

Disruption of Leaf Nutrient Remobilization in Coastal *Cycas* Trees by Tropical Cyclone Damage

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Abstract

We studied leaf nutrient status of *Cycas nitida* leaves that were damaged by Typhoon Haiyan in four contrasting locations in eastern Philippines to determine the influence of tropical cyclone (TC) damage on habitat biogeochemistry. Nitrogen resorption efficiency was below global values, but phosphorus and potassium resorption efficiencies were above global values. Stoichiometric relationships indicated P limitations, and leaf P traits tracked soil P availability. Typhoon Haiyan damage resulted in severe changes in P and K nutrient budgets for the plants, and the resulting litter was of high quality with traits that predicted rapid decomposition of the TC-generated litter. Partially desiccated leaves retained dead leaflet tissue exhibiting nutrient relations that did not differ from those of healthy green leaves, representing another means by which the TC disrupted nutrient cycling that added to the nutrients lost due to leaf abscission. Our results build on the need for a greater understanding of how TCs influence plant and community biogeochemistry and establish some background information for understanding ongoing climate change research.

Keywords: Resorption; Stoichiometry; Typhoon Haiyan

Introduction

Nutrient resorption from senescing leaves is an important trait that enables nutrient conservation for individual plants [1,2]. These remobilized nutrients are stored internally and are readily available for use as a means of reducing the dependence on newly acquired soil nutrients. When leaf senescence is allowed to proceed without interruption, the quality of resulting leaf litter is reduced by the resorption process such that the speed of litter decomposition is also reduced. Therefore, the nutrient resorption process exerts a direct effect on fitness of the individual plant and a direct effect on biogeochemical cycling of the habitat.

The proportion of nutrients that are remobilized from senescing leaves varies widely among plant species. Moreover, when rapid leaf death or leaf abscission occurs prior to the natural senescence process, nutrient recovery from the leaf may be circumvented. Indeed, this form of disrupting nutrient remobilization has been studied by experimental interruption [3,4] and has been reported for acute drought stress [5], freeze damage [6,7], and ozone stress [8].

Cycas nitida is one of two coastal species of *Cycas* found in the Philippines [9]. The plant population extends to the shore in many habitats where plants are exposed to saline conditions (Figure 1A). We have studied the traits of various habitats of this species throughout the eastern islands of the Philippines. Many of these habitats were in close proximity to the eye path of Typhoon Haiyan on 8 November 2013. We returned to some of these sites following this tropical cyclone (TC) to study some of the biogeochemical responses and the extent of damage to the agroforestry systems and the individual plants.

Our primary objective was to determine the influence of Typhoon Haiyan damage on leaf nutrient traits. The secondary objective was to determine background nutrient remobilization characteristics of this *Cycas* species, and evaluate its relationship with the variation in soil nutrient status among four sites with contrasting soils. These outcomes were used to discuss potential differences in the after-effects of TC damage among sites.

Material and Methods

Study sites

The study sites were in Samar and Leyte Islands located in the eastern periphery of the Visayan Islands in the Philippines. The lithologic units in Samar consist of various igneous rocks from the Cretaceous-Paleogene, forming the island's main nucleus enveloped by a sedimentary sequence of rocks from Miocene-Pleistocene age. Leyte Island is underlain by four lithological units: (1) a schist body, (2) an igneous complex with serpentized facies of Cretaceous to Oligocene age, (3) a sedimentary sequence similar to Samar Island during the Miocene-Pleistocene age and (4) Quaternary volcanics [10].

Samar and Leyte Islands are mediated by Type II and Type IV climates under the Modified CORONAS classification system, with most of Samar prevailing under Type II climate with no dry season and with maximum rainfall between December and January. Samar exhibits an average annual temperature of 26.8°C, average relative humidity of 80%, and mean annual rainfall of 3,634 mm. Most of Leyte except the southern part is under Type IV climate, with rainfall distributed throughout the year without a pronounced dry season, an average annual temperature of 27.5°C, and annual precipitation of 2,700 mm [11].

