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Mistletoe (*Dendrophthoe neelgherrensis* Wigh & Arn. Tiegh.) Parasitism on Yield of Nutmeg (*Myristica fragrans* Houtt.): Have We Been Underrating the Destructivity?

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ABSTRACT

The impact of mistletoe *Dendrophthoe neelgherrensis* (Wigh & Arn.) Tiegh. on nutmeg (*Myristica fragrans* Houtt.) yield was evaluated in mistletoe-infested and non–infested (control) trees during two fruiting seasons (January) in 2017 and 2019. Infested trees in season I and II had 40% and 10% of canopy covered (infestation) with the mistletoe, respectively. For yield determination, one branch was selected per whorl from each control tree. In each infested tree, one branch was selected from each non–infested whorl while two branches i.e. one infested and one non–infested, were selected from each infested whorl. The number of fruits was counted (yield) in each selected sub–lateral branch. Data were analyzed by fitting log–linear models after adjusting for over-dispersion, and comparisons were made using maximum likelihood estimates. There was no significant yield loss per tree at 10% infestation of mistletoe. However, at 40% infestation, yield dropped by 65% (from 6,238 to 2,159 fruits per tree). Yield loss in non–infested branches of infested trees was 37.2% whereas the drop was 89.6% in infested branches of those trees. Similarly, yield loss in non–infested whorls of infested trees was 48.2% whereas the drop was 84.8% for infested whorls of the infested trees. A quadratic yield pattern along the canopy was revealed, but the presence of the mistletoe was not related to the yield pattern of the tree. The study highlighted the destructive impact of mistletoe on nutmeg trees even with 10% infestation reducing the yield obtained from both the infested and non-infested branches and thus, the need for its timely control.

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INTRODUCTION

Nutmeg (*Myristica fragrans* Houtt., family Myristicaceae) is a perennial evergreen spice tree native to Maluku (Banda Islands) in Indonesia (Kew Science, 2021). The crop was introduced to Sri Lanka by the British at the beginning of the 19th century (Department of Export Agriculture, 2019). Over the years, it has attained the status of a key spice crop in Sri Lanka. In 2011, Sri Lanka was within the top five exporters for nutmeg and mace capturing about 8% of the global market while India had the largest export market share contributing to 49% of export value (Thadchaigeni *et al*., 2013). In 2018, the foreign exchange earnings of Sri Lanka from nutmeg and nutmeg products were 216.35 million US $ (Department of Export Agriculture, 2018). Nutmeg is commonly used in baking and culinary preparations, especially as a condiment. In addition, it is also known for its pharmaceutical values (Jose *et al*., 2016), and used in traditional medicine to relieve headaches, stomach aches, diarrhoea and flu symptoms. The intoxication effects of nutmeg are due to the presence of the alkyl benzene derivatives, myristicin and elemicin (Jose *et al*., 2016).

The nutmeg tree is a medium-sized, spreading or conical-shaped, thickly-leaved evergreen tree, which usually attains an average height of 4-10 m, and sometimes grows to heights of 20 m or more (Marcelle, 1995). The tree is usually single-stemmed, with profuse lateral branches arising in a slight spiral arrangement. The horizontal lateral branches radiate from the main trunk in whorls (Nagja *et al*., 2016). Sub–lateral branches fan out alternatively from these lateral branches (Marcelle, 1995). The fruit is elliptical in shape and comprises a single seed. They dehisce when ripe to reveal the purplish–brown coloured single seed covered by bright red aril. The plant yields two spices, the nutmeg (seed kernel inside the fruit) and the mace (the fleshy, red, net–like skin or aril covering the kernel) (Nagja *et al*., 2016). A well-grown single nut and mace would weigh approximately 10 g and 1 g, respectively (Department of Export Agriculture, 2019).

Parasitic plants are angiosperms that live at the expense of other plants and obtain their water, nutrient, and food requirements from their hosts (Tennakoon and Weerasooriya, 1998). Approximately 60% of the total parasitic flowering plants are root parasites. The members of the largest group of aerial parasites are mistletoes, which are sap–feeding hemi-parasites. They are known to establish long-lasting relationships with host plants (Griebel *et al*., 2017). These parasite-host relationships are complicated and can vary in different associations (Le *et al*., 2014). Further, different tree hosts are known to intrinsically offer different resources to their obligate mistletoe parasites based on their physiology and environmental parameters. Le *et al*. (2014) further argued that host-specific responses drive the intra-specific variations in mistletoe physiology. Considerable reduction in performance has been reported in many host plants, and in heavy mistletoe infestation, parasitism may result in death of the host (Press and Phoenix, 2005). For example, when parasitized by *Dendrophthoe vitelline* and *Amyema bifurcatacan,* eucalypt (*Eucalyptus* and *Corymbia* spp.) tree growth was found to be variable across space and time in plantations in New South Wales, Australia (Carnegie *et al*., 2009). This simulated analysis indicated that infection by mistletoes reduced stand basal area by 10% and stand volume by 13%.

