

Host Plant Nutrition and Outbreaks of the Coconut Caterpillar, *Opisina arenosella* Walker in Sri Lanka

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ABSTRACT

The coconut caterpillar, *Opisina arenosella*, causes locally serious outbreaks with severe defoliation to coconut palms and subsequent loss of yield. However, there appears to be a natural resistance in the host plant to *O. arenosella* attack, for infestations are confined to mature and senescing fronds and even within a heavily attacked plantation a few palms may remain unattacked or only slightly damaged. Also previous work had indicated that potassium deficiency benefited *O. arenosella*. Therefore experiments were carried out to examine the possible role in host resistance of major plant nutrients and also of certain amino acids.

Comparisons were made between plantations with a history of frequent outbreaks ('attacked') and those that had never been attacked ('unattacked'). The results showed that there were no significant differences between mean amounts of foliar potassium, nitrogen, phosphorus, calcium and magnesium at 'attacked' and 'unattacked' sites. However, these samples were taken at the end of unusually long dry seasons when differences in potassium would be expected to be relatively small because uptake is limited from dry soil. Potassium levels were highest in the youngest fronds which are those not normally attacked whereas peak amounts of nitrogen occurred in those fronds which are most susceptible to attack. Also amounts of 'amide' were notably higher at 'unattacked' sites.

It was concluded that further work was required on the relationship between major plant nutrients and levels of attack by *O. arenosella*, particularly in relation to changes in nutrient concentrations which occur at different times of the year. Thus, palms may be more susceptible to pest attack during critical periods which need to be defined in order to optimise control strategies.

INTRODUCTION

The coconut caterpillar, *Opisina arenosella* (Lep. Oecophoridae) causes serious defoliating outbreaks on coconut palms in parts of Sri Lanka and India. The outbreaks are sporadic and localised and it is thought that they occur, at least in part, because of the failure of natural enemies, which are otherwise important in maintaining the pest population at a low endemic level (Cock & Perera, 1987; Perera 1987; Perera *et al.*, 1988). There also appears to

be a natural resistance in the host plant to *O. arenosella* attack, for infestations are confined to mature and senescing fronds and even within a heavily attacked plantation a few palms may remain unattacked or only slightly damaged (Perera, 1987). Also, the caterpillar has a long developmental period which suggests that it is developing under critical nutritional conditions which could alter depending upon both inherent qualities of the palm and environmental effects on its vigour.

This paper deals with work in Sri Lanka to examine the possible role in host resistance of major plant nutrients and also of certain individual amino acids, some of which are known to improve or adversely affect insect performance on plants. In particular, previous work by Perera (1987) has indicated that potassium deficiency benefited *O. arenosella*.

Chemical analyses were made of leaf samples from (a) fronds of different ages (b) different plantations which had either a history of or no history of outbreaks.

METHODS

1. Host Plant Sampling

During March-April 1986, palms were sampled at a heavily infested plantation at Netolpitiya, nr. Tangalle, and an uninfested plantation at Horakelle, nr. Chilaw. A total of 10 palms were sampled from each site. From each individual palm, 10 leaflets were removed from every fifth frond (i.e. frond numbers 1 (youngest), 5, 10, 15, 20, etc.) and sub-samples of about 0.5 g were immediately packed in ice and then freeze-dried to 0.05 mm Hg. Subsequently all samples were stored in a deep freeze until analyses for amino acids.

In March-April 1987, eleven sites were selected according to their history of pest attack, with emphasis on comparisons between those with a history of frequent outbreaks but not currently heavily attacked ('attacked') and those that had never been attacked ('unattacked') (Table 1).

Table 1 - *Sites sampled in Sri Lanka, 1987 and 1988.*

(a) History of frequent outbreaks (subsequently referred to as 'attacked' sites)

- (i) Mahaberiattenna Farm, Digana, Kandy
- (ii) Palacholai Estate, Madurankuliya
- (iii) Sitrakala Estate, Ambalantota
- (iv) Goluwapokuna Estate, nr. Katunayake Airport
- (v) Uddappuwa Estate, Puttalam
- (vi) Siyambalagasara, Vitarandeniya
- (vii) Godawanahena Estate, Vitarandeniya

(b) History of no outbreaks (subsequently referred to as 'unattacked' sites).