The four sites that we selected for this study were minimally managed agroforests with *Cocos nucifera* as the primary crop. We selected these sites because they collectively included all of the soil types that support *Cycas nitida* populations in the country, and all four sites were damaged by Typhoon Haiyan within a few hours of each other on 8 November 2013 at the time of greatest intensity of the TC.

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Sand

The habitat with beach sand substrate was located on a small barrier island in Northwestern Samar near the San Bernardino Strait. The plants were located 20-30 m from the shore at an elevation of 2-3 m above sea level (masl). This substrate contained critically low levels of nitrogen (N) and potassium (K) and low levels of phosphorus (P).

Karst

The habitat with plants growing on karst outcrops was located on Higatangan Island, Northwest of Leyte. The plants were located 15-25 m from the shore at an elevation of 3-4 masl. The substrates in these habitats that plant roots exploit are composites of organic debris that accumulate in the solution pits of the karst outcrops. This substrate contained the highest levels of N, P, and K among the four sites.

Mineral

The habitat with plants growing in mineralized soils derived from andesite and basal flows intercalated with pyroclastics was located south of Silago in eastern Leyte. A gold and manganese reserve exists a few kilometers from this vicinity. The plants were located 90 m from the shore at an elevation of 35 masl. This substrate had moderate levels of N and K but the lowest levels of P.

Halomorphic

The habitat with these substrates was dominated by various mangrove species and *Nypa fruticans* north of Calbayog, Samar. The plants were located about 50 m from the shore at 1 masl. Low levels of N, P, and K characterized these substrates. While all four sites were prone to aerosol salt deposits, these halomorphic soils were the most saline due to ocean water intrusion and the lack of elevation that allows for leaching of salts.

TC damage and sampling

The *C. nitida* trees in these four habitats suffered typical forms of TC damage. Severe defoliation resulted in abscission of leaves in all age categories including green leaves and senescing leaves. In addition, many of the pinnately compound leaves were not abscised but some of the leaflet tissue was desiccated by the TC winds (Figure 1B)[12]. A proportion of the tissue on these leaves remained alive and functioning, but a large proportion of the tissue was attached but dead.

In order to quantify the nutrient cycling dynamics, we harvested samples from (1) healthy green leaves, (2) senescent leaves, (3) the green tissue on partially desiccated leaves, and (4) the dead tissue on the same partially desiccated leaves. Samples from six trees were harvested at each site to provide six replications. Approximately the same amount of material was collected from 6 distinct leaves on each tree. Additionally, we collected soil samples in the top 10-cm layer of rooting substrates at 1-m distance in four directions from each sampled tree. The four subsamples were mixed to provide a single soil sample per replication. The four sites used for this analysis were visited from 8-12 December 2013, roughly one month after the TC damage.

Analyses

Leaflet samples were dried at 70°C, then milled to pass through a 1-mm screen. Total carbon and nitrogen contents of leaf tissue and soils were determined by dry combustion (FLASH EA1112 CHN analyzer; Thermo Fisher, Waltham, Mass., USA). Phosphorus and potassium contents were determined by inductively coupled plasma optical emission spectrometry (Spectro Genesis; SPECTRO Analytical

Instruments, Kleve, Germany) [13]. Available P and K in soils were determined by Olsen's extractable P and DTPA extractable K.

Nutrient resorption efficiency was calculated as the change in nutrient concentration between green and senesced leaves divided by the concentration in green leaves, and represented a measure of the percentage of the nutrients that were withdrawn prior to abscission. Stoichiometric relations were calculated as C/N, C/P, C/K, N/P, N/K, and K/P. Nutrient concentrations and stoichiometry variables were analyzed by two-way ANOVA, with site and leaf type as the main factors. Stoichiometry quotients were log-transformed prior to analysis. Resorption efficiency variables were analyzed by one-way ANOVA with site as the source of variation. Resorption efficiency data were arcsine-transformed prior to analysis. Means separation for variables that were significant was conducted by Least Significant Difference. In addition, regression analysis was employed to examine how the range in soil nutrient traits among the habitats related to the range in tissue concentration and nutrient resorption efficiency.