The occurrence of mistletoe on spices and many other perennial plant species has increased during the recent past in Sri Lanka, for which the reasons are unclear (Yapa *et al.,* 2015). It is known that the ecophysiological stress of plants increases with climate change thus, making trees potentially more susceptible to mistletoe infection. This leads to increased stress of the host plants, leading to higher mortality rates (Griebel *et al*., 2017). The mistletoe species that belong to family Loranthaceae, i.e. *Dendrophthoe neelgherrensis* (Wigh & Arn.) Tieghem*, Dendrophthore falcata* (L.f.) Ethingsh., and *Scurrula cordifolia* (Wall.) G. Don*,* have been reported to infest many spice crop species including nutmeg in Sri Lanka (Yapa *et al.,* 2015). Mistletoe parasitism is known to negatively affect the physical quality characteristics of nutmeg and mace (Yapa *et al.,* 2017). However, usually, the mistletoe parasitism goes unnoticed until a substantial proportion of the host tree canopy is covered by the mistletoe, which practically delays its control measures. Further, the quantification of the impacts of parasitic plants on the yield of spice crops including nutmeg has not been conducted in Sri Lanka or elsewhere. Therefore, this study was carried out with the objective of quantifying the effect on nutmeg fruit yield due to the parasitism of mistletoe *D. neelgherrensis*, in order to adopt effective control measures. Here we report the quantified impacts of this mistletoe on the productivity of a key spice crop.

METHODOLOGY

The study was carried out during two fruiting seasons (during the month of January), season I (in 2017), and season II (in 2019), at *Bandarapola*

Estate in Matale District of Sri Lanka (7°28’00 N, 80°38’40 E and altitude 401 m). Sampling was carried out in January each year, prior to fruit maturity, in order to avoid fruit falling with maturity. The estate belonged to the WM3b agro–ecological region (Punyawardana, 2010). Nutmeg was intercropped with coconut so that a nutmeg tree was planted in between 4 coconut trees. All nutmeg trees were about 20 years old and the whole estate has been under the same management practices since establishment of the plants.

Many nutmeg trees in this estate were infested with the mistletoe species *D. neelgherrensis* (Figure 1). The identification of the parasitic plant species was carried out using voucher specimens at the National Herbarium of the Royal Botanical Gardens at Peradeniya, Sri Lanka.

a b

Figure 1. (a) A photograph showing a nutmeg tree infested with *D. neelgherrensis* in the field (see the circled area). (b) A close–up picture of *D. neelgherrensis.*

Selection of trees and design of study

Trees satisfying the selection criteria, e.g. typical conical shape without any damage to the main shape of the canopy, were selected for the study. For each fruiting season, infested and non–infested (control: completely free from *D. neelgherrensis*) trees were selected. In the season I, selected infested trees had approximately 40% (37-43%) of the canopy covered with *D. neelgherrensis*, and in season II, the infested trees had approximately 10% (8-12%) of the canopy covered with *D. neelgherrensis*. In the season I, there were only 10 infested trees satisfying the required conditions and thus all 10 trees were selected for the study.

However, there were about 20 non–infested trees satisfying the conditions in this season, and out of them, 10 trees were selected randomly as controls. In the season II, there were only 6 infested trees and 8 non–infested trees satisfying the required conditions and thus all 14 trees were selected for the study (Figure 2).

The study was planned according to the nested experimental design, with infested and non–infested trees nested within the season. According to the arrangement, the season effect was confounded with the effect of level of infestation and thus statistical analysis was not performed to investigate the effect of the level of infestation. However, this information was generated when the impact was investigated at each level of infestation.

The level of infestation was decided by a visual scoring system, depending on the extent of the canopy covered by *D. neelgherrensis*. The canopy of the nutmeg tree was pictured from at least two different sides, using the camera on a mobile phone while standing on the ground at a 2-3 m distance from the tree.

The amount of the canopy covered by the mistletoe was evaluated visually by drawing it on a paper to a scale. Then the percentage canopy covered with mistletoe was calculated as follows.

$$\textbf{Percentage canopy covered with mistletoe} = (\textbf{area of the canopy covered by mistletoe} / \textbf{total canopy area}) \times \mathbf{100}$$

