



Does plastic waste kill mangroves? A field experiment to assess the impact of macro plastics on mangrove growth, stress response and survival

Celine E.J. van Bijsterveldt^{a,b,*}, Bregje K. van Wesenbeeck^{c,d}, Sri Ramadhani^{a,b}, Olivier V. Raven^{a,e}, Fleur E. van Gool^{a,b}, Rudhi Pribadi^f, Tjeerd J. Bouma^{a,b}

^a Department of Estuarine and Delta Systems, NIOZ Royal Netherlands Institute for Sea Research and Utrecht University, P.O. Box 140, 4400 AC Yerseke, the Netherlands

^b Department of Physical Geography, Utrecht University, P.O. Box 80.115, 3508 TC Utrecht, the Netherlands

^c Unit for Marine and Coastal Systems, Deltares, 2600 MH Delft, the Netherlands

^d Department of Hydraulic Engineering, Delft University of Technology, 2600 GA Delft, the Netherlands

^e Applied Biology, HAS University of Applied Sciences, Onderwijsboulevard 221, 5223 DE 's-Hertogenbosch, the Netherlands

^f Faculty of Fisheries & Marine Sciences, Diponegoro University, Semarang 50275, Indonesia

HIGHLIGHTS

- Plastic is accumulating in mangrove forests worldwide, but impacts remain unclear.
- We studied the abundance and the effect of plastic on mangrove growth and survival.
- Plastic waste was frequently observed to cover 50% of the forest floor.
- Partial plastic cover of mangrove root zones induces extreme aerial root growth.
- Complete plastic cover of root zones causes tree death.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 25 August 2020

Received in revised form 20 October 2020

Accepted 2 November 2020

Available online 20 November 2020

Editor: Elena Paoletti

Keywords:

Mangroves
Pneumatophores
Macro plastics
Anoxia
Stress response

ABSTRACT

The value of mangroves has been widely acknowledged, but mangrove forests continue to decline due to numerous anthropogenic stressors. The impact of plastic waste is however poorly known, even though the amount of plastic litter is the largest in the region where mangroves are declining the fastest: South East Asia. In this study, we examine the extent of the plastic waste problem in mangroves along the north coast of Java, Indonesia. First, we investigate how much of the forest floor is covered by plastic (in number of items per m² and in percentage of the forest floor covered by plastic), and if plastic is also buried in the upper layers of the sediment. We then experimentally investigate the effects of a range of plastic cover percentages (0%, 50% and 100%) on root growth, stress response of the tree and tree survival over a period of six weeks. Field monitoring showed that plastic was abundant, with 27 plastic items per m² on average, covering up to 50% of the forest floor at multiple locations. Moreover, core data revealed that plastic was frequently buried in the upper layers of the sediment where it becomes immobile and can create prolonged anoxic conditions. Our experiment subsequently revealed that prolonged suffocation by plastic caused immediate pneumatophore growth and potential leaf loss. However, trees in the 50%-plastic cover treatment proved surprisingly resilient and were able to maintain their canopy over the course of the experiment, whereas trees in the 100%-plastic cover treatment had a significantly decreased leaf area index and

* Corresponding author at: Department of Estuarine and Delta Systems, NIOZ Royal Netherlands Institute for Sea Research and Utrecht University, P.O. Box 140, 4400 AC Yerseke, the Netherlands.

E-mail address: celine.van.bijsterveldt@nioz.nl (C.E.J. van Bijsterveldt).

survival by the end of the experiment. Our findings demonstrate that mangrove trees are relatively resilient to partial burial by plastic waste. However, mangrove stands are likely to deteriorate eventually if plastic continues to accumulate.

© 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Even though mangroves are widely valued for the ecosystem services they provide, forests are rapidly declining despite restoration efforts. Mangrove forests provide multiple provisioning, regulating and recreational ecosystem services, but they are most valued for their role in coastal protection (Barbier et al., 2011). In spite of this global recognition of their importance, anthropogenic influences such as land use change, cause continued mangrove decline worldwide (Alongi, 2002; Thomas et al., 2017). Many restoration and conservation projects have been initiated in recent decades to restore mangrove forests and prevent further loss (Bayraktarov et al., 2016; A. M. Ellison, 2000; Narayan et al., 2016). However, few mangrove restoration projects have been able to achieve stable mangrove canopies (e.g., A. M. Ellison, 2000; Kodikara et al., 2017; Primavera and Esteban, 2008). The lack of system understanding has been the reported cause of various failed restoration projects (A. M. Ellison, 2000; Primavera and Esteban, 2008), and achieving such an understanding of the local hydrodynamics and sediment balance has increasingly been recommended to improve mangrove settlement success (eg. Balke and Friess, 2016; Lewis III, 2005). Getting these boundary conditions right has proven to be successful for mangrove seedling planting and even natural mangrove settlement (eg. Lewis III, 2005; Van Cuong et al., 2015). However, less attention has been devoted to the more-direct anthropogenic stressors that could hamper the growth and survival of the restored young trees. The most notable anthropogenic pollution that might stress mangroves is plastic waste (Smith, 2012).

Worldwide, regions with high mangrove cover often also have serious plastic management issues. Plastic waste entering the ocean due to a lack of waste collection and disposal services is estimated to be 4.8 to 12.7 million tonnes annually (Jambeck et al., 2015). Two-thirds of the global plastic waste enters the ocean via the top 20 most polluted rivers, all situated in Asia (Lebreton et al., 2017). Similarly, Jambeck et al. (2015) found that the top four countries listed, which add the most to the marine plastic waste problem, are China, Indonesia, Philippines and Vietnam (8.8, 3.2, 1.9, and 1.8 million tonnes/year respectively). All of these countries are situated in the general region, where one-

third of the world's remaining mangrove cover is found (Bunting et al., 2018) (Fig. 1). This co-occurrence of large amounts of plastic waste and abundance of mangroves is potentially problematic. The majority of mangroves species possesses some type of aerial roots, which ensure that part of their root system remains exposed most of the tidal cycle (Tomlinson, 2016). All species rely on their aerial roots to oxygenate their root zone under periodic anoxic conditions. However, the species with upward pointing aerial roots (i.e. knee-roots and pneumatophores bearing species) are especially vulnerable to suffocation by smothering. Smothering by sediment and debris is a realistic threat as aerial roots cause flow reduction of water entering the swamp at high tide (Mazda et al., 2006), which promotes accumulation of sediment and debris in the mangrove fringe (Horstman et al., 2017). With mangrove roots being such efficient traps for particles and objects (e.g. Chen et al., 2018; Horstman et al., 2017; Martin et al., 2019), much of the floating plastic debris in the region is bound to end up in mangrove forests, potentially smothering pneumatophores and knee-roots.

To date, few studies have been conducted on the extent of the plastic problem in mangroves, as most of the marine debris studies have focused on zones with more recreational value, such as beaches (eg. Ivar do Sul and Costa, 2007; Li et al., 2016; Podolsky, 1989; Syakti et al., 2017; Willoughby et al., 1997). One of the studies on plastic in mangroves reports marine debris ridges up to 50 cm above the forest floor (Smith, 2012). Marine debris in mangroves is mostly comprised of plastic bags (Cordeiro and Costa, 2010; Debrot et al., 2013; Ivar do Sul and Costa, 2007; Kantharajan et al., 2018). If plastics remain stationary on the forest floor or inside the sediment over multiple tidal cycles (e.g., because of neap tide, or through burial in the sediment), they can create an anoxic environment and could thereby potentially induce tree suffocation (Smith, 2012). In particular, species that rely on upward pointing aerial roots for oxygen supply such as *Avicennia*, *Laguncularia* and *Sonneratia* spp. (McKee, 1996) could be at risk of suffocation caused by burial in plastic. However, despite multiple references to this potential effect in the literature (e.g., Sandilyan and Kathiresan, 2012; Smith, 2012), and some personal field observations of pneumatophore deformation due to plastic burial, to our knowledge, no manipulative studies have yet been conducted to support this hypothesis.