Results

Nutrient concentration of leaf types

Nitrogen concentration was influenced by substrate type and leaf type, as evidenced by a significant interaction ($F(9,80)=37.90$; $P<0.0001$). Green leaf N ranged from 24.2-27.6 mg g⁻¹, and naturally senesced leaf N ranged from 16.7-22.2 mg g⁻¹ (Table 1). The interaction of substrate type and leaf type also affected phosphorus concentration ($F(9,80)=4.70$; $P<0.0001$). Green leaf P ranged from 1.1-1.9 mg g⁻¹, and naturally senesced leaf P exhibited a three-fold range of 0.3-0.9 mg g⁻¹. Potassium concentration was similarly influenced by the interaction of substrate type and leaf type ($F(9,80)=130.42$; $P<0.0001$). Green leaf K concentrations were more variable among the substrates than were N or P concentrations, and exhibited a 2.59-fold difference among the substrate types. Similarly, senesced leaf K concentration greatly varied

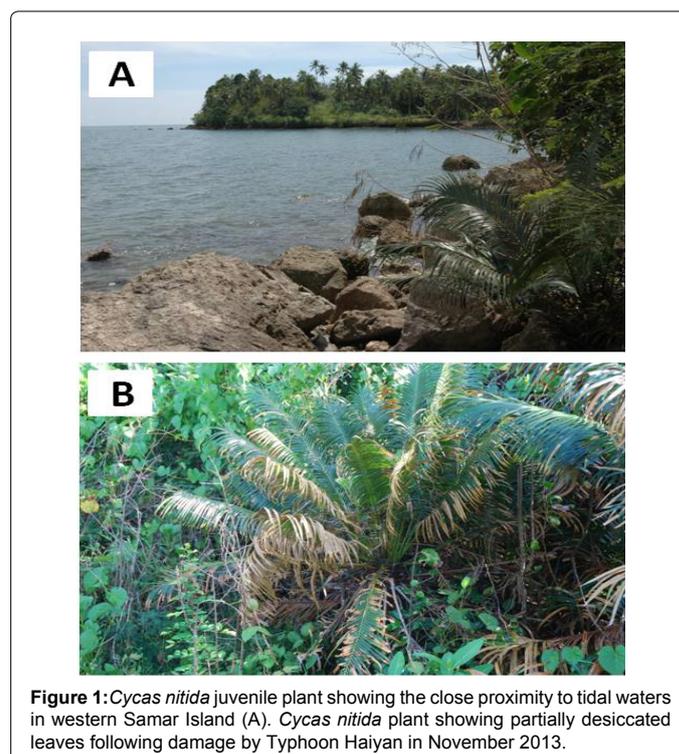


Figure 1: *Cycas nitida* juvenile plant showing the close proximity to tidal waters in western Samar Island (A). *Cycas nitida* plant showing partially desiccated leaves following damage by Typhoon Haiyan in November 2013.

Substrate	Nutrient (mg g ⁻¹)	Green		Desiccated	
		Leaf	Senesced Leaf	Green Leaflet	Desiccated Dead Leaflet
Sand	Nitrogen	27.6B	20.1A	26.1B	25.6B
	Phosphorus	1.2B	0.4A	1.1B	1.3B
	Potassium	6.4B	1.2A	6.4B	6.1B
	Carbon	498.5A	499.8A	502.2A	485.7A
Karst	Nitrogen	25.9B	22.2A	25.3B	27.0B
	Phosphorus	1.9B	0.9A	1.7B	1.9B
	Potassium	14.8B	3.3A	15.1B	14.7B
	Carbon	502.2A	504.3A	506.0A	494.7A
Mineral	Nitrogen	24.2B	16.7A	29.0C	30.2C
	Phosphorus	1.1B	0.3A	1.4B	1.2B
	Potassium	13.7B	2.9A	15.6B	15.8B
	Carbon	509.2A	518.8A	495.7A	517.2A
Halomorphic	Nitrogen	24.9B	19.6B	23.7B	24.7B
	Phosphorus	1.3B	0.4A	1.2B	1.4B
	Potassium	16.6B	4.5A	15.6B	17.0B
	Carbon	507.3A	493.5A	483.0A	473.0A

Table 1: *Cycas nitida* leaflet tissue mineral content in healthy green leaves, senesced leaves, green portions of half-desiccated leaflets, and dead portions of half-desiccated leaflets as influenced by substrate type. Numbers within rows followed by the same letter are not significantly different, n=6.