- (i) Ambakelle
- (ii) Walpita
- (iii) Welivanagoda
- (v) Palliyagedera

Twenty palms were selected at each site and samples of 6 leaflets/frond removed from fronds 5 and 14 and put separately into labelled paper bags. Samples were then oven-dried at the Coconut Research Institute (CRI) for 48 hours at 80°C and similar-aged leaves bulked and then ground up. At three 'attacked' sites, namely Kandy, Goluwapokuna and Udappuwa and two 'unattacked' sites, namely Ambakelle and Walpita more detailed sampling was undertaken. Thus at each site samples were taken from fronds 1, 5, 10, 15, 20, etc. from each of two palms in order to assess chemical changes in relation to frond age. Samples were dried and ground up as done for the bulk samples. A portion of each oven-dried sample was used for the chemical analyses for potassium, nitrogen, cellulose and silicates. At Mahaberiattenna, Palacholai, Sitrakala, Goluwapokuna, Udappuwa and Walpita replicate samples of about 0.5 g were also taken and immediately packed in ice and then freeze-dried as in 1986. These samples were used for amino acid analyses.

At each site notes were also taken of the condition of palms, palm height, number of nuts, length of leaflets and visual symptoms of potassium deficiency. The visual symptoms of potassium deficiency on each palm were placed within one of five categories ranging from zero to severe and were then quantified within the range zero = 0 to severe = 4.

In January-February 1988, seven of the eleven sites sampled in 1987 were sampled again. These comprised three 'attacked' sites namely Udappuwa, Siyambalagasara and Godawanahena and four 'unattacked' sites, namely Ambakelle, Walpita, Weliwanagoda and Palliyagedera (Table 1). Palms were sampled as in 1987 and the samples oven-dried at CRI for 48 hours at 80°C, similar-aged leaves being bulked and then ground up. A portion of each sample was used for chemical analyses for nitrogen, phosphorus, potassium, calcium and magnesium.

2. Chemical Analyses

a) *Nitrogen, phosphorus, potassium, calcium and magnesium*

Analyses were carried out at the CRI. Samples of finely ground coconut leaf were digested. Nitrogen and phosphorus digests were then analysed using an Auto-analyser and those of potassium calcium and magnesium estimated using an Atomic Absorption Spectrophotometer.

b) *Cellulose and Silicates*

Analyses were carried out at Imperial College. Polysaccharides, pectins, lignin and hemicelluloses were removed from leaf samples to leave the cellulose residue. Percentage silicate was obtained by weighing the sample of leaf material which remained after bomb calorimetry.

c) *Amino acids*

Analyses were carried out at Imperial College. Samples of finely ground coconut leaf were shaken with 2 ml of citric acid buffer (0.2N pH 2.2) and centrifuged. Samples of the supernatant were then analysed using an amino acid analyser. Briefly, the plant extract is

pumped to a 23 cm long column of Zeocarb resin from which the amino-acids are eluted sequentially by a series of buffers of increasing pH. After elution, the amino acids are detected by mixing with Ninhydrin to develop a coloured complex. The amino acids are then estimated quantitatively by a colorimeter and the results presented on a multipoint chart recorder. Results are expressed as micro-moles (μM) amino acid/100 g dried plant material.

RESULTS

1. Chemical analyses of major nutrients

a) Total foliar nitrogen

In 1987, comparisons were made between 'attacked' and 'unattacked' sites. The results show that the mean total nitrogen levels in frond 5 at the seven 'attacked' sites was 1.93% compared with a mean of 2.04% at the four 'unattacked' sites. In frond 14 the mean levels were 1.81% and 1.94% for the 'attacked' and 'unattacked' sites respectively (Table 2). Thus total nitrogen levels in fronds 5 and 14 show no significant differences in relation to whether a site is considered 'attacked' or 'unattacked'.

Table 2 - Mean % potassium and nitrogen levels in relation to frond numbers 5 and 14 and at different sites in Sri Lanka, March /April, 1987.