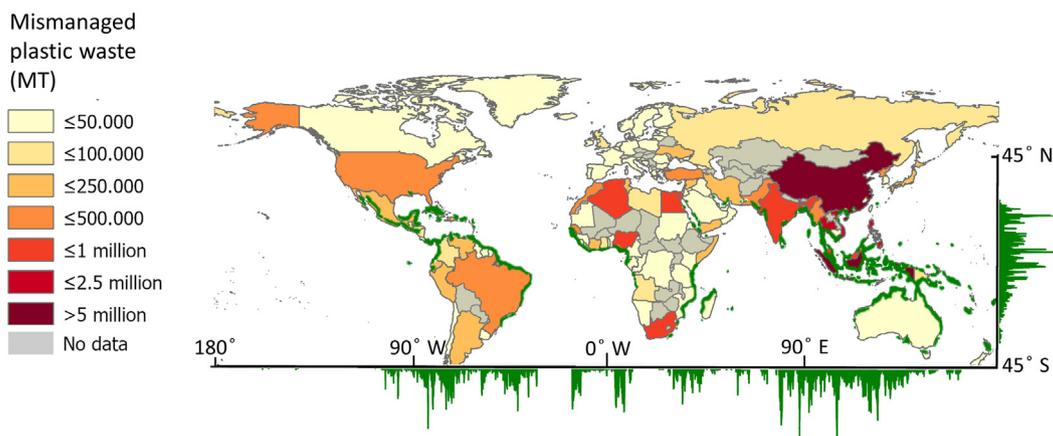


Fig. 1. A global map overlay of the estimated mass of mismanaged plastic waste (metric tonnes (MT)) at risk of ending up in the ocean in 2010 from Jambeck et al. (2015) "Plastic waste inputs from land into the ocean" (reprinted with permission from AAAS), and the global mangrove frequency distribution in 2010 along longitude and latitude, courtesy of Bunting et al. (2018) "The Global Mangrove Watch—A New 2010 Global Baseline of Mangrove Extent", illustrating that the plastic waste problem in the ocean is the largest in regions where mangroves are still the most abundant.

In this study, we aim to understand how the current plastic waste loads on the forest floor and in mangrove sediment might affect mangrove trees. We first assess the size of the current plastic waste problem in mangroves by quantifying the relatively mobile plastic fraction on the forest floor (the percentage of the forest floor covered by plastic, and the number of plastic items per m²), and by quantifying the more immobile plastic fraction buried in the rhizospheric sediment of eight coastal mangrove fringes. We then investigate how various degrees of plastic loads affect mangrove trees in terms of growth, stress and survival through the experimental application of plastic to the root systems of *Avicennia* trees.

2. Materials & methods

2.1. Site description

We used the coastline of Demak regency in Central Java as a model site to study the effect of plastics on mangroves, as this area is exemplary for many densely populated mangrove areas found in South East Asia. Java is densely populated (Fig. 2), and the northern coast holds several big cities (e.g., Jakarta, Semarang, Surabaya) that produce enormous amounts of plastic waste (Maryono et al., 2020; Syakti et al., 2017; Willoughby et al., 1997). Household waste is largely managed by burial in landfills, but most rural places lack garbage collection services. Demak's coastline stretches along 20 km from Semarang city (1.8 million inhabitants (United Nations, 2018)) in northeast direction (Fig. 2). The coastal area consists of wide plains with a gentle slope of alluvial deposits, intersected by a few large rivers (Wulan and Buyaran river) and hundreds of streams. The area used to be lined with mangrove forests that were kilometers wide. However, mangroves were replaced by paddy fields long ago, and the last remaining mangrove fringes were removed when shrimp farming was booming in the 1980s. The loss of mangrove forests, in combination with local land subsidence, has led to large scale erosion from 2003 onwards. Since the onset of coastal erosion, many aquaculture ponds have been abandoned, which has led to small mangrove stands (max 500 m wide) reappearing in old ponds

along the coast (van Bijsterveldt et al., 2020). The government is investing in mangrove restoration to expand these patches into a green-belt, but restoration is slow and existing mangrove trees appear to be stressed. This is especially the case in the seaward fringe, where plastic and sediment accumulate, wave impacts are high and erosion is looming. Plastic waste from the villages in the coastal area is not collected by the local authorities, but is instead burned per household, or it is dumped locally in places that are washed out during the monsoon or by the tide. Many of the plastics that have been washed out to sea are subsequently trapped by the coastal mangrove stands. The plastics visibly accumulate in sediment ridges on the seaward edge of the mangrove stands, where the flow velocity of the entering water drops significantly due to the drag caused by prop roots and pneumatophores. Sediment ridges often migrate landward under rough weather conditions, thereby covering mangrove root zones in their path (Chappell and Grindrod, 1984), as the debris that accumulates often rises above the level of the pneumatophores. The trees that are situated inside such a sediment-debris ridge frequently appear stressed or dead (Fig. A1). However, sedimentation with coarse sediment alone is not likely to kill mangrove trees (Chappell and Grindrod, 1984; Okello et al., 2014). The fact that these sediment ridges consist of both coarse sediment and multiple plastic layers, could potentially explain the tree mortality observed in the field. In order to investigate the nature and the effect of plastic waste in mangroves, we conducted a monitoring campaign and a field experiment.

2.2. Plastic monitoring

To assess the amount of plastic present in the field that could pose a threat to mangroves by covering pneumatophores, we quantified the presence of plastic with a size larger than 1 cm (the diameter of a pneumatophore) in two fractions: (1) the amount of relatively mobile plastic covering the forest floor, measured in terms of "the percentage of forest floor covered by plastic waste", and "the number of items per m² of forest floor". (2) The amount and the burial depth of immobilized plastic that is trapped in the upper layers of the mangrove sediment. This

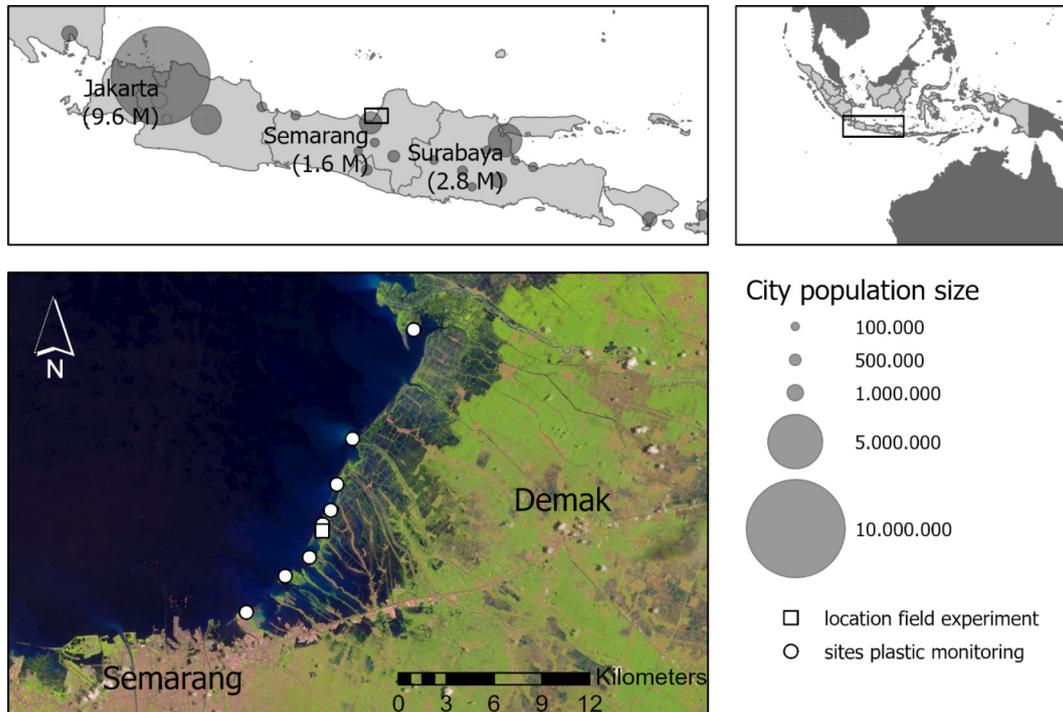


Fig. 2. Sentinel-2 satellite image of the study area, with sites of the plastic monitoring campaigns (white circles) and the location of the field experiment (white square) on the coast of Demak, located on the densely populated coast of Java, Indonesia. Population densities of Java's cities with more than 100,000 inhabitants are displayed, proportional to their population size in 2010 (demographic statistics database of the UN).

situation is especially expected to occur in the mangroves fringing the sea, where sediment and debris are deposited by the tide and waves. The mobile and immobile plastic fractions were monitored in three zones across eight mangrove fringes during a series of field campaigns in 2018 and 2019. Eight mangrove stands were selected as replicates for this study, all of which consisted primarily of *Avicennia* spp. (*Avicennia alba* and *Avicennia marina*). The mangrove stands were located along a 20 km coastline stretch of the Demak district in Central Java, Indonesia (Fig. 2). An additional site, situated 100 km westward along the coast without a large city (Semarang) in its direct vicinity, was also added to the monitoring campaign. The mobile plastic fraction, assessed in terms of the percentage of forest floor covered by plastic and the number of plastic items per m², was monitored using 50*50 cm quadrats in three different zones per site. Namely, the seaward edge of the sediment ridge in the mangrove fringe, the landward side of the sediment ridge and the mangrove basin landward of the ridge

