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SHORT COMMUNICATION

The impact of a locust plague on mangroves of the arid Western Australia coast

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Mangroves generally grow in nutrient-poor environments and maintain high levels of productivity through unique adaptations for nutrient conservation (Reef *et al.* 2010). One such adaptation in mangroves is highly efficient resorption of limiting nutrients from senescing leaves prior to abscission (Feller *et al.* 2003). Thus processes that lead to loss of foliage prior to senescence and nutrient resorption (e.g. storms and herbivory) can be detrimental to tree growth and productivity (Bryant *et al.* 1983, May & Killingbeck 1992). Furthermore, decomposition of fallen leaves by soil microbial communities (Alongi 1994, Holguin *et al.* 2001) and crabs (Nagelkerken *et al.* 2008) is another important process contributing to the recycling of nutrients that are in short supply. Therefore, processes that lead to a substantial reduction in litterfall can have a strong negative effect on nutrient cycling and forest productivity. Mangroves have long been recognized as an important source of organic carbon (both particulate and dissolved) for the surrounding tropical coastal ecosystems (Bouillon *et al.* 2008, Kristensen *et al.* 2008). Thus, processes affecting litterfall in mangroves can affect the surrounding marine food webs.

Despite high concentrations of sodium, secondary metabolic compounds and phenolic compounds in mangrove leaves, numerous insect and crab species, many of them highly host specific, feed on mangroves (Murphy 1990, Nagelkerken *et al.* 2008). In some mangrove forests, 2–10% of leaf material is consumed by herbivores prior to leaf senescence (Farnsworth & Ellison 1991, Feller 1995, Johnstone 1981, Robertson & Duke 1987). This has implications for nutrient budgets of mangrove trees, and hence also their growth and productivity.

Herbivory by locust swarms can have devastating effects on both natural and agricultural systems. The spur-throated locust, *Austracris guttulosa* (Walker) is native to tropical Australia, Indonesia, the Philippines, Papua New Guinea and other neighbouring Pacific territories (COPR 1982) and an occasional serious agricultural pest. Outbreaks develop when there are regular rains both in an outbreak area and large parts of the adjacent arid zone. Because the spur-throated locust has only one generation per year, major outbreaks take several years of favourable conditions to develop. When outbreaks do occur they can be intense and severe and can last 1–4 y (Hunter & Elder 1999). The scale of widespread successful locust breeding in 2011 had not been recorded since 1974 (Australian Plague Locust Commission bulletin, Australian Department of Agriculture, Fisheries and Forestry) causing the biggest Australian locust plague in 30 y. Swarms of *A. guttulosa* arrived at the Giralia station on the Pilbara coast, Western Australia in February 2011 (J. and D. Blake, Giralia station, pers. comm.).

Despite the fact that locust invasion areas include large areas of mangrove forests in Africa, Asia, South America, the Caribbean and Australia, we are not aware of previous studies documenting effects of locust outbreaks on mangrove forests. In this study we measured the extent and nature of herbivory by the locust *Austracris guttulosa*

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Figure 1. Herbivory by *Austracris guttulosa* (spur-throated locust) on *Avicennia marina.* Adult *A. guttulosa* feeding on *A. marina* (a). New undamaged *A. marina* leaves among leaves attacked by feeding *A. guttulosa* (b).

(Figure 1a) on the mangrove *Avicennia marina* (Forssk.) Vierh. in an arid-zone estuary in the Pilbara region of Western Australia 6 mo following the arrival of the locust swarms to the region. Using an existing fertilization experiment at the site we also tested the hypothesis that the nutritional value of the plant can affect herbivory intensity.

Our study site was within Giralia Bay (22°29′34″S, 114°19′8″E) in the Exmouth Gulf, Western Australia at the Eastern side of the Sandalwood Peninsula on the edge of a tidal creek. This bay is fringed by mangrove forests dominated by *Avicennia marina*. The forest at this site occupies the tidal gradient and is 150 m wide from the seaward to the landward edge. The seaward fringing forest (the edge of the forest fringing the creek) is regularly flooded by tide, while the scrub forest (the landward edge of the mangrove forest) is inundated less frequently, which leads to significant differences in pore-water salinity between the sites. At this arid-zone site, the soil salinity at the scrub forest is higher than at the fringing forest due to the high evaporation rates from the upper-profile soils.

