immaturity **Fixed effects**	**Estimate**	**Std. error**	**z-value**	**p-value**
Intercept	−1.81	0.14	−12.82	<0.001
Elevation	−0.29	0.13	−2.20	<0.050
Season	0.92	0.03	30.26	<0.001
Elevation:Season	−0.24	0.03	−8.18	<0.001
Kernel insect damage **Fixed effects**	**Estimate**	**Std. error**	**z-value**	**p-value**
Intercept	−3.32	0.31	−10.68	<0.001
Elevation	0.02	0.25	0.08	0.940
Season	0.27	0.05	5.01	<0.001
Elevation:Season	0.43	0.05	7.76	<0.001

affect the incidence of insect damage but interacted with rainfall to increase this insect damage at higher elevations (Table 2). The best model for insect damage explained nearly 19% of the variance ($R^2c = 0.188$), while the fixed factors explained only 3% of the variance ($R^2m = 0.029$).

4. Discussion

The results of our study suggest that inter-annual variation in rainfall, as well as elevation, impact nut quality metrics. All the metrics were significantly lower during the wet growing season. The proportion of recovered kernels decreased, and the proportion of immature nuts and insect-damaged kernels increased. Except for insect damage, these negative impacts were less at higher elevations, while elevation interacted with precipitation to mitigate against the negative impacts of a wetter growing season. As temperature is negatively correlated with elevation, lower temperatures could be vital in affecting nut quality.

Macadamias originated from regions in Australia characterized by a dry winter period, and are thus drought resistant trees through water conserving mechanisms, specifically via their leaves and stomata [43]. Stephenson et al. [44] found that very heavy rainfall during the nut maturation stage was detrimental to kernel recovery. In contrast, moderate rainfall of about 100 mm/month was associated with high kernel recovery. Arguably, excessive rain during the kernel-filling stage of the macadamia nut, could decrease kernel filling, likely due to the reduction of photosynthesis under cloudy conditions. Kernel recovery is sensitive to reduced photosynthate supply [37]. Also, high rainfall and its link to high air humidity during the nut growth and maturation stages can negatively affect kernel recovery. High air humidity suppresses transpiration, negatively affecting mineral uptake and kernel growth. Additionally, excess water in high-rainfall areas can cause leaching of macronutrients (e.g., nitrogen) in the soil, and removes much of the oxygen resulting in a shortage of microelements (e.g., iron) [45].

Macadamias can be successfully grown at various elevations, e.g., 700 m a.s.l. in Costa Rica, 550–1500 m a.s.l. in Malawi, and 550–1600 m a.s.l. in Guatemala. However, low altitudes, e.g., below 450 m a.s.l. in the lower Ntchisi (Malawi) area, are too hot for good growth and tree health [46]. Several studies suggest that macadamias are better suited to lower elevation areas: e.g., <476 m a.s.l. in Hawaii [47] and <600 m a.s.l. in South Africa [48]. Trees planted at high elevations grow relatively