(Fig. 3a). Quadrat data were collected three times: after the wet season of 2017–2018, after the dry season of 2018 and finally after the dry season of 2019. The percentage plastic cover within each 50*50 cm quadrat was estimated and the number of plastic items in the first 2 cm of sediment was counted. The percentage plastic cover per quadrat was always estimated by the same researcher to ensure consistency. In addition, a validation dataset was obtained by taking pictures of the field quadrats. The pictures in which plastic was clearly identifiable -in practice these were sandy sites where canopy shadow and biofouling of plastic was limited - were subsequently used to manually digitize all visible plastic per quadrat with image processing software (Fiji ImageJ, version 1.52u). The quantified plastic area was then divided by the surface area of the quadrat and multiplied by 100% to obtain the actual plastic percentage per quadrat. The field estimates validated against the plastic percentages obtained from pictures of those quadrats revealed a linear relationship ($R^2: 0.88, p < 0.0001$), indicating that the

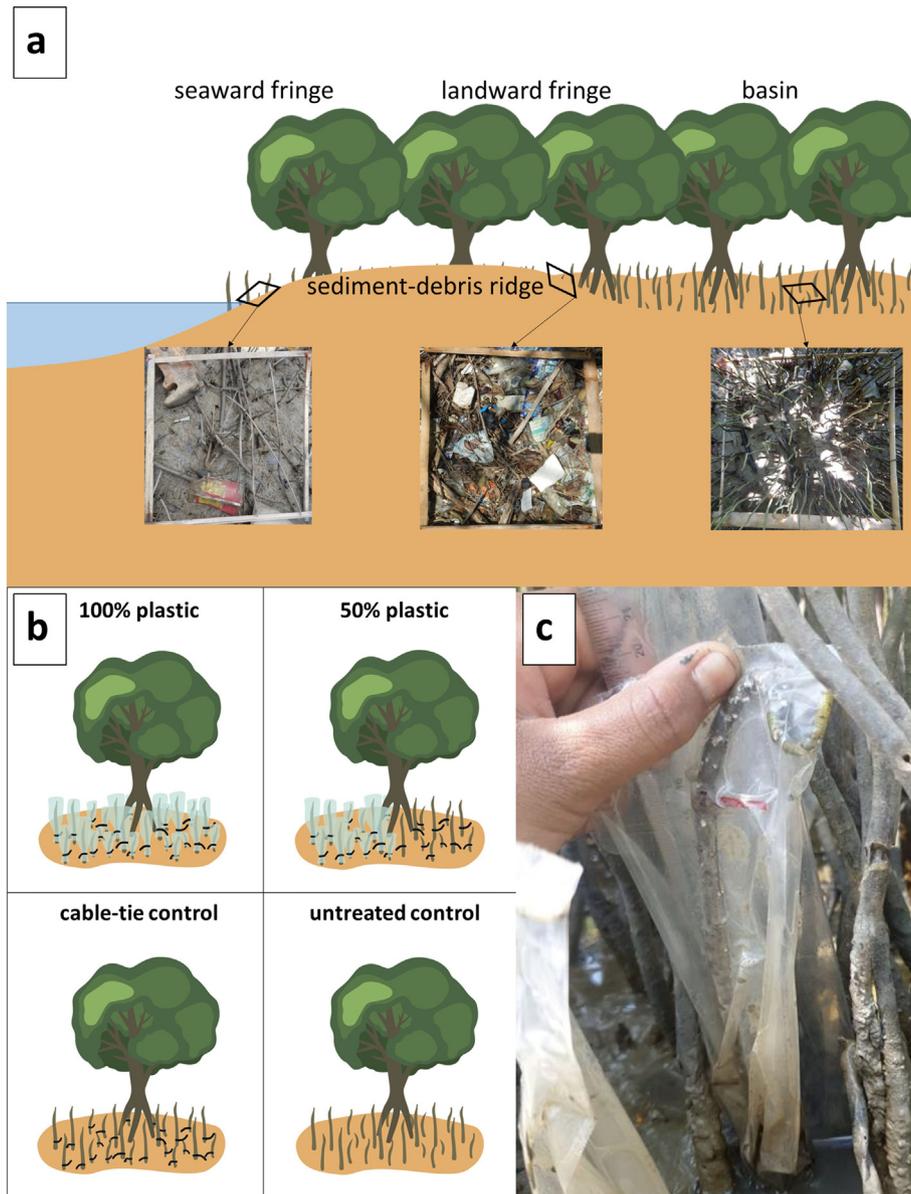


Fig. 3. a. Quadrat placement and core locations across a coastal mangrove stand: water line at low tide (seaward fringe), landward of the sediment ridge (landward fringe), mangrove basin (basin). b. Conceptual representation of the four plastic suffocation experiment treatments: 100% of the root zone covered by plastic, 50% of the root zone covered by plastic, cable tie control and untreated control (UTC). c. Plastic suffocation method, a plastic bag tied to the base of individual pneumatophores with a cable tie. Additional cable tie markings were used on 10 pneumatophores per tree at 5 cm from the top (the red cable tie inside the plastic bag in the picture) to quantify pneumatophore extension over the course of the experiment.

field estimates were perhaps not always 100% accurate, but at least reproducible across field sites. Thus, the estimated percentage of the forest floor covered by plastic and the number of plastic items were monitored per quadrat in each zone, replicated over nine sites and repeated during three field campaigns, resulting in 27 quadrat observations per zone and amounting to a total of 81 quadrat assessments. The immobile plastic fraction that was buried inside the sediment was monitored by collecting sediment cores in each zone (Fig. 3a). In total, 9 cores were collected per zone, divided over nine sites and repeated during two field campaigns resulting in 18 cores per zone and 54 cores in total. Cores were collected using a 50 cm transparent PVC tube (\varnothing 5.3 cm) with a saw head. Coring was done by slowly rotating the saw head into the sediment, cutting through plastic layers instead of pushing them down. The number of plastic layers and the depth of the plastic layers were quantified in each core. The coring depth varied among locations between a depth of 14 cm and 35 cm, due to differences in sediment type or cable root density. Therefore, to standardize across locations, only plastic layers detected within the first 14 cm of the sediment were considered for comparison between the zones.

2.3. Suffocation experiment

To investigate the effect of plastic waste on mangrove trees with pneumatophores, we conducted a manipulative experiment on 42 young *A. marina* trees to quantify root growth, litter fall and tree survival in response to various degrees of plastic suffocation over a period of six weeks. The trees that were selected for the experiment were located on the seaward fringe of one mature mangrove stand. This site had been selected because it was an expanding mangrove forest, and the young trees that relatively recently colonized the mudflat were still largely disconnected from each other. This was essential in order to apply treatments to individual trees. The downside of using the seaward fringe of the mangrove stand was that i) the trees were relatively exposed to waves (Fig. A3) and ii) the trees showed some size and age differences, with larger trees towards the back and smaller trees out on the mudflat. The 42 trees that were selected for the experiment were disconnected from other individuals and were relatively similar in size (mean height: 1.8 m (+/- 0.4 m)). To overcome potential bias in tree mortality caused by confounding variables such as salinity, waves or size rather than by the treatments, the 42 trees were assigned to the four plastic treatments based on their height in such a way that all treatments had the same variation of tree size and tree position relative to the sea. The trees were then subjected to one of the four treatments: 100% of the pneumatophores covered by plastic (13 trees), 50% of the root zone covered by plastic (11 trees), an untreated control (10 trees) and a cable tie control (8 trees) (Fig. 3b). In the two plastic cover treatments, trees received a plastic bag on individual pneumatophores, tied to the bottom of each root with a cable tie (Fig. 3c). This method of plastic application does not fully resemble the way pneumatophores are smothered by both sediment and plastic, as observed in the field. However, preliminary experiments revealed that this was the most reliable method to keep the treatments reproducibly in place over longer periods of time. The effect of the cable tie fixation method was accounted for in the cable tie control treatment. Trees in the 100% treatment received plastic bags on 100% of the pneumatophores in their root zone. Trees in the 50% treatment received plastic bags on 50% of their aerial roots (Fig. 3c). The 50% treatment was applied to pneumatophores in the root zone in the shape of a semi-circle to mimic the effect of partial suffocation by a migrating sediment-ridge. The effect of different amounts of plastic cover was assessed in terms of (1) pneumatophore growth (new pneumatophore development and pneumatophore extension), (2) tree stress (litter fall and leaf area index) and (3) tree survival.