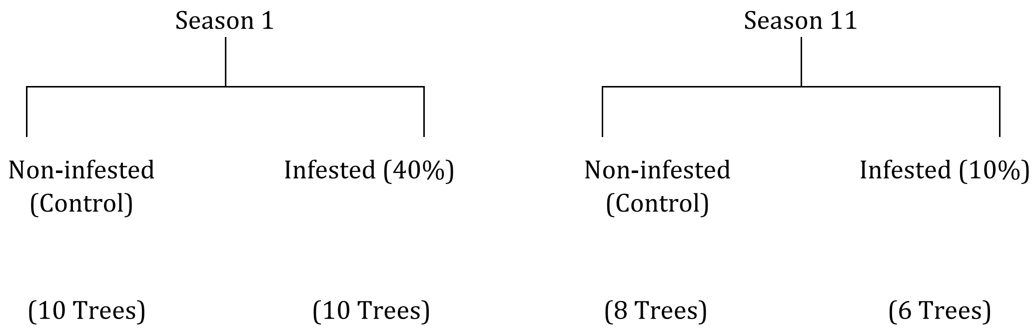

Figure 2. Selection of number of trees for the study in the two-fruiting season

Data collection

The fruit counting was done before the fruits ripened as the fruits tend to easily fall upon ripening. The sampling of branches from selected trees was carried out as follows: from each control tree, for each whorl, one out of the five lateral branches was selected randomly, and the fruit number in selected branches was counted separately. When taking the fruit count from the selected lateral branch, the count was taken for each sub–lateral branch (Figure 3) separately. The fruits in the topmost branches in the crown (final five to eight whorls of the plant) were counted together as it was difficult to count them separately due to the height, and also because the branches became smaller with the tree height. From infested trees, for each infested whorl, an infested lateral branch was also selected, and in addition, a healthy lateral branch was selected randomly for each non–infested whorl. Fruit counting was done separately in each sub–lateral branch.

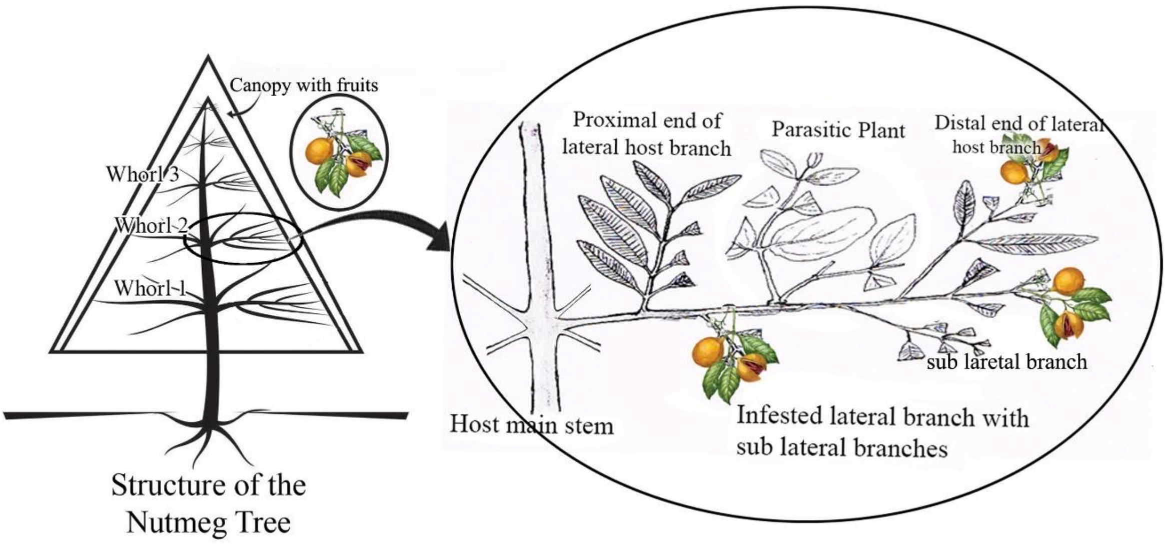

Figure 3. Branching pattern of nutmeg that was considered for sampling in the infested trees

Statistical analysis

The major focus of the analysis was to evaluate the effect of *D. neelgherrensis* infestation on yield (fruit number) of nutmeg followed by the effect of the season. In infested trees, the yield of infested and non–infested lateral branches, and the infested and non-infested whorls were compared. When the lateral branch was infested, the yield of infested and non–infested sub–lateral branches were compared. According to the arrangement of the study, control and infested trees were nested within seasons. Therefore, first, the season effect was studied, and then depending on the outcome, further analysis was done as follows.