Since 2004, nine replicate trees in the seaward fringing forest and in the landward edge of the mangrove forest have been receiving one of three nutrient treatments annually as described in Lovelock *et al.* (2011). Briefly, nine replicate trees in each of the two forests have been fertilized with either nitrogen (N, as urea), phosphorus (P, as triple superphosphate) or were designated as controls (unfertilized). Since 2005 the growth response of the trees was measured annually as stem extension rates of five representative unbranched terminal twigs on each tree. Twigs measured in 2011 were tagged and measured in August 2010 when they had one or two leaf pairs. In order to estimate the extent of herbivory for each tree we counted the total number of leaves showing signs of herbivory or that were missing entirely, and the total number of leaf scars (nodes) for the five marked twigs on each tree (Figure 1b). Herbivory intensity was defined as the proportion of leaves attacked and was calculated as the ratio between the number of leaves showing signs of herbivory and the potential number of leaves produced since August 2010 based on leaf scars (nodes) where each node represents a leaf pair.

Soil pore-water salinity was measured at the base of each tree. Pore-water was extracted from 30 cm depth using a suction device (McKee 1993), analysed using a handheld refractometer (model 300011, Sper Scientific, Scottsdale AZ, USA) and reported in practical salinity units (PSU).

Data were analysed in a linear model (ANCOVA) with nutrient treatment and site as factors, salinity of the pore-water as a cofactor and the herbivory intensity as the variable. The proportions of attack were arcsine-transformed. Statistical analysis was performed using R for Mac OS X 2.13.2.

All the trees in this study lost significant amounts of foliage to locust attack. On average the locust significantly damaged 45% of the leaves of *A. marina*, with values ranging from 15–100% of the foliage on each tree either damaged or missing entirely.

Site (seaward fringing vs. landward facing) had a significant effect on the proportion of leaves damaged or lost (ANCOVA, $F_{(1,42)} = 4.67$, $P = 0.04$). Landward trees exhibited higher herbivory intensity than seaward trees, with 58% of the foliage significantly damaged or lost in landward trees compared with only 32% for the seaward trees.

Salinity significantly affected herbivory intensity (ANCOVA, $F_{(1,42)} = 30.7$, $P < 0.001$). However, as pore-water salinity was significantly higher in the landward facing forest, 59.2 ± 3.5 PSU than in the seaward forest, 47.4 ± 2.5 PSU ($t_{(45)} = 14.0$, $P < 0.001$), the effect of salinity was confounded by site. Within each site, salinity was not correlated with herbivory (Pearson's $r = 0.10$, $P = 0.63$ for the landward forest and $r = -0.01$, $P = 0.97$ for the seaward forest, Figure 2a).

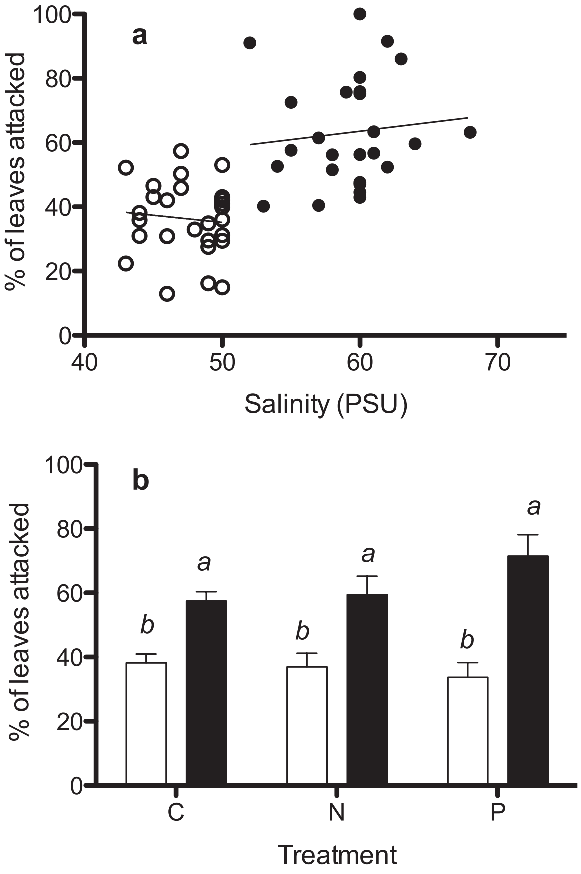

Figure 2. Herbivory intensity by *Austracris guttulosa* on *Avicennia marina.* The percentage of leaves attacked by locust in *A. marina* trees as a function of pore-water salinity along the landward (closed circles) and seaward (open circles) edges of the mangrove forest. Non-significant linear regressions between herbivory and salinity are shown for each site ($\beta = 0.52$, $P = 0.59$ for landward $\beta = -0.45$, $P = 0.63$ for seaward) (a). The average (± SE) proportion of the leaves attacked by locust in *A. marina* trees fertilized with nitrogen (N) phosphorus (P) or unfertilized controls (C) along the landward (closed bars) and seaward (open bars) edge of the mangrove forest. Different letters indicate significant differences at $P < 0.05$ (b).