	Potassium Bulked		Nitrogen Bulked	
	5th	14th	5th	14th
<i>Attacked Sites</i>				
Maha-Kandy	1.84	1.29	2.09	1.85
Palacholai	1.46	0.68	1.82	1.67
Sitrakala	1.70	1.18	1.91	1.71
Goluwapokuna	1.78	1.50	1.93	1.99
Uddappuwa	1.09	0.62	1.87	1.81
Siyambalagasara	1.49	1.30	1.84	1.82
Godawanahena	1.10	0.63	2.07	1.82
Mean	1.49	1.03	1.93	1.81
<i>'Unattacked' Sites</i>				
	5th	14th	5th	14th
Ambakelle	1.60	1.06	1.82	1.74
Walpita	1.67	1.22	2.07	2.00
Weliwangoda	1.12	0.78	2.16	1.93
Palliyagedera	1.43	0.91	2.12	2.07
Mean	1.46	0.99	2.04	1.94

In 1988, mean total nitrogen levels in frond 5 at three 'attacked' sites was 2.17% compared with a mean of 2.28% at four 'unattacked' sites. In frond 14 the levels were 1.96% and 2.11% for the 'attacked' and 'unattacked' respectively (Table 3). Thus, as in 1987, although mean nitrogen levels were higher at 'unattacked' sites, those differences were not significant. Furthermore the pattern of change in mean levels of nitrogen in relation to frond age was similar in the 'attacked' and 'unattacked' sites, the lowest nitrogen levels occurring in the youngest and oldest leaves, with peak amounts in frond 10.

b) Foliar phosphorus

In 1988, the mean phosphorus levels in frond 5 at 'attacked' sites was 0.140% compared with 0.158% at 'unattacked' sites. In frond 14 the mean levels were 0.129% and 0.114% for the 'attacked' and 'unattacked' sites respectively (Table 3).

Table 3 - Mean % potassium, nitrogen, phosphorus, calcium and magnesium in relation to fronds 5 and 14 at 'attacked' and 'unattacked' sites, January / February, 1988.

	K		N		P		Ca		Mg	
	5th	14th	5th	14th	5th	14th	5th	14th	5th	14th
<i>Attacked Sites</i>										
Udappuwa	1.15	0.66	1.90	1.77	0.154	0.135	0.20	0.29	0.25	0.28
Siyambalagasara	1.38	1.03	2.27	2.00	0.129	0.117	0.30	0.43	0.28	0.35
Godawanahena	1.00	0.65	2.33	2.10	0.148	0.134	0.44	0.59	0.35	0.43
Mean	1.18	0.78	2.17	1.96	0.144	0.129	0.31	0.44	0.29	0.35
<i>Unattacked Sites</i>										
Ambakelle	1.30	1.09	2.25	2.09	0.143	0.132	0.35	0.36	0.30	0.32
Walpita	1.70	1.23	2.27	2.23	0.162	0.147	0.31	0.30	0.19	0.25
Weliwanagoda	1.14	0.79	2.30	2.00	0.165	0.142	0.33	0.41	0.30	0.40
Palliyagedera	1.33	0.90	2.31	2.10	0.163	0.140	0.33	0.48	0.32	0.36
Mean	1.37	1.00	2.28	2.11	0.158	0.140	0.33	0.39	0.28	0.33

c) Foliar potassium

The results of samples collected during the period March-April 1987 showed that the mean potassium level in frond 5 at seven 'attacked' sites was 1.49% compared with a mean of 1.46% at the four 'unattacked' sites. In frond 14 the mean levels were 1.03% and 0.99% for the 'attacked' and 'unattacked' sites respectively (Table 2). Potassium levels varied notably between some individual sites. For example, in frond 14 the level varied within 'attacked' sites from 0.62% at Udappuwa to 1.50% at Goluwapokuna. Thus potassium levels in fronds 5 and 14 show no significant differences in relation to whether a site is 'attacked' or 'unattacked'. In contrast, the visual symptoms of potassium deficiency were notably more severe at the 'attacked' sites (mean value 1.8) than at 'unattacked' sites (mean value 0.5). Also, on average, fewer nuts were produced in 'attacked' than in 'unattacked' sites (Table 4).