- (1) Root growth was assessed based on two variables: (1) the number of new pneumatophores that were formed over the course of the experiment and the extension of existing pneumatophores. New

pneumatophore growth was assessed only at the end of the experiment by counting the number of bright green pneumatophores (at low tide) that were smaller than 5 cm. Root extension of existing pneumatophores was quantified by measuring the increase in distance between a cable tie applied 5 cm from the top of a pneumatophore at baseline, and the distance from the same cable tie to the tip of the pneumatophore six weeks after treatment application. This method was preferred over measuring the total length of pneumatophores at baseline and at the end of the experiment because our preliminary experiments revealed that vertical pneumatophore growth occurs primarily from the root apex. In addition, this root growth monitoring method had the advantage that large changes in sediment level between baseline and the end of the experiment could not influence the measurements in root growth. The cable tie method was applied to 10 randomly selected pneumatophores per tree (red circle in Fig. 3c). The 50% treatment received cable tie markings on 20 pneumatophores, 10 in the plastic treated part of the root zone, and 10 in the uncovered part of the root zone.

- (2) Tree stress was quantified by two independent methods: weekly litter fall underneath each individual tree, and the leaf area index (LAI) at the end of the experiment. Litter fall was quantified by collecting leaves weekly from nets suspended underneath each individual tree, and subsequently weighing the dry biomass (dried in a stove for 48 h at 60 °C) in the lab. Litter fall data from the third week after treatment application were excluded from the analysis because a storm during that week has likely blown many of the leaves from the nets. Leaf area index per tree was quantified by remote sensing at the end of the experiment. That is, all trees were mapped with a drone (DJI Phantom 4) six weeks after the start of the experiment from an altitude of 50 m. Individual drone images were stitched to one mosaic image of the study area with a 10 cm resolution. The original tree canopy was then digitized by hand, following the contour of branches, twigs and the suspended leaf litter net. Healthy vegetation was subsequently extracted from the original image bands (RGB) using the Normalized Green Red Difference Index (NGRDI) (Lussem et al., 2018) with a threshold of 0. Overlay analysis of the vegetation extraction with the original canopy polygons then resulted in a LAI value per tree at the moment of final harvest.
- (3) Tree survival until the end of the experiment was assessed as a response variable, and compared to the tree survival in the untreated control group. Tree survival in the untreated control group was used as the background survival rate, because tree mortality during the experiment would occasionally occur as result of rough weather conditions. This effect was accounted for by testing the survival rates in the 100%-, 50%- and cable tie treatments against the survival in the untreated control.

2.4. Statistical analysis

The distribution of plastic monitored in the field across the three zones of interest was analysed by Kruskal-Wallis non-parametric test for each of the plastic fractions (percentage plastic cover, number of items per m², burial depth and number of layers per core). The difference between treatments in terms of root extension was tested by Analysis of Variance (ANOVA), using tree ID as a blocking factor and plastic treatment as the explanatory factor. The effect of the four treatments on the number of new roots was tested with a generalized linear model (GLM) assuming a quasipoisson distribution. The effect of the plastic treatments on weekly litter fall were also analysed by GLM, using treatment and the interaction between treatment and week number as explanatory variables and litter fall per week as response variable assuming a Gamma distribution. Leaf area index, as a proportion, was highly skewed and the effect of the treatments on the leaf area index were therefore analysed with the Kruskal-Wallis non-parametric test.

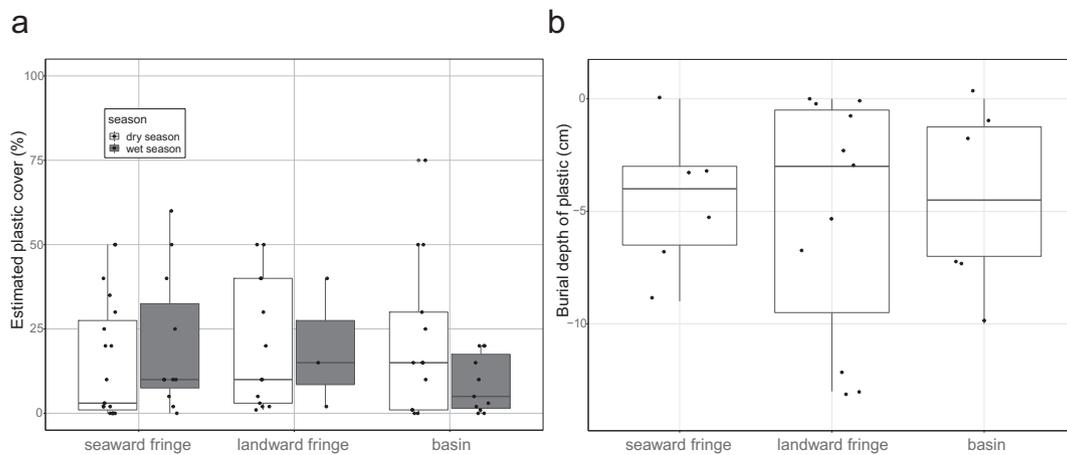


Fig. 4. Median (black line within box), 1st and 3rd quantile (box range) and 95% of the observation range (whiskers) of **a.** the estimated percentage of the forest floor covered by plastic per zone after the wet season and after the dry season **b.** the depth of plastic layers present in the upper 14 cm of the sediment across mangrove zones (seaward fringe, landward fringe and basin).

The difference in tree survival and expected natural survival for each treatment was tested statistically with a one-sided binomial test using the survival rate of the untreated control group as the expected natural survival. Statistics were executed in R studio (R Core Team (2013), version 1.0.143).

3. Results

3.1. Plastic monitoring

The number of plastic items on the forest floor was generally high, ranging from 0 to 236 plastic items per m^2 , with an average of 27 items. The number of items differed significantly between the three defined sedimentation zones in mangroves, with significantly higher numbers found in the landward fringe (mean \pm SE: 44.8 ± 9.3 number of items) than in the seaward fringe (29.4 ± 8.6 SE) and in the mangrove basin (17.3 ± 4.0 SE) ($p < 0.05$). Surprisingly, no significant effect of season was detected on the number of plastic items in the quadrats. Estimated percentage of the forest floor covered by plastic in Demak's mangroves varied between 0 and 75%, with an average of 17% of the forest floor covered by plastic. However, in contrast to the number of plastic items, no significant differences were found across mangrove zones or between seasons for the percentage of forest floor covered by plastic (Fig. 4a). Furthermore, cores from the different zones across mangrove stands revealed that there was an immobilized plastic fraction. When considering all data from the cores, plastic was found buried in the sediment up to at least 35 cm depth (Fig. A2), which was the maximum core depth. However, due to a large variation in coring depth, only the plastic layers up to 14 cm were taken into account for a comparison between the zones. This comparison showed that plastic layers were present in the upper 14 cm of the sediment in all zones, and no distinction could be made between the zones in terms of average plastic layer depth or the number of plastic layers up to 14 cm (Fig. 4b).