In order to have a comprehensive understanding of the impact of *D. neelgherrensis* infestation on yield, the effect of the mistletoe infestation on yield components was studied. The yield components such as fruit number per whorl, lateral branch, and sub–lateral branch were studied after adjusting for yield patterns, when such pattern was detected within the canopy. It was hypothesized that the whorl yield increased from the bottom of the canopy until halfway through the height of the canopy and, decreased from that point upwards. As the number of whorls was not consistent across trees, this aspect was considered by means of a relative position of the whorl (a value between 0–1). A higher relative position implied that the whorl was located more towards the top, and a lower relative position indicated the whorl was more towards the bottom of the canopy. The data collected were fruit counts and thus, the analysis was done by fitting log linear–models. The goodness of fit of the models was evaluated using deviance (G^2) statistic (McCullagh and Nelder, 1989). The effects of the factors were evaluated using changes in the deviance (ΔG^2) statistic of type 3 analysis, also known as likelihood ratio (LR) (Agresti, 2007). Data were investigated for over-dispersion (McCullagh and Nelder, 1989), too. The over-dispersion, if any, was considered in the analysis and the standard errors were adjusted accordingly (McCullagh and Nelder, 1989; Agresti, 2007) using Pearson scaling method (Agresti 2007). The difference between levels of factors was studied using the maximum likelihood estimates. The PROC GENMOD of SAS statistical package (University Edition) was used for the statistical analysis.

RESULTS AND DISCUSSION

Comparison of yield between the two fruiting seasons

The yields of two fruiting seasons were compared first, according to the nested arrangement of the study. When the log–linear model was fitted for the season effect, goodness of fit statistic (G^2) was 51637.0 with 32 df and thus over-dispersion was exhibited. When the model was refitted after accounting for over-dispersion using Pearson scaling method, G^2 was 36.8 with 32 df. The likelihood ratio type 3 statistic for the season effect after accounting for over-dispersion was 35.67 with 1 df ($P < 0.0001$). The small P value clearly indicated the difference in yield between two seasons. The maximum likelihood estimates for the season I relative to season II was 2.0385 with the standard error of 0.4472. Thus, the season I yield (4,198 fruits per tree) was much higher than that of season II (547 fruits per tree), regardless of the level of mistletoe infestation.

Impact of the level of mistletoe infestation on nutmeg yield

Since the season effect was significant and separate control trees were there for each season, the effect of infestation was studied by fitting the log–linear model for each season separately. When log–linear model was fitted to study the effect of infestation in season I where the level of infestation was 40%, the goodness of fit statistic, G^2, was 29773.3 with 18 df and thus over-dispersion was exhibited. When the model was refitted after accounting for over-dispersion using Pearson scaling method, G^2 was 23.1 with 18 df. The likelihood ratio type 3 statistic resulted from the model for infestation effect after accounting for over-dispersion was 16.07 with 1 df ($P < 0.0001$) and thus, the effect of infestation was evident. The parameter estimate for the control relative to the infested (40%) was 1.0619 with the standard error of 0.2835 and $P < 0.0001$. This clearly indicated that the fruit number in control trees (6,238 per tree) was much higher than that of trees with 40% infestation (2,159 per tree) (Figure 4).

Similarly, when the analysis was done for season II where the level of infestation was 10%, the G^2 was 1118.9 with 12 df and thus over-dispersion was exhibited in season II as well. When over-dispersion was accounted, G^2 was 12.2 with 12 df and likelihood ratio type 3 statistic for infestation was 0.56 with 1 df ($P = 0.4550$), indicating that the fruit number has not decreased by 10% level of infestation. The maximum likelihood estimate for the control relative to the 10% level of infestation was 0.1669 with the standard error of 0.2247 and $P = 0.4576$. From the maximum likelihood estimate too, it was clear that there was no difference in fruit number between control and 10% infestation (Figure 4).

When the above analysis was performed by pooling data from both seasons, the results were similar to those from the analysis done for season I. The G^2 for the pooled model was 85844.1 with 32 df and 33.9 with 32 df, respectively, before and after accounting for over-dispersion. The likelihood ratio type 3 statistic for the infestation effect after accounting for over-dispersion was 6.25 with 1 df ($P = 0.0124$) and thus, the impact of the infestation was evident. The parameter estimates for the control relative to the infested trees was 0.8887 with the standard error of 0.3756 and $P = 0.0181$. The estimated fruit number per tree for the control and infested trees were 3,727, and 1,534, respectively (Figure 4).