Table 4 - Index of visual potassium deficiency in relation to 'attacked' and 'unattacked' sites and mean yield of nuts, March / April, 1987

Attacked Sites	Mean Index of Potassium Deficiency *	Mean No. Nuts/ Palm
Maha-Kandy	1.8	25.3
Palacholai	2.4	7.8
Sitrakala	-	-
Goluwapokuna	2.0	25.7
Uddappuwa	2.7	36.6
Siyambalagasara	0.6	20.6
Godawanahena	1.2	36.7
Mean	1.8	25.5
<i>Unattacked Sites</i>		
Ambakelle	0.5	51.6
Walpita	0.6	44.2
Wellwanagoda	0.4	27.8
Palliyagedera	0.4	33.5
Mean	0.5	39.3

* No visual deficiency symptoms = 0
 Very slight deficiency symptoms = 1
 Slight deficiency symptoms = 2
 Moderate deficiency symptoms = 3
 Severe deficiency symptoms = 4

The samples in 1987 were taken at the end of an unusually prolonged dry season. Potassium uptake is inhibited in dry soil conditions (Jeganathan *et al.*, 1976) and foliage is likely to be drained by the demands of developing nuts which contain high levels of potassium. Therefore differences in foliar potassium between 'attacked' and 'unattacked' sites may only be apparent immediately following the seasonal rains when it is known that potash uptake rises considerably (Jeganathan, *et al.*, 1976). Thus in 1988 samples were taken during late January - early February which should have coincided with the end of the rains. Unfortunately, rainfall was below average in November and virtually ceased afterwards. However, the results showed that the mean potassium levels in frond 5 at the three 'attacked' sites was 1.18% compared with a mean of 1.37% at the four 'unattacked' sites. In frond 14 the mean levels were 0.78% and 1.00% for the 'attacked' and 'unattacked' sites respectively (Table 3). As in 1987, there was notable variation between some sites irrespective of whether the site was 'attacked' or 'unattacked'. Therefore, although 'attacked' sites showed overall lower amounts of potassium, such differences were not significant.

In detailed studies of changes in potassium with frond age, the pattern of change in levels of potassium was similar in the 'attacked' and 'unattacked' sites. Thus potassium was highest in frond 1 with the lowest levels occurring in the oldest fronds.

d) Foliar calcium

In 1988, mean calcium level in frond 5 at 'attacked' sites was 0.31% compared with a mean of 0.33% at the 'unattacked' sites. In frond 14 the mean levels were 0.44% and 0.39% respectively (Table 3).

e) Foliar magnesium

In 1988, mean magnesium level in frond 5 at 'attacked' sites was 0.29% and at 'unattacked' sites was 0.28%. In frond 14 the mean levels were 0.35% and 0.33% respectively (Table 3).

2. Chemical analyses of silicates and Cellulose

Young larvae may have difficulty in initially penetrating and feeding upon the characteristically tough foliage of coconut. Thus differences in cuticular toughness may represent an important host resistance mechanism. Therefore, samples of different aged fronds from Walpita ('unattacked' site) and Goluwapokuna ('attacked' site) were analysed for silicate and cellulose content. The results showed that both mean % silicate and cellulose were similar at the two sites but the mean % cellulose was highest in the youngest leaves, varying from a mean of 31.7% in frond 1 to 17.3% in frond 25.

3. Chemical analysis of individual amino acids

The results of chemical analyses of the freeze-dried samples collected at Horakelle (uninfested) and Netolpitiya (infested in 1986) are shown in Table 5. The youngest fronds at Horakelle had considerably larger amounts of total named amino acids than older fronds, although this is not evident in the samples from Netolpitiya. The larger amounts of amino acids in the youngest fronds at Horakelle are principally due to 'amide' (probably asparagine + glutanine) although larger amounts of other amino acids, notably glycine, valine, alanine and threonine, are also present. When the individual amino acids are considered as a % of the total named amino acids the greatest changes occur in the 'amide', which varied at Horakelle from 30% in frond 1 to about 13-17% in fronds 10-30 and at Netolpitiya from 26% in frond 1 to about 9-13% in fronds 10-25. In contrast, % of glutamic and aspartic acid at Horakelle were in notably smaller amounts in the younger fronds than in older fronds.

In 1987, comparisons between Walpita ('unattacked' site) and Goluwapokuna ('attacked' site) showed that the levels of total named amino acids were higher at the 'unattacked' than the 'attacked' site, principally because of the larger amounts of 'amide' (Table 6). Also the mean level of aspartic acid at the 'unattacked' site was notably lower than at the 'attacked' site (Table 6).

Thus in both 1986 and 1987 amide was present in larger amounts in uninfested and 'unattacked' sites than those which were infested and 'attacked'. Furthermore in 1986 larger amounts of 'amide' were present in younger fronds than in the older fronds, the latter being known to be more susceptible to pest attack.