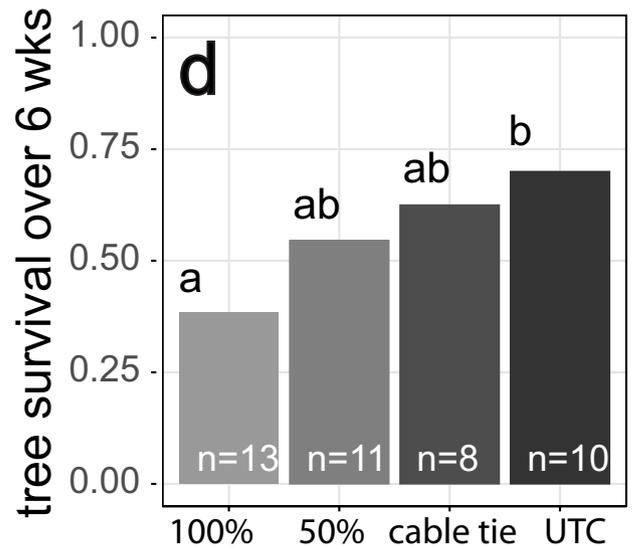
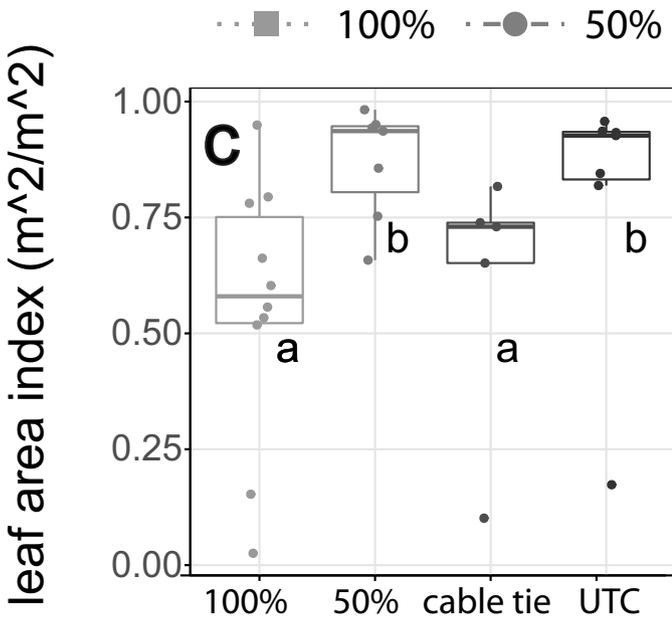
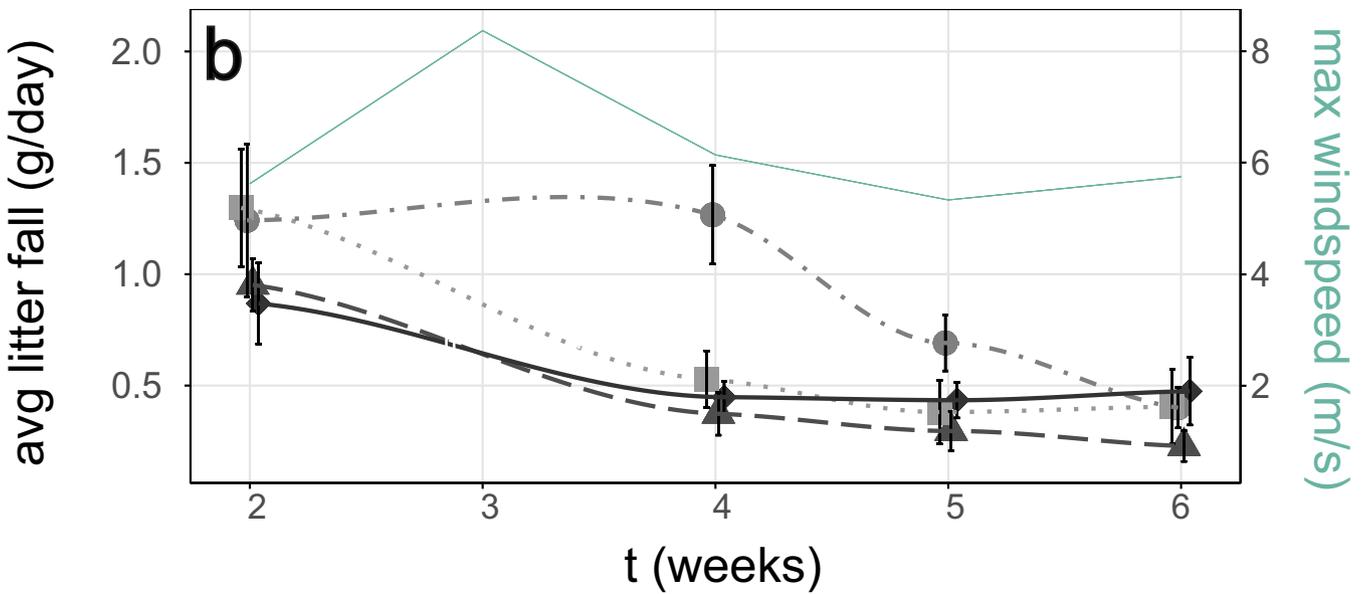
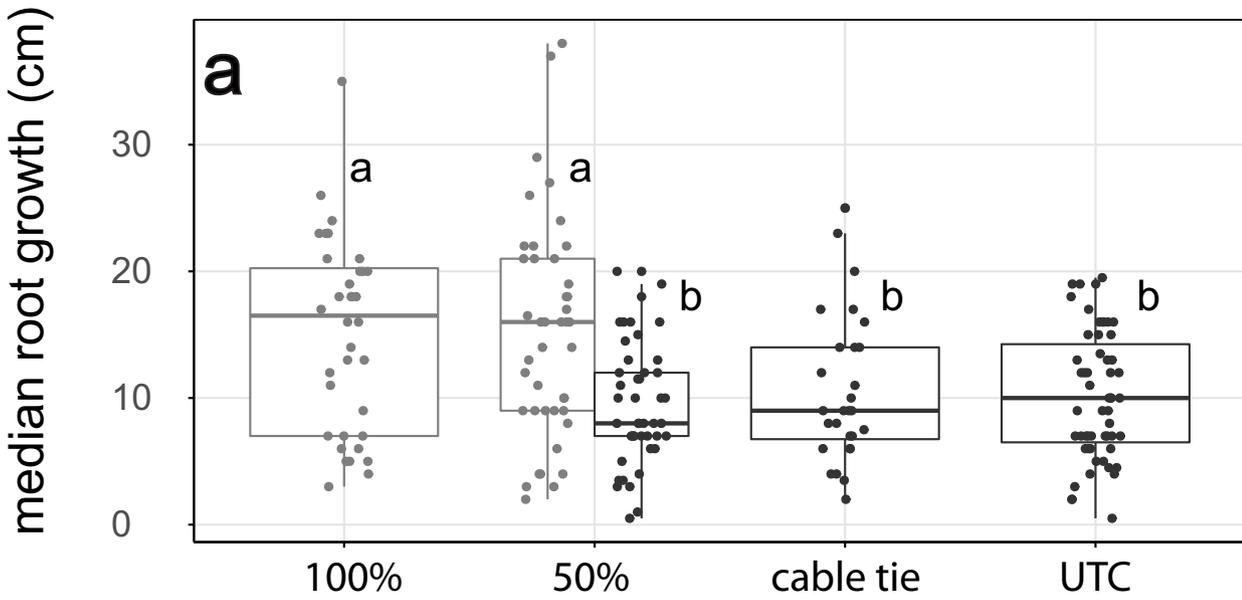
3.2. Mangrove response to plastic suffocation

Simulation of different plastic cover percentages revealed that mangroves in all treatments developed new roots, with an average

(\pm SE) number of new roots of $73 (\pm 25)$, $87 (\pm 14)$, $48 (\pm 15)$ and $100 (\pm 38)$ for 100%, 50%, cable tie control and untreated control treatments, respectively, and with no significant differences in root development between the treatments ($p < 0.5$). In contrast, trees did invest significantly in root growth of existing pneumatophores in response to plastic suffocation ($F = 9.4$, $df = 4$, $p < 0.001$). Trees that had 100% of their root zone covered by plastic showed significantly more pneumatophore extension than trees in the cable tie and untreated control treatments. Pneumatophore growth in the 100% plastic treatment was 6.1 cm ($p < 0.001$), 4.9 cm ($p < 0.05$) and 5.2 cm ($p < 0.001$) higher than uncovered roots in the 50%, cable tie control and untreated control treatments, respectively, over a period of six weeks. Interestingly, trees that had 50% of their root zone covered with plastic showed a similar growth response, though only in the roots that were covered by plastic, indicating a very localized response to plastic suffocation (Fig. 5a). In the plastic covered part of the 50%-treatment, roots showed an average pneumatophore extension that was 6.2 cm ($p < 0.001$), 5.0 cm ($p < 0.01$) and 5.3 cm ($p < 0.001$) higher than the root growth in the uncovered half of the 50% treatment, cable tie control and untreated control, respectively, over a period of six weeks.

In addition to the response in root growth, trees also showed other signs of stress in response to the plastic treatments. The average daily litter fall trends of the 100%- and 50%-treatments appear to start higher than the cable tie and untreated control treatment over the first two weeks of the experiment (Fig. 5b), suggesting an immediate stress response to suffocation. The litter fall in the 100%-plastic treatment then showed a strong drop between week 2 and 4, following a storm in the third week of the experiment (depicted on the second y-axis of Fig. 5b). Trees in the cable tie and untreated control treatments showed a similar drop in litter fall after the storm, which suggests that the storm removed all loosely attached leaves. In contrast, litter fall in the 50%-treatment remained stable over the same period, and only started to drop after week 4. By the end of the experiment, only the 100% treatment and cable tie treatments showed a reduced LAI as a result of the litter fall, as displayed in Fig. 5c, suggesting that the cable tie fixation method itself may also have induced a stress response. Interestingly, the 50% treatment did not have a significantly lower LAI than the untreated control by the end of the experiment (Fig. 5c), despite showing

Fig. 5. **a** Median ($\pm 95\%$ obs range) root extension (cm) over the course of 6 weeks in response to the different treatments. Pneumatophores covered by plastic (grey boxes) extended significantly more than uncovered pneumatophores (black boxes) ($p < 0.01$). **b.** Tree stress response based on average (\pm SE) litter fall in gram dry weight per day for per treatment plotted over the course of the experiment. Weekly averages of maximum daily wind speed displayed on the second y-axis. **c.** Tree stress response based on median leaf area index ($\pm 95\%$ obs range) per treatment after the experiment. **d.** Tree survival displayed as the proportion of trees per treatment that survived the suffocation experiment (original number of trees per treatment is indicated with "n=").



high litter fall rates throughout the experiment in general. Overall, these trend differences between the litter fall and LAI data suggest that these stress parameters are less obvious response indicators of plastic suffocation than root extension.