with a 3.75-fold difference among the substrate types. For all four habitats, the leaves that were partially desiccated by Typhoon Haiyan exhibited N, P, and K concentrations that did not differ between the green and dead leaflet tissues (Table 1). Carbon concentration varied among the substrate and leaf types in an interactive manner ($F(9,80) = 3.34$; $P=0.0016$). However, leaf C concentration did not differ among the leaf types for any of the substrates (Table 1). The significant interactive effect was likely a result of the idiosyncrasies brought about by the different ranking of means among leaf types for each of the substrate types.

Stoichiometry of leaf types

The interaction of substrate type and leaf type was significant for log C/N ($F(9,80) = 66.17$; $P<0.0001$), log C/P ($F(9,80) = 31.64$; $P<0.0001$), and log C/K ($F(9,80) = 38.65$; $P<0.0001$). These quotients were greatly increased in senesced leaves when compared with green leaves, due to the decline in N, P, and K of senesced leaves combined with no concomitant decline in C (Table 2). The stoichiometric relationships of N, P, and K were variable because all three nutrients decreased to varying degrees from green to senesced leaves. Log N/P was influenced by the interaction of substrate type and leaf type ($F(9,80) = 19.19$; $P<0.0001$). Because P was reduced to a greater percentage than N when comparing green and senesced leaves, the quotient N/P of senesced leaves increased 71% to 158% above that of green leaves (Table 2). Log N/K was also significantly affected by the interaction of substrate type and leaf type ($F(9,80) = 29.65$; $P<0.0001$). The decline in K concentrations from green to senesced leaves was greater than the decline in P, so the quotient N/K of senesced leaves increased even more than N/P, and ranged from 200% to 325% above that of green leaves. The interaction of substrate type and leaf type was also significant for log K/P ($F(9,80) = 56.21$; $P<0.0001$). Senesced leaf K/P was lower than that of green leaves, with the karst substrate exhibiting the greatest decline (Table 2).

The leaves that were partially desiccated by Typhoon Haiyan exhibited N/P, N/K, and P/K values that were similar to green leaf tissue (Table 2). Without exception, these stoichiometric relationships of the partially desiccated leaves were dissimilar from those of naturally senesced leaves.

Nutrient resorption altered by TC damage

Natural nutrient resorption patterns were calculated from healthy green leaves and senesced leaves. Nitrogen resorption efficiency varied among substrate types ($F(3,20) = 25.95$; $P<0.0001$), and was greatest in mineral substrates and least in karst substrates (Figure 2). Phosphorus resorption efficiency similarly varied among substrate types ($F(3,20) = 201.30$; $P<0.0001$), and exhibited a pattern among the substrate types that was similar to that of N resorption efficiency. Substrate type significantly influenced potassium resorption efficiency ($F(3,20) = 33.67$; $P<0.0001$), and was greatest in sand and least in halomorphic substrates.