Table 5 (i) Amounts of individual named amino acids (μM /100 mg dry material) at Horakelle (uninfested site) March / April, 1986.

FronD No	1	5	10	15	20	25	30
<i>Amino Acid</i>							
Aspartic Acid	535.3	406.9	554.6	488.9	486.8	394.8	434.1
Threonine	489.6	88.7	109.2	134.3	135.6	77.8	103.9
'Amide'	1910.9	448.6	325.3	302.5	327.7	231.8	350.6
Glutamic Acid	269.7	243.4	249.9	179.4	235.3	170.7	184.3
Proline	282.5	62.4	72.8	99.3	44.6	66.8	72.8
Glycine	243.2	33.5	44.4	64.8	33.3	30.2	43.7
Alanine	801.9	249.3	357.7	280.7	308.9	269.4	258.5
Valine	295.5	21.5	31.9	38.5	18.0	23.8	106.5
Methionine	30.1	0.8	2.5	0.1	2.2	6.6	9.6
Isoleucine	119.8	26.0	33.5	32.9	36.3	30.2	30.5
Leucine	81.3	23.3	28.7	25.6	36.8	18.8	38.1
Tyrosine	124.3	27.3	26.5	28.3	34.0	37.7	22.6
Phenylalanine	74.6	51.3	65.2	57.6	74.6	63.8	49.7
Amino butyric	376.3	179.1	187.9	163.9	189.7	141.8	168.0
Histidine	146.1	54.9	67.5	60.5	101.5	73.6	86.1
Lysine	159.1	74.1	71.5	72.5	88.6	50.1	106.6
Arginine	383.6	262.5	90.4	59.8	97.1	67.7	53.9
Total	6350.8	2253.6	2319.5	2089.6	2251.0	1755.6	2119.5

Table 5 (ii) Amount of individual amino named acids (μM /100 mg dry material) at Netolpitiya (heavily infested site) March / April, 1986.

FronD No	1	5	10	15	20	25
<i>Amino Acid</i>						
Aspartic Acid	250.0	396.8	310.7	286.4	247.9	146.9
Threonine	33.2	49.8	61.7	48.2	34.8	27.9
'Amide'	356.4	215.6	194.1	127.9	112.6	83.0
Glutamic Acid	179.9	182.7	140.5	129.9	119.6	76.0
Proline	65.9	55.5	71.6	88.2	23.4	106.4
Glycine	20.0	18.8	21.2	22.3	16.1	12.0
Alanine	149.4	258.2	219.3	164.8	152.4	203.3
Valine	8.7	11.6	27.4	64.6	23.5	0.0
Methionine	4.6	2.0	1.1	0.1	4.2	0.0
Isoleucine	16.1	18.9	30.8	19.7	30.4	11.4
Leucine	16.3	17.3	29.1	32.1	29.8	4.4
Tyrosine	2.7	7.9	21.5	17.8	19.9	5.7
Phenylalanine	34.5	44.7	63.4	55.1	40.4	60.2
Amino butyric	100.0	154.5	162.2	130.7	195.1	131.7
Histidine	39.5	36.5	69.4	42.7	41.3	23.4
Lysine	20.4	57.8	53.4	40.0	41.3	50.8
Arginine	54.9	40.8	8.2	10.0	27.8	0.1
Total	1352.5	1569.4	1485.6	1280.5	1160.5	943.2

Table 6 (i) *Amounts of individual amino named acids (μM /100 mg dry material) at Goluwapokuna ('unattacked' site) March / April, 1987.*

<i>Fron</i> d No	1	5	10	15	20
<i>Amino Acid</i>					
Aspartic Acid	110.1	154.9	194.9	100.1	102.2
Threonine	187.5	214.5	253.4	252.1	181.6
'Amide'	704.5	535.5	970.4	848.1	606.4
Glutamic Acid	216.1	183.8	126.7	139.5	210.9
Proline	19.3	68.9	64.9	95.3	166.5
Glycine	111.4	114.9	149.4	130.5	103.9
Alanine	279.5	296.2	325.4	277.6	262.7
Valine	114.1	91.4	128.6	128.5	100.1
Methionine	0.1	0.1	0.0	0.1	0.1
Isoleucine	54.0	63.7	54.7	62.2	57.8
Leucine	47.4	48.8	63.7	69.1	52.0
Tyrosine	219.5	169.8	149.2	149.9	143.2
Phenylalanine	119.4	73.7	151.1	116.0	87.6
Amino butyric	138.8	234.9	434.7	213.4	181.4
Histidine	130.1	94.0	156.9	113.3	132.2
Lysine	114.7	94.9	174.8	91.9	119.8
Arginine	555.0	329.0	360.1	192.7	224.4
Total	3121.5	2769.0	3758.7	2980.3	2732.8