Ultimately, the stress applied to the trees by the plastic treatments resulted in higher mortality rates (Fig. 5d). The trees in the 100% plastic cover treatment suffered significantly from the plastic and showed a significantly lower survival than the trees in the untreated control treatment ($p = 0.02$). Trees in the 50% treatment also appeared to be mortality-affected by the plastic, with slightly over half of the trees surviving the experiment. However, this was not found to be significantly different from the expected survival ($p = 0.2$). The expected survival was based on the survival of the trees in the untreated control treatment over the course of the experiment. The survival of these trees was relatively low as well (70%), which is most likely the result of a storm in the third week. Nevertheless, plastic clearly affected tree mortality on top of the storm.

4. Discussion

Plastic waste is a growing problem in coastal regions and seas, as plastics accumulate in local ecosystems. Deterioration of coastal ecosystems and the increase of plastic waste in these systems could especially impact people that are directly dependent on these habitats for ecosystem services, such as food and coastal defence. In this study, we attempted to understand the extent of the plastic waste problem in mangrove forests in a rural, though relatively densely populated, area on the coast of Java, where people largely depend on aquaculture and fisheries. These rural communities benefit from healthy mangrove ecosystems for both coastal defence and for shrimp, crabs and commercial fish species. We therefore assessed the extent and the hypothesized negative effect of the omnipresent plastic waste on mangrove growth and survival. Overall, plastic is extremely abundant in mangrove forests and can be found in every plot at multiple depths. In addition, our results indicate that large quantities of plastic negatively affect ecosystem health and tree survival.

In more detail, our results confirm that plastic waste is trapped by mangrove forests. We found multiple sites where a large part of the forest floor (>50%) was covered with plastic waste (Fig. 4b), and plastic counts were up to 236 items per m^2 . These amounts of plastic are not uncommon in mangrove areas near cities. For instance, Rahim et al. (2020) found plastic waste numbers of 378 items per m^2 in Kendari Bay, Indonesia. Although these quantities of plastic are worrisome in and of itself, the plastic that only covers the forest floor and not the exposed pneumatophores probably poses little threat to the mangroves. Aerial roots in the form of pneumatophores are interconnected by below-ground cable roots. Blowing through such a cable root will push bubbles out of lenticels in multiple pneumatophores (Scholander et al., 1955). This interconnectivity between pneumatophores originating from the same cable root possibly minimizes the effect of scattered plastic on the sediment surface, which might only cover a few pneumatophores per cable root. The remaining pneumatophores can keep the sediment oxygenated at all times. In addition, the plastic can still be re-suspended by the tide, thereby only causing temporary suffocation. In contrast, plastic that is deposited on top of pneumatophores during sedimentation events can remain in place for weeks or months, depending on when the next storm hits. Our findings from the sediment cores suggest that a part of the plastic is present in the forest sediment for prolonged periods of time, as more than half of the plastics found in the cores were buried below 2 cm in the sediment (Fig. 4b). The finding that plastic is not only trapped but also buried in mangrove sediment is in accordance with Costa et al. (2011), who found plastics in various degrees of degradation buried up to at least 20 cm depth in a mudflat of a mangrove fringe in Brazil. If the plastic that was buried in the sediment at our field sites was present in the same abundance as the visible plastic layer on the sediment surface, this could cause a similar suffocating effect as the 100% and 50% treatments in the experiment.

In the field, plastic bags are of course rarely tied to pneumatophores as they were applied in the experiment, and an experimental set-up where the plastic was applied to aerial roots in a more "natural" way could have made the results more easily interpretable. However, despite an apparent loss in LAI in the cable tie control treatment, the tree mortality was not affected by cable tie application method itself, nor did the trees show a pneumatophore growth response when only the cable ties were applied. Furthermore, if the plastic would have been applied in a more realistic manner, covering both the sediment and the pneumatophores, this would only have increased the suffocating effect of the treatments, as oxygen penetration into the sediment through both the sediment surface and the pneumatophores would have been impaired. This would have complicated root respiration by trees even more than the current treatments, making the effects of plastic suffocation with the current set-up conservative estimates. Despite these considerations regarding the methodology, our results show that trees that were treated with 100% plastic cover of their root zone responded with extreme root elongation in an attempt to outgrow the suffocating substance, displayed increased litter fall after treatment application and failed to re-establish a canopy during the experiment. Unsurprisingly, most trees that were completely covered by plastic died in the course of the experiment. In contrast, a more realistic plastic cover of 50% showed that mangrove trees can be resilient to partial plastic suffocation, as the trees of the 50% treatment showed substantial investment in root growth similar to that observed in the 100% trees, but had an intermediate survival compared to the 100% plastic cover, and untreated control treatments.

Resilience to recurring anoxic conditions is a trait of all mangrove species, and in addition to evolutionary root adaptations, most mangrove species can adjust to prolonged inundation events as well (Youssef and Saenger, 1996). Acclimation strategies for coping with inundation events can function as mechanisms to overcome plastic suffocation. However, only few studies report field observations related to mature trees in anoxic conditions. For example, Snedaker et al. (1981) reported that *Avicennia germinans* trees survived an oil spill, although pneumatophore growth was atypical, with pneumatophores showing a crooked appearance. These root anomalies were similar to observations in our experiment and other heavily polluted field sites (Fig. A4). Bendy roots may suggest that trees tried to outgrow the suffocating substance. In a study by Ellison (1999), massive sedimentation caused by a hurricane suffocated multiple mangrove species. Mortality was not an immediate result of defoliation, as Ellison noted, because multiple individuals exhibited renewed leaf growth after the hurricane. This side note suggests that the trees did not die immediately from suffocation, but instead reacted similarly to what we appear to see in our 50% treatment; trees that were stressed by suffocation were initially able to endure the anoxic conditions due to heavy investment in root growth and potential foliage renewal. Nevertheless, in Ellison's study, mass mortality occurred sometime between the hurricane and their field observations.

The fact that mangroves can die despite foliage renewal, raises some interesting topics for further research: our experiment was conducted over a relatively short period of six weeks, and although this appeared to be sufficient to observe direct effects of plastic on mangrove trees, the ultimate effect of the 50% plastic waste cover remains unclear. Therefore, it would be interesting to know what the effect is of the current plastic waste levels on the overall life expectancy of mangrove trees. Longer term studies are needed to investigate changes in life span under partial plastic burial and other long term effects, such as the potential leakage of chemicals from decomposing plastic waste (Gao and Wen, 2016), or the effect of plastic during different seasons.

Notwithstanding the uncertainties regarding long-term effects of plastic on mangroves, our study demonstrates for the first time that mangroves are affected by large amounts of plastic on pneumatophores, and that these quantities of plastic are not uncommon in mangrove fringes. In addition, the plastic waste disposal into the environment is

only expected to increase in the future (Jambeck et al., 2015). Managers should therefore confront this problem alongside traditional mangrove conservation and restoration. Mangroves are relatively cheap ecosystems to restore compared to other marine ecosystems (Narayan et al., 2016), but median restoration costs for mangroves still range from 1191 USD/ha in developing countries, and up to 38,982 USD/ha in developed countries (Bayraktarov et al., 2016). Meanwhile, overall restoration success currently remains one of the lowest compared to restoration success in other marine ecosystems such as coral reefs, saltmarshes and oyster reefs (Bayraktarov et al., 2016). The success rate of mangrove restoration could potentially be increased if, in addition to budgets for planting mangroves, budgets for mitigation of potential stressors such as plastic waste reduction are also made available.