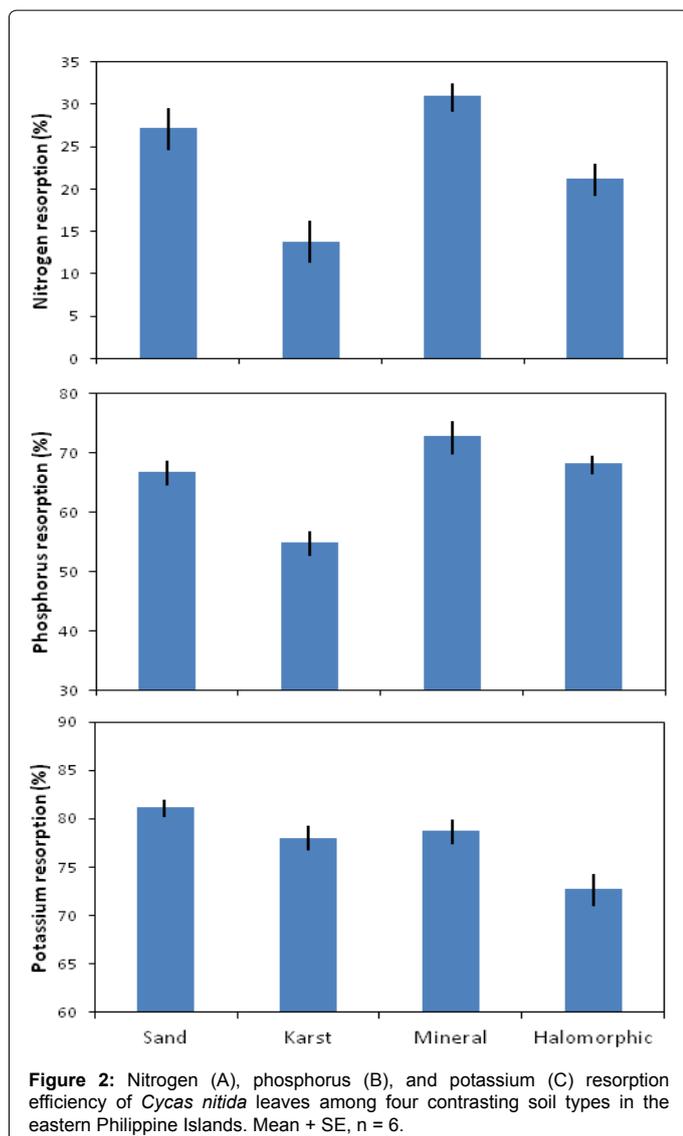
We found no evidence of nutrient resorption from the dead leaf portions in the leaves that were differentially desiccated by Typhoon Haiyan. The N, P, and K concentrations of the dead portions of these leaves did not differ from those of the green portions of the same leaves (Table 1).

Soil nutrients influence leaf nutrients

Total soil N concentration ranged from 0.4 to 13.3 mg g⁻¹. Nitrogen resorption efficiency exhibited a linear decline and N concentration of senesced leaves exhibited a linear increase with increased soil N concentration (Figure 3). In contrast, healthy green leaf N concentration was unaffected by soil N concentration ($P=0.4963$). Available P concentration in the soils ranged from 8.4 to 28 μg g⁻¹. Phosphorus resorption efficiency also declined with increased soil P concentration (Figure 3). Unlike N, both green and senesced leaf P concentration was positively related to soil P concentration. Available soil K was more

Substrate	Quotient	Green		Desiccated	
		Leaf	Senesced Leaf	Green Leaflet	Desiccated Dead Leaflet
Sand	C/N	18A	25B	19A	19A
	C/P	417A	1257C	473B	381A
	C/K	78A	416B	79A	79A
	N/P	23B	51C	25B	20A
	N/K	4A	17B	4A	4A
Karst	K/P	5B	3A	6B	5B
	C/N	19AB	23C	20B	18A
	C/P	272AB	554C	290B	257A
	C/K	24A	156B	35A	34A
	N/P	14A	24B	15A	14A
Mineral	N/K	2A	7B	2A	2A
	K/P	8B	4A	9B	8B
	C/N	21B	31C	17A	17A
	C/P	463B	1736C	354A	434B
	C/K	37A	179B	32A	33A
Halomorphic	N/P	22A	56B	21A	25A
	N/K	2A	6B	2A	2A
	K/P	12BC	10A	11AB	13C
	C/N	20A	25B	20A	19A
	C/P	400B	1226C	403B	334A
Halomorphic	C/K	31A	111B	31A	28A
	N/P	19A	49B	20A	17A
	N/K	1A	4B	2A	1A
	K/P	13B	11A	13B	12AB

Table 2: The influence of substrate type on *Cycas nitida* leaflet tissue stoichiometry in healthy green leaves, senesced leaves, green portions of half-desiccated leaflets, and dead portions of half-desiccated leaflets as influenced by substrate type. Numbers within rows followed by the same letter are not significantly different, n=6.



variable among the habitats than were N and P, and ranged from 20-1324 $\mu\text{g g}^{-1}$. Despite this 66-fold range, soil K concentration did not influence K resorption efficiency ($P=0.9722$), green leaf K concentration ($P=0.0689$), or senesced leaf K concentration ($P=0.3182$). Factors other than available K in the rooting substrate were causal for the differences in K resorption efficiency among the habitats (Figure 2).