The nutrient treatment did not significantly affect the herbivory intensity at either the seaward or the landward sites (ANCOVA, $F_{(2,42)} = 0.93$, $P = 0.40$, Figure 2b). Trees receiving P fertilizer in the landward edge of the forest appeared to be attacked more heavily by locusts but not significantly so (ANCOVA, site × treatment $F_{(2,42)} = 0.83$, $P = 0.44$).

Stem extension rates were on average (± SD) 106 ± 69.5 mm y^{-1} and were independent of pore-water salinity ($F_{(1,53)} < 0.001$, $P = 0.99$), site ($F_{(1,53)} = 1.53$, $P = 0.22$) and the nutrient treatment (ANOVA, $F_{(2,53)} = 1.97$, $P = 0.15$). These values are significantly lower than the average growth rate of the same trees over the past 5 y, which was 227 ± 152 mm y^{-1} (paired t-test, $P < 0.001$). Fertilization significantly increased tree growth during previous years at this site (Lovelock *et al.* 2011).

The locust outbreak had a significant impact on the mangrove canopy. Under normal rates of herbivory on *Avicennia marina*, it is estimated that a fraction ranging between 2% and 10% of the primary production in a mangrove forest is removed by grazing insects (Feller 1995, Johnstone 1981, Robertson & Duke 1987). Although we did not measure the leaf area lost to herbivory, the attack on the leaves had a significant impact on leaf area. We made a conservative estimate from visual inspection that attacked leaves that were not entirely eaten or prematurely abscised lost on average more than 33% of their leaf area. The loss of such a significant portion of the foliage prior to senescence can have far-reaching consequences for mangrove productivity, reproduction and survival and could explain the significantly lower rates of stem extension recorded in 2011 compared with previous years.

Locust herbivory can potentially impact the export of detrital material from the mangroves. Previous work estimated mangrove litter production at this site to be roughly 350 g C m^{-2} y^{-1} (Lovelock *et al.* 2009). Thus, for the entire mangrove area of the Exmouth Gulf (161 km^2), more than 56 Gg y^{-1} of carbon enter the estuary as leaf litter; the largest source of C for the estuary (Lovelock *et al.* 2009). Extensive defoliation, as observed in this study can consequently impact marine secondary production in the region and affect nutrient cycling. Conversely, through the conversion of plant material to nutrient-rich frass and through the abundance of dead bodies of locust, locust outbreaks may also be delivering a significant resource pulse to the system.

Scrub trees, those on the landward edge of the forest experienced a higher intensity attack than the trees facing the creek. Geographical location was the main driver of spatial heterogeneity in the intensity of herbivory, probably due to the proximity of landward trees to the terrestrial environment. Position in the intertidal zone has been previously suggested as an important factor in herbivory in mangroves (Feller & Chamberlain 2007) and should be taken into account when modelling forest-wide herbivory rates.

Herbivory intensity was higher in the high-salinity scrub forest, but we did not find a significant correlation between pore-water salinity and the intensity of locust attacks on leaves within each site. This corroborates previous findings that herbivory is not correlated with Na^+ or Cl^- concentrations in the leaves (Johnstone 1981, Lacerda *et al.* 1986). It is well known that leaf Na^+ concentration in mangroves is strongly linked to soil pore-water salinity (Ball 1988, Parida *et al.* 2004) especially in salt-secreting mangroves such as *A. marina*, where both salt accumulation in leaf tissues and salt secretion on to the leaf surface are positively correlated with soil salinity

(Ball 1988, Tomlinson 1986). Therefore we can infer that the locust did not discriminate against leaves containing higher salt concentrations.

Neither did we find support for the hypothesis that increased nutrient concentrations in the plant (mainly N) altered the incidence of herbivory. Our previous work at this site (Lovelock *et al.* 2011) revealed that nitrogen fertilization significantly increased foliar N concentrations (and decreased C:N ratios) relative to P fertilized and control trees. Our findings support previous studies that conclude that nutrient availability does not affect the herbivory intensity of all mangrove herbivores (Farnsworth & Ellison 1991, Feller 1995, Feller & Chamberlain 2007). It is important to note that P fertilization did not significantly alter green-leaf phosphate concentrations in these trees (Lovelock *et al.* 2011) so the lack of significant response in herbivory could be due to the lack of increased P concentrations in the leaves of P-treated trees.

In this study we have shown that while locust plagues are rare occurrences, their impact on mangrove forests can be large. The causal mechanisms behind locust outbreaks are primarily climate-related consistent with ENSO patterns of climate variability (Stige *et al.* 2007, Todd *et al.* 2002). For some regions recent evidence suggests that changes in rainfall patterns are leading to more frequent outbreaks of some locust species (Cheke & Tratalos 2007). More frequent outbreaks of locust in mangrove forests can be another threat mangrove ecosystems will face due to climate change and can alter the energetics of mangrove forests.

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