5. Conclusions

Plastic waste is trapped by mangrove forests, and can be present in high quantities both on the forest floor and in the sediment. Layers of plastic that are deposited on top of mangroves' aerial roots can cause an immediate local response, as trees invest in root growth to outgrow the anoxic conditions. Mangrove trees that are partly covered by plastic show a root-growth response and are seemingly stressed, but appear to be able to endure partial suffocation. Mangrove trees in which the root zones are entirely covered by plastic will ultimately die. Our findings suggest that mangrove trees are stressed by the current plastic pollution levels, especially near sources of mismanaged plastic. Mangrove restoration projects could therefore benefit from plastic management alongside conventional restoration efforts such as planting or habitat rehabilitation.

Data availability

Data in support of this manuscript are available at: <https://doi.org/10.4121/13109561>

CRediT authorship contribution statement

Celine E. J. van Bijsterveldt: Methodology, Formal Analysis, Investigation, Writing-Original Draft, Visualization, Supervision. **Bregje K. van Wesenbeeck:** Conceptualization, Validation, Writing-Review & Editing, Supervision. **Sri Ramadhani:** Formal Analysis, Investigation, Writing – Review & Editing, Visualisation. **Olivier V. Raven:** Methodology, Formal Analysis, Writing – Review & Editing, Visualisation. **Fleur E. van Gool:** Methodology, Writing – Review & Editing. **Rudhi Pribadi:** Resources, Writing-Review & Editing, Supervision. **Tjeerd J. Bouma:** Conceptualization, Methodology, Validation, Writing-Review & Editing, Supervision.

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.

Acknowledgements

The authors would like to thank Silke Tas and Alejandra Gijón Mancheño and the wider BioManCo team for the fruitful brainstorm sessions and critical feedback. Anneliese Suryaningtyas and Alifiansyah Deto Rahmana Putra for their efforts in preliminary experimental setups. We are grateful for the beautiful drone image created by Faiz Hamza Adriano who flew the drone at the study site and Lennart van IJzerloo for the post processing. In addition, we would like to thank Co-REM UNDIP, and in particular Muhammad Helmi and Aris Ismanto for facilitating the research project in Indonesia. Last but not least, we would like to thank Eko Budi Priyanto and Kuswanto from Wetlands

International and the local fishermen Bapak Slamet and Bapak Nur and their family for facilitating our work in the field.

Funding

This work is part of the BioManCO project with project number 14753, which is (partly) financed by NWO Domain Applied and Engineering Sciences, and co-financed by Boskalis Dredging and Marine experts, Van Oord Dredging and Marine Contractors bv, Deltares, Witteveen+Bos and Wetlands International. The BioManCO project is a collaboration between TU Delft, NIOZ and UNDIP and makes use of the framework set up by Building with Nature Indonesia, a program by Ecoshape, Wetlands International, the Indonesian Ministry of Marine Affairs and Fisheries (MMAF), the Indonesian Ministry of Public Works and Housing (PU) and other partners.

Appendix A



Fig. A1. Typical sediment ridge with accumulated plastic waste in a mangrove fringe of Demak regency, Java, Indonesia. Note the reduced canopy cover of trees located inside the sediment ridge.

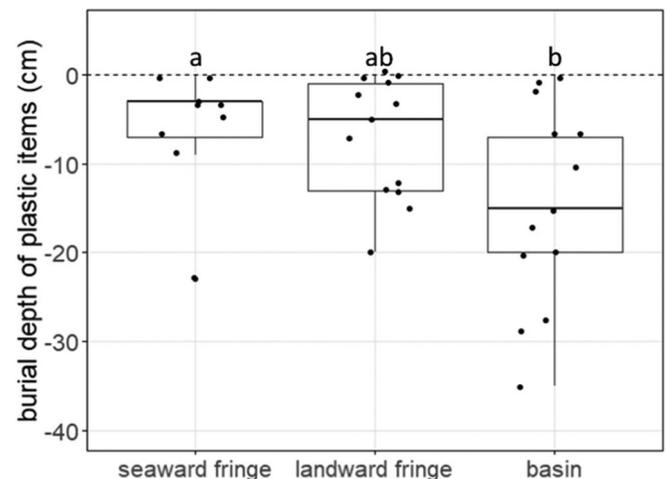


Fig. A2. The burial depth of plastic layers across mangrove zones (seaward fringe, landward fringe and basin).

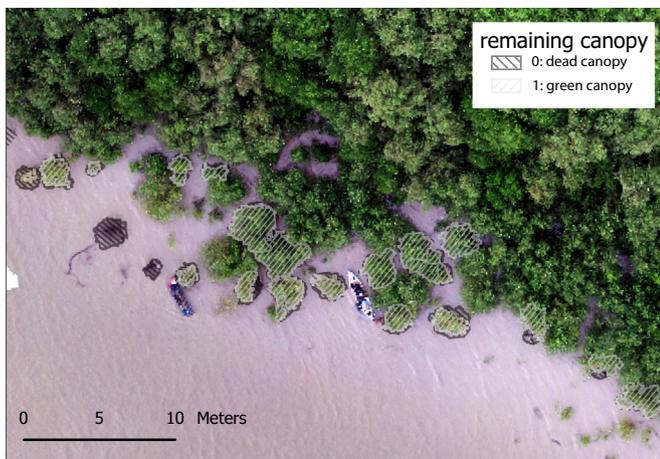


Fig. A3. Drone image of part of the study area, white hatched filled polygons (1) indicate vegetation based on Normalized Red Green Difference Index above zero, and black hatched filled polygons (0) display lost canopy cover compared to baseline.



Fig. A4. One of the many mangrove trees with crooked pneumatophores fringing a river mouth. The pneumatophores are entangled in plastic waste, cloths and diapers discharged by the river.

References

- Alongi, D.M., 2002. Present state and future of the world's mangrove forests. *Environ. Conserv.* 29, 331–349. <https://doi.org/10.1017/s0376892902000231>.
- Balke, T., Friess, D.A., 2016. Geomorphic knowledge for mangrove restoration: a pan-tropical categorization. *Earth Surf. Process. Landf.* 41 (2), 231–239. <https://doi.org/10.1002/esp.3841>.
- Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* 81 (2), 169–193.
- Bayraktarov, E., Saunders, M.I., Abdullah, S., Mills, M., Beher, J., Possingham, H.P., ... Lovelock, C.E., 2016. The cost and feasibility of marine coastal restoration. *Ecological Applications* 26 (4), 1055–1074.
- Bunting, P., Rosenqvist, A., Lucas, R.M., Rebelo, L.M., Hilarides, L., Thomas, N., ... Finlayson, C.M., 2018. The global mangrove watch - A new 2010 global baseline of mangrove extent. *Remote Sensing* 10 (10). <https://doi.org/10.3390/rs10101669>.
- Chappell, J., Grindrod, J., 1984. Chenier plain formation in northern Australia. *Coastal Geomorphology in Australia* 1 (1), 197–231.
- Chen, Y., Li, Y., Thompson, C., Wang, X., Cai, T., Chang, Y., 2018. Differential sediment trapping abilities of mangrove and saltmarsh vegetation in a subtropical estuary. *Geomorphology* 318, 270–282. <https://doi.org/10.1016/j.geomorph.2018.06.018>.
- Cordeiro, C.A.M.M., Costa, T.M., 2010. Evaluation of solid residues removed from a mangrove swamp in the São Vicente estuary, SP, Brazil. *Mar. Pollut. Bull.* 60 (10), 1762–1767. <https://doi.org/10.1016/j.marpolbul.2010.06.010>.
- Costa, M.F., Silva-Cavalcanti, J.S., Barbosa, C.C., Portugal, J.L., Barletta, M., 2011. Plastics buried in the inter-tidal plain of a tropical estuarine ecosystem. *J. Coast. Res.* 64, 339–343.

