Growth Pattern in Tropical Mangrove Tress of Bunaken National Park, North Sulawesi, Indonesia

Abstract. Seasonal growth patterns and growth rate variation in tropical mangroves of Bunaken National Park (BNP) were investigated. Dendrometer bands were installed on trees from twelve different sites in tropical mangroves of Bunaken National Park (BNP) to 10 measure stem growth rates. Growth rates measured in trees at the twelve sites varied significantly from 0.83 ± 0.27 to 1.71 ± 0.31 mm month⁻¹. Growth rates were higher on Sonneratia alba (1.65 ± 0.69 mm month⁻¹), low on Rhizophora stylosa, Xylocarpus moluccensis, Avicennia marina, Ceriops tagal (0.82 ± 0.16 , 0.82 ± 0.18 , 0.85 ± 0.18 , 0.88 ± 0.28 mm month⁻¹, respectively), and medium on $\textit{Rhizophora apiculata, Bruguiera parviflora, Bruguiera gymnorrhiza, Rhizophora mucronata (1.19 \pm 0.16, 1.22 \pm 0.69, 1.25 \pm 0.49, 1.25 \pm 0.40, 1.2$ 1.31 ± 0.22 mm month⁻¹, respectively). Statistically, growth rates were higher in trees with initial girths more than 50 cm compared to trees with initial girth less than 50 cm on B. gymnorrhiza, C. tagal and R. mucronata, but these were slower for R. apiculata and S. alba. Growth rates varied among different site conditions, and the effect of soil water salinity on these was significant at higher intertidal sites. Growth rates exhibited seasonal patterns, and these were correlated positively with rainfall and negatively with temperature. The effect of the 2015-2016 El Nino was significant on reduced growth rates.

20 Keywords: dendrometer, El Nino, growth rate, tropical mangrove

1

11

12

13

14

15

16

17

18

19

21

INTRODUCTION

22 Mangrove is a relatively small group of higher plants which have been peculiarly successful in colonising tropical and 23 sub-tropical intertidal habitats at the interface between land and sea (Clough 1979; Duke 1992; Kathiresan and Bingham 24 2001: Maxwell 2015). Mangroves, which are tolerant to salt and brackish waters (Spalding et al. 1997), have developed 25 complex morphological, anatomical, physiological, and molecular adaptations allowing survival and success in their high-26 stress habitat (Srikanth et al. 2015). Despite of all the ecological services and economic benefits associated with mangrove 27 ecosystems, about 2.1% (2,834 km²) of the existing worldwide mangrove area was estimated to be lost each year during 28 the second half of the 20th century (Valiela et al. 2001) and a total loss of 1.97% (1,646 km²) from 2000 to 2012 (Hamilton 29 and Casev 2016).

30 Mangroves in many tropical locales exhibit seasonal diameter growth patterns, often as a consequence of distinctive 31 32 wet and dry seasons, and their seasonal patterns of growth are often related to rainfall, temperature, and relative moisture regimes (Krauss et al. 2006). Mangrove trees of the same species may show different growth rates due to specific 33 environmental factors such as nutrients, salinity or inundation frequency of any localities (Suarez et al. 1998). According 34 to Menezes et al. (2003), abiotic factors may influence the individual growth rates, but their effect on the forest structure is 35 modified by biotic factors, such as neighbourhood competition.

36 As in many tropical tree species, annual growth rings are commonly said to be absent in mangroves (Gill 1971; Tomlinson 1986), although these are claimed to be present in Rhizophora mucronata from the Kenyan coast (Verheyden et 37 38 al. 2004). It is proposed by Roberts et al. (2011) that the use of growth ring for age and growth rate determinations should 39 be evaluated on a case by case basis. In the absence of annual growth rings, dendrochoronological technique may not be 40 applied, and that in this case, dendrometer band to measure increments in circumference growth offers an alternative to document fine-scale growth increments (Krauss et al. 2006). In practice, the growth rates of mangrove species may be a 41 42 useful indicator of site conditions resulting from change (Krause et al. 2006), key data of demographic processes to 43 investigate the development of mangrove forests (Menezes et al. 2003), necessary for the establishment of sustainable 44 silvicultural practices (Devoe and Cole 1998), important to generate a population model to determine cutting limits for 45 harvesting of the mangrove trees (Rajkaran and Adams 2008), and a fundamental measurement to understand tree biology 46 and physiology (Nasim et al. 2013).