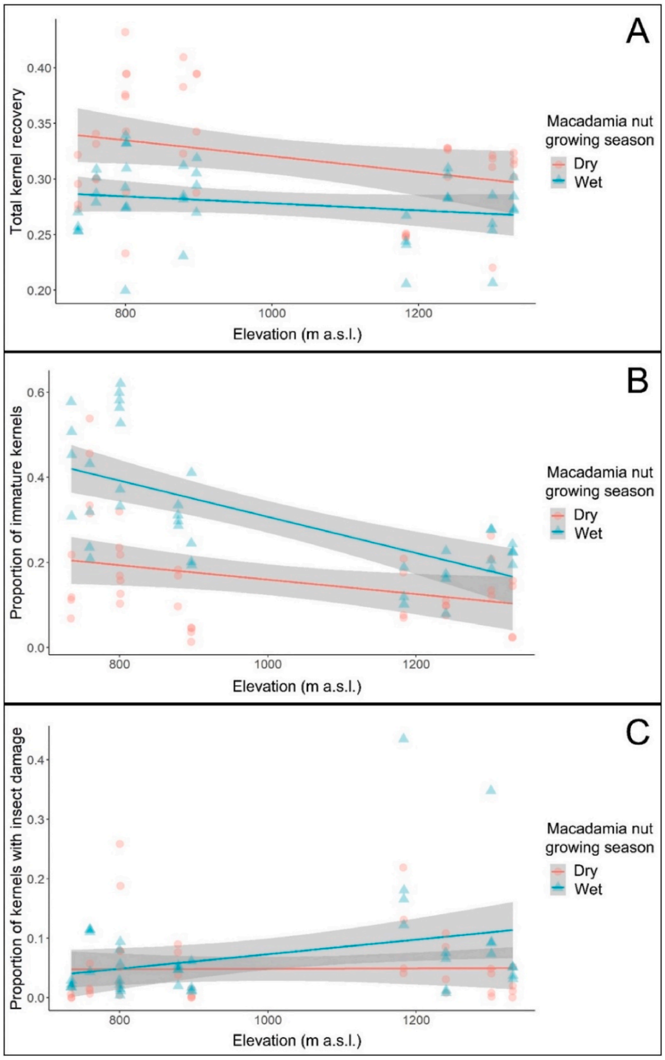

Fig. 4. Effects of the elevation gradient and the macadamia nut growing season (dry vs. wet growing season) on total kernel recovery (A), the proportion of immature kernels (B), the proportion of kernels with insect damage (C). Regression line and 95% confidence interval are indicated for each growing season.

slower, have thicker shells and lower total kernel recovery. In our study, TKR decreases slightly with elevation, especially in the wet growing season. Nevertheless, elevation had no significant effect on TKR, while higher elevations significantly mitigated the negative impact of higher rainfall on TKR during the wet growing season.

The GLMM model explained a small amount of variation in TKR. TKR depends on many other factors, besides rainfall seasonality and temperature, these include cultivars, genetic factors, physiological disorders in the nut, early germination, on-farm management and insect damage [16,36,37]. Some of these factors, such as cultivars, irrigation strategies, landscape context and volant vertebrate predators were included as random factors in the model. Shell thickness affects TKR, edibility and the highly valued kernel size. Since the shell accounts for most of the macadamia nut's weight, TKR is an essential element of the economic profit of macadamias, along with the tree yield and the other criteria of nut quality, such as immaturity and insect damage. Therefore, TKR directly depends on kernel immaturity, and we can assume that kernel recovery is also influenced by factors causing immature kernels [16,36,37].

In the model for kernel immaturity, marginal R^2 values contributed most to the conditional R^2, suggesting that the fixed factors (rainfall and elevation) play a larger role than landscape context, the volant vertebrate predators and farm in affecting this metric. The incidence of immature kernels was much higher in the wet year (31% vs. 16%). Although water deficit during nut development can cause premature nut drop of immature nuts with low oil content and poor quality, excessive rain during nut maturation can adversely affect kernel quality and induce immature nut drop [44,49,50]. The wetter summer season would cause an increase in pest insect abundance and damage. Insect damage is not only direct through spoiling the kernel, but also indirect through triggering immature nut drop [14,35]. Relative humidity, rainfall, and temperature are important predictors for determining the population size and pest damage potential of various heteropteran stink bug species [51]. These sucking insects can feed both on the kernel of mature nuts after the shell has hardened and on the kernel of developing nuts, resulting in injuries that cause their abortion before reaching maturity [52]. On the other hand, nut borers lay their eggs on the husk (pericarp), and the larvae burrow through the husk and shell to feed on the kernel. Nut borer larval feeding on the husk can cause immature kernel and premature nut drop, particularly during the oil accumulation stage, due to the damage of the connective tissue between the embryo (kernel) and the pericarp [16].

Our study showed that the incidence of insect damage on the kernels was significantly higher in the wetter year (7.2% vs. 4.9%). This increase in insect damage was primarily due to early and late stink bug damage, while nut borer damage seems to have been slightly lower in the wetter year. It is important to note that we examined insect damage only on the kernels. However, most nut borer damage is on husks through larval feeding, not on the kernels [26,28]. Consequently, nut borer damage could be underestimated, not only in our study but also by the macadamia industry in general. Immature kernels represented a large portion of total kernel weight during both growing seasons (reaching 31% in the wet growing season), compared to the proportion of kernels with insect damage (up to 7.2% in the wet growing season). This demonstrates the importance of further investigating the link between stink bug/nut borer damage and kernel immaturity and their actual and future impacts on the macadamia industry under changing climate conditions.

Precipitation gradients and pest pressure are confounded [1]. Major stink bug infestations can occur during austral summer up to autumn, while significant infestations of macadamia nut borers *T. batrachopa* usually occur from November to January [14]. Based on Taylor et al. [53], populations of the significant stink bug species in South Africa, the two-spotted stink bug *B. distincta* and the green vegetable bug *Nezara viridula* Linnaeus, 1758, generally begin to build up during late spring (October to November) in response to warmer conditions and peak in summer (from November to February). Monitoring of the macadamia nut borer *T. batrachopa* and the false codling moth *T. leucotreta*, in a macadamia farm in Levubu showed that their populations seem to peak each year around December and January [53].