Table 6 (ii) *Amounts of individual amino named acids (μM /100 mg dry material) at Goluwapokuna ('attacked' site) March / April, 1987.*

<i>Fron</i> d No	1	5	10	15	20	25
<i>Amino Acid</i>						
Aspartic Acid	287.0	326.1	324.1	279.3	275.6	257.5
Threonine	185.5	140.9	253.7	254.4	141.8	123.2
'Amide'	307.1	179.5	285.4	336.7	189.6	152.0
Glutamic Acid	119.5	86.4	111.2	108.4	71.7	110.7
Proline	80.6	68.2	86.1	52.2	44.2	2.7
Glycine	84.1	69.4	94.8	122.5	54.2	26.2
Alanine	245.8	181.5	253.4	234.6	136.4	124.5
Valine	47.7	44.5	83.1	77.3	23.4	15.1
Methionine	0.0	0.0	0.0	0.0	0.0	0.0
Isoleucine	39.7	30.7	56.4	55.2	22.8	19.7
Leucine	38.1	26.2	46.6	45.1	21.1	2.0
Tyrosine	51.6	37.6	96.8	126.7	29.5	24.2
Phenylalanine	47.8	49.6	74.8	49.4	37.2	33.4
Amino butyric	281.0	287.3	336.5	269.5	229.9	181.5
Histidine	31.9	41.8	77.1	82.9	47.9	39.3
Lysine	46.0	48.8	134.5	128.7	53.5	49.1
Arginine	119.2	118.4	334.8	396.3	57.7	105.5
Total	2012.6	1736.9	2649.3	2619.2	1436.3	1266.6

DISCUSSION

The occurrence of an outbreak of *O. arenosella* depends upon a complexity of factors which probably involves the synchronisation of the pest with availability of susceptible hosts, both during initial pest invasion and subsequent population increase. Host plant susceptibility may be an inherent characteristic. For example, young larvae of *O. arenosella* develop more rapidly and survive better on mature than on young foliage (Perera & Cammell unpublished data). Also there may be considerable variation in the levels of pest attack in individual palms within the same plantation (Perera, 1987), which is probably, at least partially, due to inherent characteristics.

Host plant susceptibility to *O. arenosella* attack may also vary in relation to environmental and nutritional factors. Developmental rate and survival of larvae is seemingly negatively correlated with levels of foliar potassium (Perera, 1987). Although in this paper there is little evidence that 'attacked' sites have lower mean levels of potassium than 'unattacked' sites, differences may be evident at certain times of the year because of the association between rates of potassium uptake by the palms and rainfall. Thus uptake is limited from dry soil and in these circumstances there is potash deficiency in the tree because of the continuing heavy demands for potash by developing nuts. This situation is likely to be exacerbated in the higher yielding palms of the non-outbreak areas, although nutrients are more likely to be added by growers to compensate for demand where higher-yielding palms are grown.

Host plant susceptibility to pest attack and other major nutrients is also seemingly unrelated. However, the potassium/ nitrogen ratio may be important in terms of the variation in the performance of the larvae on different-aged fronds, since the youngest leaves contain most potassium and relatively little nitrogen whereas the ratio of nitrogen to potassium is highest in fronds 10-15, which are those preferred by *O. arenosella*.

Clearly more work is required on the relationship between major plant nutrients and levels of pest attack. Nutrient concentrations are known to vary during a season (Jeganathan *et al.*, 1976) and therefore palms may be more susceptible to pest attacks during critical periods which need to be defined in order to optimise control strategies. Also, the mechanisms of host plant resistance are poorly understood.

The initial analyses for individual amino acids has shown that these may vary considerably both between different-aged fronds and different localities. This was particularly notable in relation to amounts of 'amide'. However, whether such differences are influencing susceptibility to pest attack requires further work, particularly in relation to possible patterns of change both within and between different seasons.

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