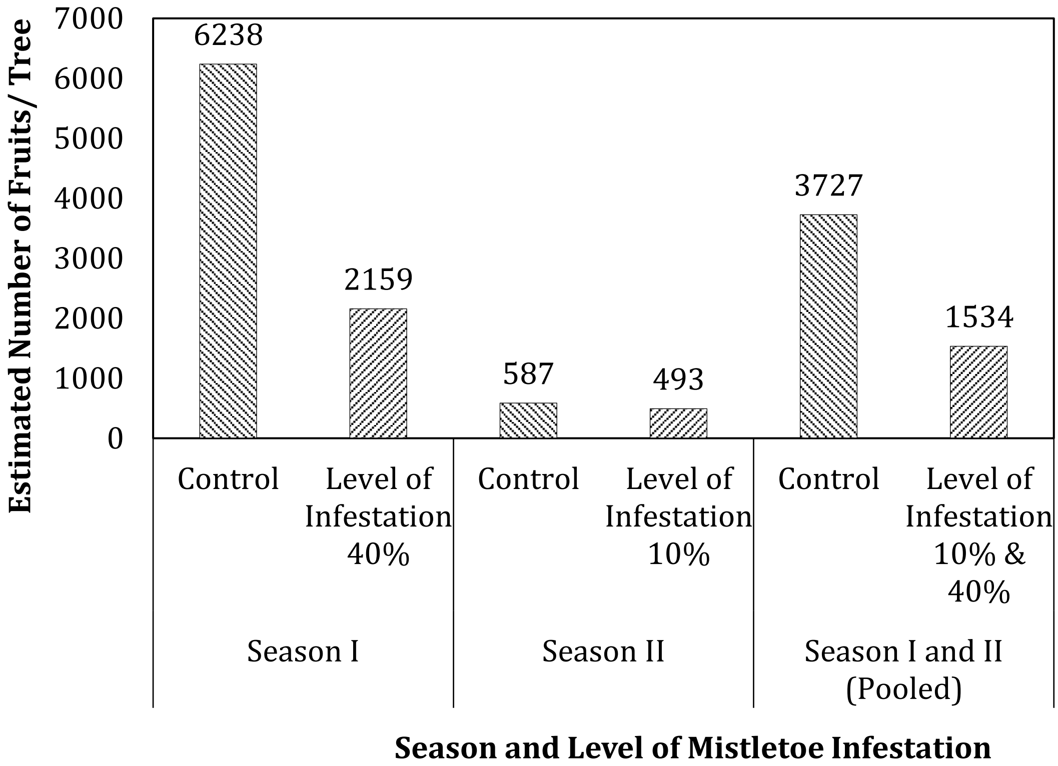

Figure 4. Estimated number of fruits per tree in different seasons and levels of infestation

Pattern of fruit yield in different whorls

The yield of infested whorls was compared to verify whether the yield reduction in infested trees was due to the reduction of yield in infested whorls. The analysis was first done with the yield of whorls in control trees, and then with the yield of non–infested whorls in infested trees, using season I data. When fitting models to study these two aspects, the position effect of whorls was also taken into account since it was hypothesized that position of whorl had an impact on the yield.

When the model was fitted to study the effect of infestation on the yield of a whorl after adjusting for the whorl position effect, the goodness of fit statistic G^2 was 40323.1 with 166 df. Since over-dispersion was exhibited, the model was refitted after accounting for over-dispersion using the Pearson scaling method. Then the G^2 was 193.2 with 166 df. From this model the likelihood ratio type 3 statistic for the interaction between whorl and infestation was 43.51 with 9 df (P=0.55), revealing that there was no interaction between whorl and infestation with respect to fruit number. Then the model was refitted after removing the interaction effect and accounting for over-dispersion using the Pearson scaling method, which resulted in a G^2 of 199.7 with 175 df. In the model, the position effect was taken into consideration by having a linear term and a quadratic term of the whorl position. The likelihood ratio type 3 statistic for linear and quadratic position effects were 6.15 with 1 df (P = 0.01) and 5.25 with 1 df (P = 0.02), respectively. Furthermore, the maximum likelihood estimates for the two terms were 5.4374 with the standard error of 2.1881, and –3.6168 with the standard error of 1.5807, respectively. These results proved the hypothesis that there was a pattern in the fruit yield in different whorls, i.e. first, the yield increased from the bottom towards the top, up to the middle area, and then it decreased.

Impact of mistletoe infested branch on yield

When the model was fitted for season I data to study the impact of infestation on yield in a branch after adjusting for the whorl position and after taking into account of over-dispersion, the G^2 was 607.69 with 646 df. The likelihood ratio type 3 statistic for infestation was 75.47 with 2 df (P<0.0001) indicating an impact of infestation on yield in a branch. However, there was no interaction between the infestation and the relative position of the whorl. Here, the impact of infestation was studied by considering branches of 3 types, *viz*, (i) infested branch of an infested tree, (ii) non–infested branch of an infested tree, and (iii) branch of non–infested (control) tree. The maximum likelihood estimates (standard errors) for the difference between type (i) and type (ii) from the type (iii) were −2.2615 (0.4855) ($P < 0.0001$) and −0.4656 (0.0818) ($P < 0.0001$), respectively. In addition, the maximum likelihood estimate (standard error) for the difference between type (i) and type (ii) was −1.7959 (0.4896) ($P = 0.0002$). The estimated fruit numbers of the above three types of branches are illustrated in Figure 5.