Discussion

A relatively infrequent but intense large scale disturbance event such as a TC may exert extreme damage to coastal agroforestry settings. The direct damage of a TC on a coastal habitat may last a few hours, but subsequently influence management decisions for years. Likewise, resistance during and resilience following a TC may be influenced by vegetation management decisions of a coastal habitat during the years prior to the event. These interactive effects are poorly understood and not adequately studied for TCs. Moreover, research on the influence of TCs on island ecosystems in the western Pacific has not been adequate [14].

We have addressed these needs by showing that the direct TC damage to *C. nitida* populations in the Philippines influences biogeochemical processes by disrupting the natural processes associated

with senescence-driven nutrient resorption prior to leaf abscission. For the individual plant, loss of entire green leaves due to the TC-force winds leads to direct loss of the entire nutrient capital of those leaves. The reduction in fitness and plant health following severe defoliation is more acute for taxa like *Cycas* species with persistent, long-lived leaves [15] than for species with ephemeral, short-lived leaves. Additionally, wind-induced partial leaf desiccation during a TC disrupts nutrient retrieval from the damaged leaf tissue, and this dead leaf tissue is retained suspended in the canopy by the partially functioning leaves.

For the ecosystem, the copious amount of green leaf tissue that is added to the litter layer alters nutrient additions to the soils through two mechanisms. First, the volume of litter creates a pulse of inputs that may exert lasting effects on increased ecosystem nutrient availability. Second, the stoichiometry of this litter pulse reveals high quality litter that the detritivore community may decompose more rapidly than litter derived from natural senescence processes. This chemical trait increases the speed of release of nutrients that are stored in the litter layer. The combined effects of litter volume and elevated litter quality can cause TC-generated litter to release copious amounts of nutrients into the ecosystem [16].

For the dead leaf tissue that remains affixed to partially live leaves, we have confirmed one of our earlier predictions concerning how this form of damage will influence biogeochemical cycling [12]. The quality of this suspended form of litter is of high quality, with chemical traits that do not differ from the live green leaf tissue. Confirmation of our other predictions about how the nutrients stored in this suspended dead leaf tissue will be released over time remains to be resolved through long-term studies that employ repeated sampling techniques.

Cycads are a lineage of ancient dioecious gymnosperms that have persisted for hundreds of millions of years [17]. Cycads are members of the Cycadales, which includes more than 330 species [18] and comprise the most threatened group of plant species on Earth [19,20]. The genus *Cycas* is the most speciose cycad genus, with more than 100 described taxa [18]. To our knowledge, this is the first empirical look at macronutrient stoichiometry for any *Cycas* species. Robust data sets have been parsed to indicate that leaf N:P above 16 suggests P limitation to plant biomass production, N:P below 14 suggests N limitation, and N:K above 2.1 or K:P below 3.4 indicate K limitation [21-25]. Our N:P mean was 19.6, indicating primarily P limitation. Our N:K mean was 2.4 which indicated K limitation in relation to N availability, and the K:P mean of 9.7 signified K sufficiency in relation to P availability.

To our knowledge, this is also the first report for any *Cycas* species that includes a close look at leaf nutrient resorption traits. On average, plants withdraw about 50% of leaf N and P prior to leaf abscission [1,26], and withdraw about 70% of the leaf K prior to leaf abscission [27]. Our average N resorption efficiency of 23% was much lower than the global average, while our average P resorption efficiency of 65% and K resorption efficiency of 78% were higher than global values. Assessments of a range in plant species have shown that species that associate with N-fixing root symbionts express reduced N resorption efficiency in comparison to other species [28,29]. Therefore, we expected to find relatively low N resorption efficiency for *C. nitida*, since this and other cycad species utilize the services of N-fixing cyanobacteria within specialized root structures [17]. These findings indicate that the loss of green leaves during a TC event may damage the P and K economies of *C. nitida* to a greater degree than N economy.