- Debot, A.O., Meesters, H.W.G., Bron, P.S., de León, R., 2013. Marine debris in mangroves and on the seabed: largely-neglected litter problems. *Mar. Pollut. Bull.* 72 (1), 1. <https://doi.org/10.1016/j.marpolbul.2013.03.023>.
- Ellison, A.M., 2000. Mangrove restoration: do we know enough? *Restor. Ecol.* 8 (3), 219–229.
- Ellison, J.C., 1999. Impacts of sediment burial on mangroves. *Mar. Pollut. Bull.* 37 (8–12), 420–426. [https://doi.org/10.1016/S0025-326X\(98\)00122-2](https://doi.org/10.1016/S0025-326X(98)00122-2).
- Gao, D.W., Wen, Z.D., 2016. Phthalate esters in the environment: A critical review of their occurrence, biodegradation, and removal during wastewater treatment processes. *Sci. Total Environ.* 541, 986–1001. <https://doi.org/10.1016/j.scitotenv.2015.09.148>.
- Horstman, E.M., Mullarney, J.C., Bryan, K.R., Sandwell, D.R., 2017. Deposition gradients across mangrove fringes. *Coastal Dynamics* 228, 1874–1885.
- Ivar do Sul, J.A., Costa, M.F., 2007. Marine debris review for Latin America and the wider Caribbean region: from the 1970s until now, and where do we go from here? *Mar. Pollut. Bull.* 54 (8), 1087–1104. <https://doi.org/10.1016/j.marpolbul.2007.05.004>.
- Jambeck, J., Geyer, R., Wilcox, C., Siegler, T.R., Perryman, M., Andrady, A., Law, K.L., 2015. Plastic waste inputs from land into the ocean. *Science* 347 (6223), 769–772. <https://doi.org/10.1126/science.1260352>.
- Kantharajan, G., Pandey, P., Krishnan, P., Bharti, V., Deepak Samuel, V., 2018. Plastics: a menace to the mangrove ecosystems of megacity Mumbai, India. *ISME/GLOMIS Electronic Journal* 16 (1), 1–5.
- Kodikara, K.A.S., Mukherjee, N., Jayatissa, L.P., Dahdouh-Guebas, F., Koedam, N., 2017. Have mangrove restoration projects worked? An in-depth study in Sri Lanka. *Restor. Ecol.* 25 (5), 705–716. <https://doi.org/10.1111/rec.12492>.
- Lebreton, L.C.M., Van Der Zwet, J., Damsteeg, J.W., Slat, B., Andrady, A., Reisser, J., 2017. River plastic emissions to the world's oceans. *Nat. Commun.* 8, 1–10. <https://doi.org/10.1038/ncomms15611>.
- Lewis III, R.R., 2005. Ecological engineering for successful management and restoration of mangrove forests. *Ecol. Eng.* 24 (4 SPEC. ISS), 403–418. <https://doi.org/10.1016/j.ecoleng.2004.10.003>.
- Li, W.C., Tse, H.F., Fok, L., 2016. Plastic waste in the marine environment: a review of sources, occurrence and effects. *Sci. Total Environ.* 566–567, 333–349. <https://doi.org/10.1016/j.scitotenv.2016.05.084>.
- Lussem, U., Bolten, A., Gnyp, M.L., Jasper, J., Bareth, G., 2018. Evaluation of RGB-based vegetation indices from UAV imagery to estimate forage yield in grassland. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives* 42 (3), 1215–1219. <https://doi.org/10.5194/isprs-archives-XLII-3-1215-2018>.
- Martin, C., Almahasheer, H., Duarte, C.M., 2019. Mangrove forests as traps for marine litter. *Environ. Pollut.* 247, 499–508. <https://doi.org/10.1016/j.envpol.2019.01.067>.
- Maryono, M., Seruyaningtyas, K., Roynaldi, A.D., Hastuti, C.M., Rahma, N.N., Sudarno, Hadiyanto, 2020. Regional model development of plastic waste monitoring: basic framework from population and public market in Central Java-Indonesia. *IOP Conference Series: Earth and Environmental Science* 448 (1), 0–12. <https://doi.org/10.1088/1755-1315/448/1/012098>.
- Mazda, Y., Magi, M., Ikeda, Y., Kurokawa, T., Asano, T., 2006. Wave reduction in a mangrove forest dominated by *Sonneratia* sp. *Wetl. Ecol. Manag.* 14 (4), 365–378. <https://doi.org/10.1007/s11273-005-5388-0>.
- McKee, K.L., 1996. Growth and physiological responses of neotropical mangrove seedlings to root zone hypoxia. *Tree Physiol.* 16, 883–889 Retrieved from. <http://www.ncbi.nlm.nih.gov/pubmed/14871780>.
- Narayan, S., Beck, M.W., Reguero, B.G., Losada, I.J., Van Wesenbeeck, B., Pontee, N., ... Burks-Copes, K.A., 2016. The effectiveness, costs and coastal protection benefits of natural and nature-based defences. *PLoS ONE* 11 (5), 1–17. <https://doi.org/10.1371/journal.pone.0154735>.
- Okello, J.A., Robert, E.M.R., Beeckman, H., Kairo, J.G., Dahdouh-Guebas, F., Koedam, N., 2014. Effects of experimental sedimentation on the phenological dynamics and leaf traits of replanted mangroves at Gazi bay, Kenya. *Ecology and Evolution* 4 (16), 3187–3200. <https://doi.org/10.1002/ece3.1154>.
- Podolsky, R.H., 1989. Entrapment of sea-deposited plastic on the shore of a Gulf of Maine Island. *Mar. Environ. Res.* 27 (1), 67–72. [https://doi.org/10.1016/0141-1136\(89\)90019-6](https://doi.org/10.1016/0141-1136(89)90019-6).
- Primavera, J.H., Esteban, J.M.A., 2008. A review of mangrove rehabilitation in the Philippines: successes, failures and future prospects. *Wetl. Ecol. Manag.* 16, 345–358. <https://doi.org/10.1007/s11273-008-9101-y>.
- R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <http://www.R-project.org/>.
- Rahim, S., Widayati, W., Anuluddin, K., Saleh, F., Alfirmar, Sahar, S., 2020. Spatial distribution of marine debris pollution in mangrove-estuaries ecosystem of Kendari Bay. *IOP Conference Series: Earth and Environmental Science* 412 (1), 0–8. <https://doi.org/10.1088/1755-1315/412/1/012006>.
- Sandilyan, S., Kathiresan, K., 2012. Plastics - a formidable threat to unique biodiversity of Pichavaram mangroves. *Curr. Sci.* 103 (11), 1262–1263.
- Scholander, P.F., Van Dam, L., Scholander, S.I., 1955. Gas exchange in the roots of mangroves. *Am. J. Bot.* 42 (1), 92–98.
- Smith, S.D.a., 2012. Marine debris: a proximate threat to marine sustainability in Bootless Bay, Papua New Guinea. *Mar. Pollut. Bull.* 64, 1880–1883. <https://doi.org/10.1016/j.marpolbul.2012.06.013>.
- Snedaker, S.C., Jimenez, J.A., Brown, M.S., 1981. Anomalous aerial roots in *Avicennia germinans* (L.) L. in Florida and Costa Rica. *Bull. Mar. Sci.* 31 (2), 467–470.
- Syakti, A.D., Bouhroum, R., Hidayati, N.V., Koenawan, C.J., Boulkamh, A., Sulistyio, I., ... Wong-Wah-Chung, P., 2017. Beach macro-litter monitoring and floating microplastic

- in a coastal area of Indonesia. *Marine Pollution Bulletin* 122 (1–2), 217–225. <https://doi.org/10.1016/j.marpolbul.2017.06.046>.
- Thomas, N., Lucas, R., Bunting, P., Hardy, A., Rosenqvist, A., Simard, M., 2017. Distribution and drivers of global mangrove forest change, 1996–2010. *PLoS One* 12 (6), 1–14. <https://doi.org/10.1371/journal.pone.0179302>.
- Tomlinson, P.B., 2016. Root systems. *The Botany of Mangroves*, 2nd ed. Cambridge University Press, pp. 90–108 <https://doi.org/10.1017/CBO9781139946575.008>.
- United Nations, 2018. Population Division World Urbanization Prospects 2018. Retrieved May 20, 2020, from <https://population.un.org/wup/Download/>.
- van Bijsterveldt, C.E.J., van Wesenbeeck, B.K., van der Wal, D., Afiati, N., Pribadi, R., Brown, B., Bouma, T.J., 2020. How to restore mangroves for greenbelt creation along eroding coasts with abandoned aquaculture ponds. *Estuar. Coast. Shelf Sci.* 235 (June 2019), 106576. <https://doi.org/10.1016/j.ecss.2019.106576>.
- Van Cuong, C., Brown, S., To, H.H., Hockings, M., 2015. Using *Melaleuca* fences as soft coastal engineering for mangrove restoration in Kien Giang, Vietnam. *Ecol. Eng.* 81, 256–265. <https://doi.org/10.1016/j.ecoleng.2015.04.031>.
- Willoughby, N.G., Sangkoyo, H., Lakaseru, B.O., 1997. Beach litter: an increasing and changing problem for Indonesia. *Mar. Pollut. Bull.* 34 (6), 469–478. [https://doi.org/10.1016/S0025-326X\(96\)00141-5](https://doi.org/10.1016/S0025-326X(96)00141-5).
- Youssef, T., Saenger, P., 1996. Anatomical adaptive strategies to flooding and rhizosphere oxidation in mangrove seedlings. *Aust. J. Bot.* 44 (3), 297–313. <https://doi.org/10.1071/BT9960297>.