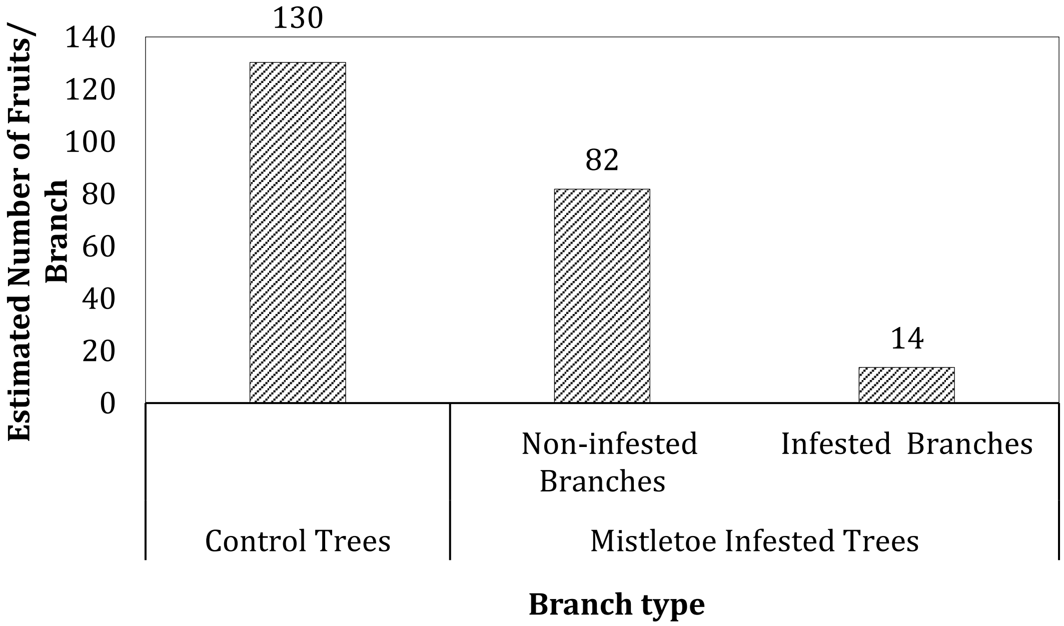

Figure 5. Variation of fruit number in nutmeg branches with the infestation of *D. neelgherrensis* at 40% infestation level

Impact of mistletoe infested whorl on yield

When the impact of infestation on yield in a whorl was evaluated by means of 3 types of whorls, *viz*, (i) infested whorl of an infested tree (at least one branch is infested), (ii) non–infested whorl of an infested tree, and (iii) whorl of a non–infested tree, the outcome was consistent with that of the comparison between 3 types of branches. The effect was also studied after adjusting for the whorl position and the model initially exhibited over-dispersion ($G^2 = 46664.8$ with 192 df). However, when over-dispersion was taken into account, the G^2 was 213.6 with 192 df. The Maximum likelihood estimates (standard errors) for the difference between type (i) and type (ii) from the type (iii) were −1.8837 (0.5347) ($P < 0.0001$) and −0.6571 (0.1193) ($P < 0.0001$), respectively. Furthermore, the maximum likelihood estimates (standard error) for the difference between type (i) and type (ii) was −0.6938 (0.2674) ($P = 0.0095$). The estimated relative yields in terms of the number of fruits, after adjusting for other effects and computed based on parameter estimates for whorls of type (i), (ii) and (iii), were 59, 203 and 391, respectively (Figure 6). This clearly showed the impact of infestation in terms of the number of fruits. Moreover, this analysis also confirmed the quadratic (concave upward) yield pattern in terms of whorl position. The parameter estimates (standard error) for the linear term and the quadratic term of the whorl position were 2.1108 (0.8300) and −2.1809 (0.7646), respectively.