Chemical traits of fresh litter exert direct influences on the rates of subsequent litter decomposition, with higher nutrient content speeding

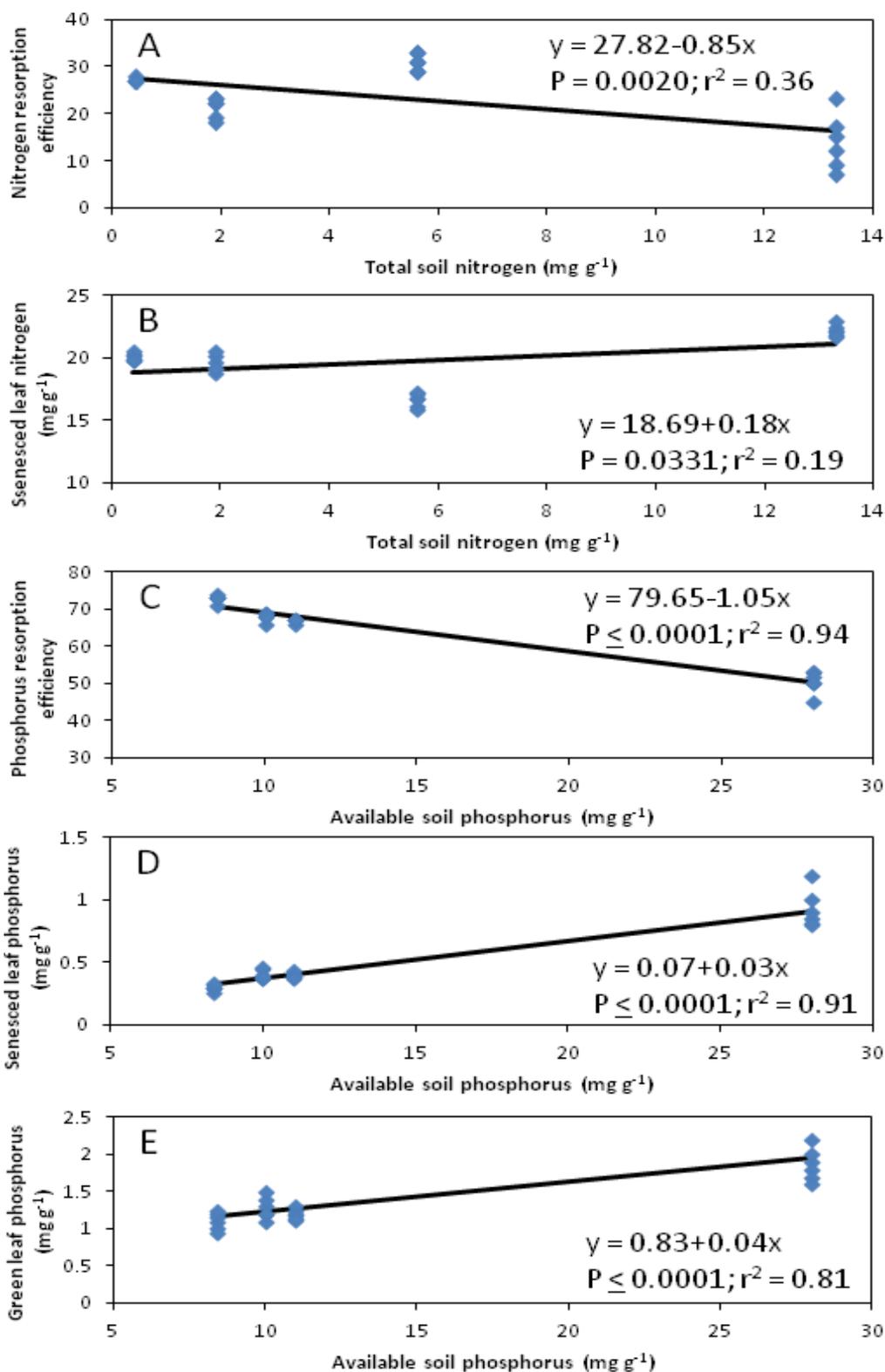


Figure 3: The influence of soil nitrogen on leaf nitrogen resorption efficiency (A) and senesced leaf nitrogen concentration (B) of *Cycas nitida*. The influence of available soil phosphorus on leaf phosphorus resorption efficiency (C), senesced leaf phosphorus concentration (D), and green leaf phosphorus concentration (E) of *Cycas nitida*.