Relative to the model for immaturity, rainfall and elevation explained considerably less variation in the best model for insect damage. Differences in landscape context (surrounding vegetation) and farm management (e.g., insect pest control practices) between the farms could partly explain this. None of our sampling units received pesticide treatments, but pesticide drift is still possible from adjacent tree blocks that were treated and would also affect insect colonization. Although we did not have exact data on these variations and only included them as random factors, we noticed that the farms at lower altitudes had heavier pesticide applications. In contrast, one high-altitude farm applied no pesticides. Additionally, the farms located at higher altitudes had surrounding vegetation that was less transformed. The extent of macadamia orchards also decreases at higher elevations, covering smaller areas than at lower elevation sites where agricultural intensification has been much higher.

The other random factor used in our model for insect damage was the cage exclusion treatment. This prevented volant vertebrate predators of pest insects (i.e., insectivorous bats and birds) from reaching the sampled macadamia trees. A previous study in macadamia orchards of Levubu based on exclusion experiments demonstrated that prevented biocontrol by birds and bats resulted in a significantly higher percentage of insect-damaged kernels and in yield losses of up to 60%. This biocontrol was higher near natural vegetation but still significant in human-modified landscapes [54]. Other similar studies have tested bird and bat predation effects in the tropics by using exclosures, and found that bird and bat predation reduced insect abundances [55–57].

Elevated bat foraging activity in orchards during late wet summer season, decreased in the dry season and corresponded with seasonal changes in abundance of heteropterans and lepidopterans [18,53,58]. Generally, fluctuating arthropod numbers influence the foraging behaviour of birds and bats. This pattern is more pronounced under more-extreme seasonal rainfall conditions [59]. For example, the breeding season for insectivorous birds coincides with the flush of insects associated with the rains in tropical areas of Africa characterized by a 4-to-6-months dry season [60]. In tropical moist forests of Central America, a general increase in insect abundance during the rainy season has been noted and correlated with the tendency for most insectivorous birds to breed at that time [61].

In the southern aspect of the Soutpansberg mountain range, bat activity and species richness of bats declined monotonically with increasing altitude [62,63]. In our study, the observed increase in the incidence of insect damage at higher altitudes during the wet growing season could result from reduced activity of insectivorous birds and bats at these higher altitudes. Bats and birds can reduce herbivorous insect densities and damage in tropical and subtropical agroecosystems [17,18,53,54,58,64–68]. Encouraging their populations on a local level around agricultural lands can thus be a powerful and cost-effective way of controlling pest insects instead of relying entirely on environmentally harmful chemical insecticides [69].

It should be noted that the proportion of unsound kernels in our study (around 38% in the wet growing season and 21% in the dry growing season), composed of immature kernels and kernels with insect damage, is much higher than the average of 3–4% usually reported by the South African macadamia industry. This could be partly due to our relatively small sample size or because half of the sampling units were covered with an exclusion cage, preventing natural pest control by bats and birds; hence exceptionally high insect damage is not surprising [54]. Additionally, a substantial number of clearly defective nuts-in-shell (e.g., extremely small size, visible damage) do not reach the nut processing factories and thus not reported by the macadamia industry, which suggests that the extent of macadamia crop losses linked to nut immaturity and insect damage is severely underestimated.

5. Conclusion

We demonstrated in this study the effects of elevation and inter-annual rainfall variability during the macadamia growing season on nut quality and insect damage. Expected climatic changes, especially changes in precipitation and ambient temperature, and their strong effects on ecological and trophic interactions make it imperative to study them together to better understand how climate change impacts crop production and future biodiversity. The average of the IPCC CLIM5 climate models [70] and multiple studies on projections of future changes in precipitation [71] predict that wet subtropical regions where macadamias are grown will experience increased precipitation. This, coupled with changes in rainfall timing [33] may result in water excess during vital phases of the macadamia crop production (e.g., nut development), which will lower the nut yield and quality, and thus increase crop losses, affecting the profit of large-scall farmers and the livelihood of smaller-scale farmers. The general trend suggests that the wetter and warmer conditions predicted for these regions could aggravate these losses for the macadamia industry. At the same time, cooler temperatures at higher altitudes could be a significant mitigating factor.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