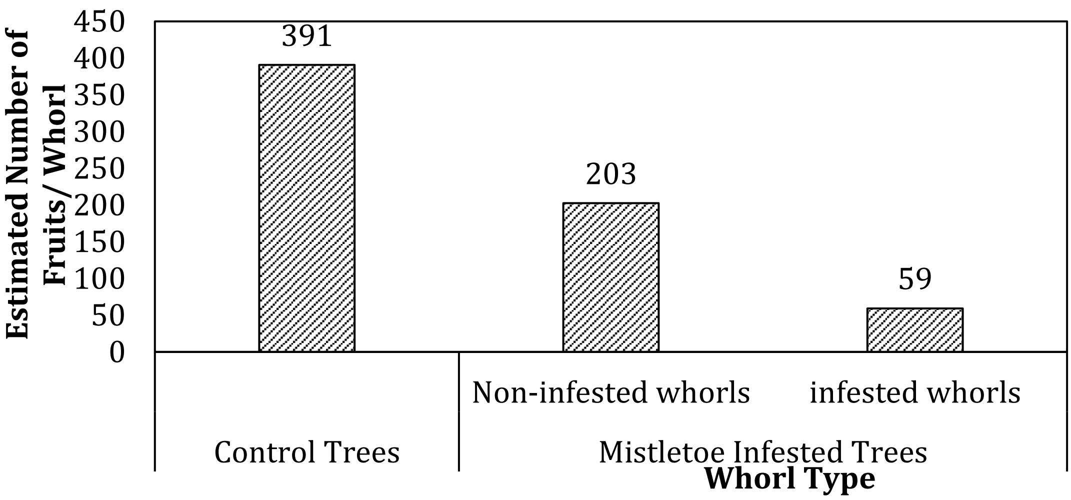

Figure 6. Variation of fruit number in nutmeg whorls with the infestation of *D. neelgherrensis* at 40% infestation level

Yield between the seasons

The initial analysis of the results clearly showed the seasonal differences of the yield, where the yield in season I was much higher than that of season II, regardless of the level of infestation. Many perennial crops, including nutmeg exhibit seasonal bearing habit, and a high variation of yield during different years (Vikram *et al*., 2018) due to alternate bearing, a common phenomenon in perennial fruit–bearing trees. This is thought to occur due to the negative impact of high fruit load on the vegetative growth and next year's flowering and hypothesized to be a consequence of varying dominance of developing fruits and shoot meristems (Smith and Samach, 2013). When nutmeg yields high in one year, it will be usually followed by a relatively lower yield in the subsequent year. Further, nutmeg also shows the variation in terms of fruit weight and number, e.g. when the number of fruits is high, the weight of a fruit is low, and *vice versa* (Wahyuni and Bermawie, 2019). Nutmeg is known to have a low rate of fruit set of 33.7% and a high post–set fruit drop of up to 74.4% (Nazeem and Sivaraman Nair, 1981). In India, a fruit number of 3,000 or above was considered as high–yielding (Vikram *et al*., 2018), and in Sri Lanka, 10,000 nuts per tree per year is considered as a good trait to be used in the selection programmes (Department of Export Agriculture, 2019). In the present study, the fruit count was taken before the fruits ripened (e.g. before the fruits start falling) and may have contributed to the observed higher fruit numbers per tree.

Impacts of the mistletoe on nutmeg yield

Results of the study clearly showed the detrimental effect of *D. neelgherrensis* on the yield of nutmeg. *Dendrophthoe neelgherrensis* is an obligate hemi–parasite and they attach to branches forming haustoria, which is a specialized, multi–cellular organ, tapping into the xylem of the tree (Yoshida *et al*., 2016) creating an association with the host which can last for a considerable period of time (Griebel *et al*., 2017). Mistletoe draws the xylem sap containing water, nutrients, and carbon-containing compounds to complement their full carbon requirements (Shen *et al*., 2013; Le *et al*., 2014; Griebel *et al*., 2017), and also exchange materials such as water, nutrients, proteins, nucleotides, pathogens, and retrotransposons between the host and the parasite through haustoria (Griebel *et al*., 2017). Therefore, infestation by mistletoe can cause severe reduction of nutrients reaching the distal end of the host branch, e.g. after the point the mistletoe is attached (Tennakoon *et al.,* 2011; Griebel *et al*., 2017). The mistletoe is known to deprive its hosts of metabolites produced in other parts of the host. Some mistletoes are known to draw large amounts of photosynthates from their hosts, and concentrate in their endophytic system and aerial shoots (Hull and Leonard, 1964). As the infestation gradually grows and the mistletoe establishes in the host plant, and the exploitation of the host by the mistletoe also increases. When mistletoes are well-established, they can significantly modify the functional processes of the host tree (Griebel *et al*., 2017). This could be clearly observed in the study during the two seasons, with different levels of mistletoe infestation.

The results of the analysis of the two seasons indicated no yield reduction at least up to 10% infestation. However, a definite and drastic yield reduction occurred when the level of infestation increased up to 40% (Figure 4). In fact, this supplemented the fact that yield loss was significantly higher at 40% infestation compared to 10% infestation. The percentages of yield drop due to 40% infestation was 65% and this tallied with the outcome from the maximum likelihood estimates. This outcome implied that there is no real need for using a control measure when the mistletoe infestation is 10% of the canopy or less. The planters need not panic just by seeing a mistletoe appearing on a nutmeg tree but instead, they can plan to control them before reaching a higher level of infestation. Nevertheless, control measures may have to be adopted when the infestation level increases beyond 10% since the damage response to the level of infestation is not linear. For example, Yapa *et al*. (2017) showed that with a 20% infestation by the same mistletoe, *D. neelgherrensis*, the fruit quality of nutmeg significantly decreased. However, they did not estimate the drop in fruit quantity in that study.