up decomposition and higher carbon/nutrient quotients slowing down decomposition [30,31]. In this study using one gymnosperm species and four contrasting habitat types, we found that C:N variation of senesced leaves among the habitats was constrained, but C:P varied 3.1-fold and C:K varied 3.7-fold. These differences illuminate one of the ways in which TC damage may alter subsequent litter decomposition in a heterogeneous manner among various sites. The pulse of high quality green leaf litter caused by a TC may speed up the decomposition in habitats with the higher C/nutrient quotients to a greater degree than habitats with the lower C/nutrient quotients. Loss of biodiversity leads to myriad ecological changes, including a reduction in the speed of cycling of litter carbon and nitrogen [32]. Changes in carbon and nutrient traits of composite fresh litter may be one of the drivers of these changes in overall decomposition speed when biodiversity declines.

Studies of the role of soil nutrient availability on nutrient resorption processes have not adequately revealed canonical relationships. However, some reports revealed a modest adjustment in resorption efficiency reflective of natural variations in soil nutrient status [28,33]. Moreover, manipulations of soils nutrients through fertilizer inputs have been shown to alter leaf nutrient stoichiometry [34]. Our results indicate P relations of *C. nitida* leaves appear to be tightly linked to soil P availability, but N and K relations are less dependent on soil resources. The range in soil K was much greater than the range in soil P, yet P resorption efficiency tracked soil P and K resorption efficiency was not influenced by soil K.

The Philippines is one of the world's biodiversity hotspots [35-38]. In line with global trends [39], the natural systems that support that biodiversity are in decline with 97% of original forest irreversibly converted to other land uses [40]. The Economics of Ecosystems and Biodiversity (TEEB) initiative [41] and other international efforts to mainstream an understanding of the value of ecosystem capital rely on case studies to build an adequate database. Efforts to address the underlying causes of the decline, and the contributions that the Philippines may offer global TEEB initiatives are hindered by lack of research on the organisms. Indeed, basic research on oceanic islands has not been adequately connected to the urgent needs for biodiversity conservation [42,43].

The impact of TCs on small islands may exert extreme pressures on the coastal communities [14]. For example, coastal flooding caused by TCs will likely worsen in the future [44]. The science and mitigation of island species extinctions [45] may advance with more case studies that document the influence of TCs on coastal biodiversity. These studies would benefit by focusing on imminent factors such as the immediate impact of TCs on biogeochemical cycling in coastal communities, as we have done in this study, rather than on long time-scales [46]. These efforts to better understand the biogeochemistry of coastal agroforestry settings will also inform the need to better understand ecosystem capital [47] in those settings. The coastal communities in the Philippines are under tremendous pressure for conversion to utilitarian use by humans, and conversion to minimally managed agroforests represents one of the most common forms of habitat conversion for coastal settings. In light of the global momentum of land conversion for human use, Hahs and Evans [48] argue for a much better understanding of how the converted habitats affect the ecology of resident organisms. Moreover, research on island systems could be improved by recognizing the interactions of terrestrial, ocean, and human systems that combine to create the island ecotone [49]. We restricted the habitats for evaluation in this study to coastal agroforestry habitats, a decision that addresses all of the above concerns.

In summary, large scale disturbances such as regional drought, freeze events, or tropical cyclones may influence plant behavior and ecosystem traits for many years after the event. The study of tropical cyclone issues in the tropical and subtropical climates has lagged behind the study of disturbances in temperate climates. We have studied the aftermath of Typhoon Haiyan in the Philippines to show that nutrient remobilization during leaf aging and senescence can be disrupted by the few hours of a tropical cyclone event in a manner that is similar to other large scale disturbances. The damage may influence nutrient budgets and cycling for individual plants, particularly P and K budgets, and consequently demand thoughtful management decisions during extended recovery. Moreover, in agroforestry settings the disturbance may influence nutrient cycling at the community level for extended periods of time following the event. Climate change studies predict major alterations in frequency of intense tropical cyclones. A greater understanding of how TCs influence plant and community level responses is needed to form the foundation that will serve as background information during ongoing climate change research.

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