The support of the Department of Science and Technology (DST) and the National Research Foundation (NRF) in South Africa is acknowledged through the South African Research Chairs Initiative (SARChI) Chair on Biodiversity Value and Change in the Vhembe Biosphere Reserve [Grant number 87311], hosted at the University of Venda. We gratefully acknowledge the support of the German Federal Ministry of Education and Research (BMBF) and the German Federal Government through the SALLnet project (South African Limpopo Landscapes Network) within the framework of the SPACES II program (Science Partnerships for the Adaptation to Complex Earth System Processes in Southern Africa). Additionally, we thankfully acknowledge the support of Prof. Wayne Twine (University of the Witwatersrand) through the project ACyS (Annual Cycle and Seasonality) of the ACCESS program (Alliance for Collaboration on Climate and Earth System Science). CW is grateful for funding by the Deutsche Forschungsgemeinschaft (DFG) [Project number 493487387]. We also thank Hamza Bouarakia for his aid with the map of the study area. Furthermore, we sincerely thank all participating macadamia farmers, managers and landowners (Alan Whyte, Phillip Potgieter, Marius Mostert, Murray Stewart, Pierre Thomas, Jacques Bouwer, Gertien Le Roux, Louis Jordaan, Dave Pope, Richardt Bouwer, Derrick Bouwer, Andy Tonks, Greame Whyte) for allowing us to conduct our experiments on the ten farms, and for their cordial cooperation and assistance.

Appendix A

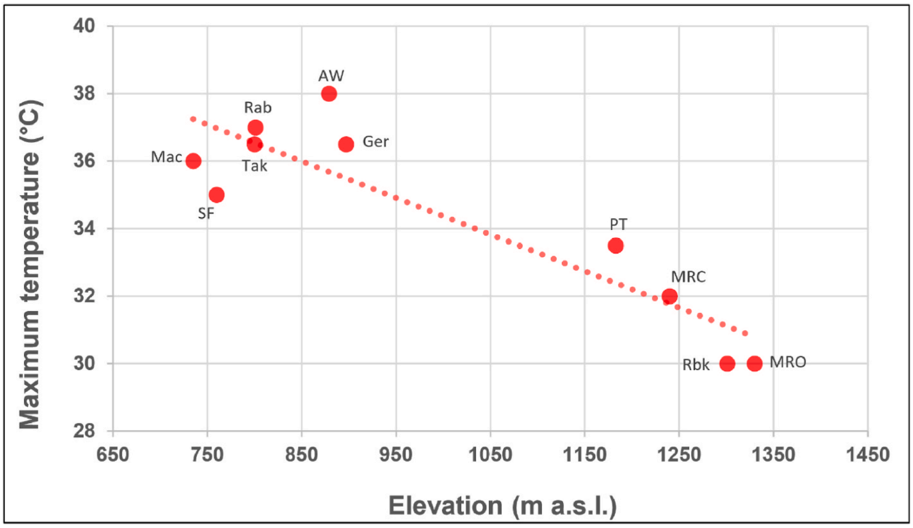

Fig. A.1. Maximum temperature (during the summer season of 2019–2020, referred to as the "dry" year in our study), recorded at the ten farms located at different elevations in Levubu region (Limpopo, South Africa). Linear regression forecast is also indicated.

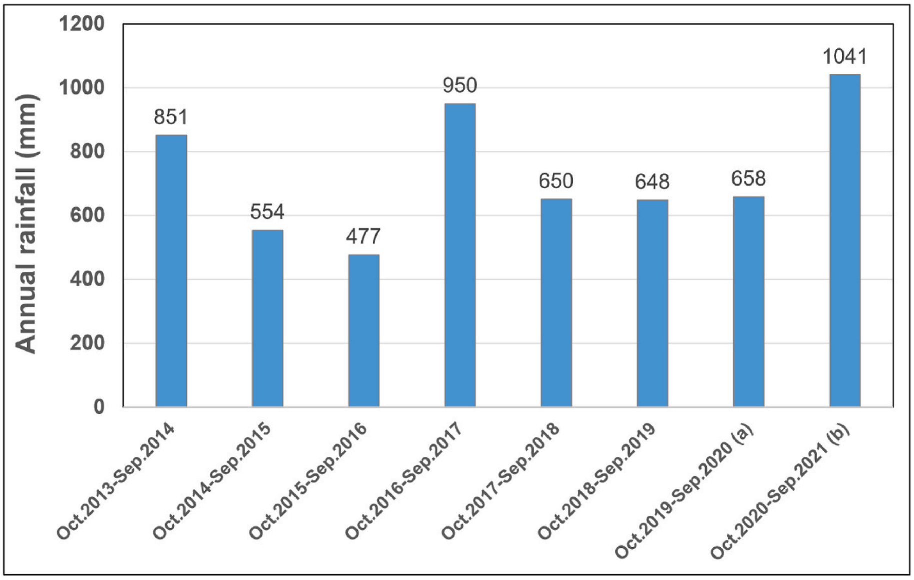

Fig. A.2. Annual rainfall for eight successive years (October 2013–September 2021), recorded at the highest part of the elevation transect (1330 m a.s.l.) in Levubu region (Limpopo, South Africa). a: the "dry" year in our study, b: the "wet" year.

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