The mangrove forests of Bunaken National Park (BNP) are among the most distinctive and unusual in Southeast Asia, 47 48 because of the species that the forests contain and the ecological processes that are now taking place (Davie et al. 1996) 49 Djamaluddin 2004). It is believed that the interplay between geophysical, geomorphic and biological factors has supported 50 the mangrove distribution and diversity in the intertidal environments of the Park. Last study reported that there were at 51 least 27 plant species distributed over ten sub-habitat types (Djamaluddin 2018). A common dieback phenomenon 52 53 associated with big trees of several species within the Park is also an important factor. While we do not know the lifespan of mangrove trees, this dieback is presumed to relate to old age. Long lifespan of mangroves in this area may be supported 54 55 by their stable physical intertidal environments and the absence of catastrophic events (Djamaluddin 2004).

In this study, the growth dynamic of nine common encountered species in BNP was investigated. This study was 56 designed to examine growth rates of trees growing at different conditions of intertidal environment over a period of 59 Commented [W1]: research purposes?

Commented [W2]: Method?

Commented [W3]: how about the value of economic losses?

Commented [W4]: Explain that?

Commented [W5]: Roberts or Robert?

-	Commented [W6]: Nasim or Nazim		
-	Commented [W7]: not in the library		
-	Commented [W8]: what do you mean? explain briefly?		

57 months, including the period of the 2015-2016 El Nino. This allowed for comparison of growth rates by sites with 58 different conditions of tidal inundation and soil water salinity, by species from the same climatic zone and between the 59 same trees species of large sizes and small sizes. In addition, seasonal pattern of growth rates was investigated using data 50 of stem growth rates over several continuous wet and dry seasons, and growth dynamic in relation to rainfall and 52 temperature was analysed. This study was conducted to test the hypothesis that growth rates are influenced by conditions 53 of intertidal environments, and that distinct wet and dry seasons may have a consequence on seasonal pattern of growth 54 rates

MATERIALS AND METHODS

65 **Description of climate**

64

66 The rainfall in the study area is strongly affected by the wind systems (Djamaluddin 2004). The north-westerly winds 67 blow over the South China Sea and bring moisture during September and April. In November, these winds arrive in the 68 North Sulawesi via the Sulawesi Sea and to the west coast of South Sulawesi in late of November or early of December. 69 Dry south-easterly winds blow from the wintery Australian land mass towards Eastern Sulawesi. These dry winds cause a 70 short dry season in Manado from August to October. Based on data released by Manado Meteorology and Geo-physic Office, the total annual rainfall ranges from 2,501 to 3,000 mm. During 1973 to 2016, the annual temperature of North 71 72 Sulawesi varies little between 25.5 °C and 27.0 °C. The minimum annual mean temperature of 25.5 °C is recorded in 1984 73 and the maximum of 27.0 °C in 2015.

74 Data collection and analysis

75 Four canopy trees were selected from each of the twelve different sites to measure stem growth rate in the form of girth 76 increment. These sites represented conditions at high intertidal environment including Site 1 (highly accreting inland fringe habitat; $01^{\circ}22'00.50^{\circ}$ N, $124^{\circ}33'18.84''$ E), Site 2 (less steep and eroding landward habitat; $01^{\circ}22'01.53''$ N, $124^{\circ}33'16.09''$ E), Site 3 (less steep landward habitat; $01^{\circ}22'05.50''$ N, $124^{\circ}33'16.37''$ E), Site 11 (freshwater influenced 77 78 79 habitat; 01°19'43.85" N, 124°31'14.14" E); low intertidal environment or seaward fringe habitat including Site 4 80 (01°22'24.37" N, 124°33'10.31" E), Site 5 (01°22'20.01" N, 124°33'04.72" E), and Site 7 (01°22'13.57" N, 124°32'58.41" E); middle intertidal environment including Site 10 (01°21'38.79" N, 124°32'40.84" E); tidal stream edge or river levee 81 habitat including Site 6 (01°22'21.08" N, 124°33'09.00" E) and Site 8 (01°22'07.20" N, 124°33'04.20" E); and transgressed 82 83 bedrock coast habitat including Site 12 (01°19'43.17" N, 124°31'45.00" E).

The growth rates of selected trees were measured every two months during July 1999 to June 2001 and March 2014 to December 2016, using fixed dendrometer bands made with DYMO labelling tape produced by DYMO Esselte Pendaflex Corporation. These bands were attached around tree trunks using a spring and expand as the tree grows. The extent of girth expansion was measured on the tape using a micrometre.