Impact of the mistletoe infestation on yield in branches and whorls

In terms of the estimated fruit number of the three types of branches studied, there were significant differences. The yields were 14, 82 and 130 for the infested branch of an infested tree, non–infested branch of an infested tree, and branch of non–infested tree respectively (Figure 5). These results clearly indicated that the yield of branches in infested trees was lower than that of control trees. There was a yield decrease of about 37% in non–infested branches of an infested tree, compared to the yield in a branch in a control tree. In addition, the yield of an infested branch in an infested tree was about 90% lower than the yield of a branch of a control tree. In fact, the yield of an infested branch was 83% lower compared to the yield of a non–infested branch of an infested tree. Thus, the findings revealed that when the tree was infested, the yield of both infested and non–infested branches of the same tree was decreased. It was also interesting to note that there was no interaction between the impact of infestation and whorl position, which implied that the impact of the infestation was consistent across whorls.

Figure 6 clearly illustrated the impact of infestation in terms of the yield at the level of whorl: The estimated relative yields for the infested whorl of an infested tree (at least one branch was infested), non–infested whorl of an infested tree and whorl of non–infested tree, were 59, 203 and 391, respectively. When the tree was infested with *D. neelgherrensis*, the yield in a non–infested whorl in infested trees dropped by 48% compared to the yield in whorls of non–infested trees. Further, the yield dropped by 71% in the infested whorls, compared to the non-infested whorls of the same tree. Altogether, there was a 85% yield decrease in an infested whorl compared to that of a whorl in control trees. This result confirmed the outcome from the comparison of different types of branches, e.g. when a whorl is infested, healthy whorls of the infested tree are also negatively affected.

Yapa *et al.* (2017) reported that the mistletoe infestation significantly decreased the fresh and dry weights of whole fruit, nutmeg nut, mace, and pericarp. Further, the infestation significantly decreased the length and width of the nutmeg nut and the thickness of the pericarp. The present study indicated that *D. neelgherrensis* infestation drastically decreases the nutmeg yield by reducing the fruit number, and size/ weight of the nut and mace. Being a hemiparasite, *D. neelgherrensis* does this by exploiting the host tree reserves. Although mistletoe leaves are capable of photosynthesizing, many mistletoe species acquire large amounts of heterotrophic carbon from the host phloem sap, deprive the host of its nutrients which accumulate in the parasite leaves, acquire water from the host, modify energy balance, and thereby significantly modifying the functional processes of the host tree (Griebel *et al*., 2017). Mistletoe abundance is reported to be increasing within many existing distributions, and aggravation of climatic stress in the form of prolonged droughts has intensified tree mortality rates with mistletoe infestations (Griebel *et al*., 2017). Tree declining and mortality of such trees have been reported by many workers (*Zweifel et al., 2012;* Mutlu *et al.,* 2016; Niranjan and Sinniah, 2016; DeSiervo *et al*., 2018; Szmidla *et al.*, 2019). For instance, declining of *Grevillea robusta* L., a shade tree of tea plantations, has been reported by Niranjan and Sinniah (2016) in Sri Lanka, and mistletoe infestation has been named as one of the primary causes of the decline. Links have also been established between the increase in tree mortality rates following mistletoe infestation (Griebel *et al*., 2017). Prolonged droughts are anticipated to aggravate in many ecosystems under the predicted changes in climate. Therefore, in the future, control of the mistletoes in economically important tree species including spice crops such as nutmeg may become extremely important.

The analysis of the present study proved that there is a pattern in the fruit yield in different whorls of the nutmeg tree. The yield in whorls increases with the increase of the canopy height, reaches the maximum around the mid–height of the canopy, and decreases with the further increase of canopy height. With such a pattern it is natural that if a whorl is infested in mid–canopy area the yield loss will be higher. However, no interaction between whorl and infestation suggested that the presence of the mistletoe is not associated with the branching pattern.

Statistical analysis of this study exposed the fact that over-dispersion is a common phenomenon in analyzing count data and over-dispersion should be taken into account when analyzing such data. In the presence of over-dispersion, not taking account of over-dispersion will lead to underestimation of the standard errors of estimates and thereby misleading conclusions that could be made (Samita and Thattil, 1996; Agresti, 2007).

CONCLUSIONS

In conclusion, we were able to quantify the damage due to the mistletoe, *D. neelgherrensis*, in the form of yield of nutmeg. When *D. neelgherrensis* covers more than 10% of the canopy of the nutmeg tree, the control measures have to be definitely adopted, since the effect of the mistletoe is felt not only in infested whorls and branches but across all the branches and whorls of the tree. Although the present study was conducted with *D. neelgherrensis* as the mistletoe and nutmeg as the host, the detrimental effects may be similar in other mistletoes-host associations, too. Hence, the inferences of this study will be valuable in providing recommendations for the control of mistletoes in spice and other tree crops.

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