Before the setting up of dendrometer in August 1999, data of structural attributes, soil water salinity, and tidal 88 inundation were measured during July 1999. Structural attributes in the form of species composition and height of tree 89 90 canopy were assessed to descript structural attributes of ecological mangrove communities at sample sites. Field 91 determination of the flora were confirmed by a range of systematic reviews (e.g. Ding Hou 1958; Tomlinson 1986; Noor et 92 al. 2006). The canopy height was measured directly by means of a long fixed stick for trees with height up to 5 m and, for taller trees, it was indirectly measured by using of a clinometer (SUNTO MC 1 Type). Surface soil sample were taken at 0 93 94 to 300 mm depth at five random points in every location, and soil water salinity was measured using a Hand-Held 95 Refractometer (Atago Master-S/Mill) of water samples of a known volume eluted through sediment samples. Level of tidal 96 inundation was observed at all sites during early neap-tide, full moon-tide and late neap-tide. A pole gage was used to 97 measure level of tidal inundation. Data of rainfall and temperature were based on the reports from Manado Meteorology 98 and Geo-Physic Office

99 In analysing the differences in stem growth rate by species and sites, the one-way analysis of variance (ANOVA) was applied. Regression Analysis was used to analyse the effect of rainfall and temperature on stem growth rate. The twelve sites that were regarded as having different environmental conditions and community attributes can be seen in Figure. 1 and these are summarised in Table. 1. **Commented [W9]:** the results of this study will then be used like what? Or what research can be done from the results of this study?

Commented [W10]: Does sea wave height affect the growth of mangroves? if yes, add data on tidal waves

Commented [W11]: Explain?

103

104

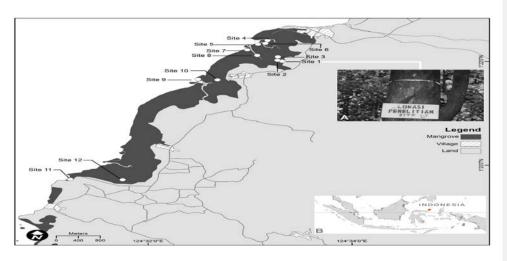


Figure 1. Locations of the twelve sites sampled at Southern Section of Bunaken National Park. Inserted Figure. 1A is dendrometer on trees number 3 at Site 1, inserted Figure. 1B is map of Indonesia with red dot indicating study location on Sulawesi Island and equator line across the Country

 Table 1. Description of the twelve sites sampled where four canopy trees in each site were selected for the measurement of stem growth

 rate: SD (Standard Deviation) of five random soil samples, tidal inundation frequency represented number of day month⁻¹ a site being

 inundated by seawater

Site	Species of Tree	Initial Tree	Average	Soil Water Salinity	Tidal Inundation
	Sampled	Girths (cm)	Height of	(average \pm SD, μ g L ⁻¹)	Frequency
	-		Canopy (m)		(%)
Site	1 A. marina	61.5 - 98.4	17	14.3 ± 0.47	< 13
Site	2 C. tagal	17.0 - 22.8	2.5	19.5 ± 0.00	13 – 22
Site	3 R. apiculata	16.0 & 18.5	4	19.0 ± 0.00	22 - 30
	C. tagal	21.4 & 30.0	4	19.0 ± 0.00	22 - 30
Site	4 R. apiculata	39.0 & 41.5			
	R. mucronata	22.5	6	14.0 ± 0.00	45 - 50
	B. gymnorrhiza	29.0			
Site	07	91.5 &			
	R. mucronata	104.5	8	14.0 ± 0.02	45 - 50
		30.0 & 40.0			
Site		93.5		18.0 ± 0.82	30 - 45
	B. gymnorrhiza	71.0	7		
	X. moluccensis	55.0	,		
	R. apiculata	15.0			
Site		34.0		18.0 ± 0.00	45 - 50
	S. alba	47.5	8		
	R. apiculata	47.5	0	1010 = 0100	10 00
Site	8 A. marina	118.0			
	B. parviflora	38.5	8	17.5 ± 0.21	30 - 45
	R. apiculata	53.5 & 59.5			
Site		72.5 & 88.0			
	S. alba	64.0 &	22	14.0 ± 0.00	45 - 50
		118.5			
Site	R. apiculata	102.0 &			
10	B. gymnorrhiza	105.0	22	19.7 ± 1.25	30 - 45
		90.0 & 96.0			
Site	C. tagal	50.0 -	12	6.5 ± 0.50	13 – 22
11		102.0	12	0.5 ± 0.50	13 - 22
Site	S. alba	129.5	27	13.3 ± 0.47	> 90

12	R. apiculata	79.0	
	R. mucronata	104.0	
	A. marina	99.0	

116

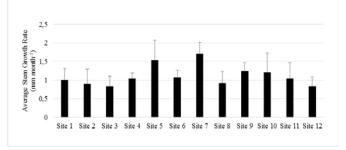
117

RESULTS AND DISCUSSION

118 Variation between sites

119 Figure 2 shows the stem growth rates at different sites. The result from the ANOVA statistical test suggested that the 120 differences in stem growth rate were significant between the twelve sites (F(11,324) = 5.848, p-value = 0.00, < 0.05). The highest growth rates were found in trees at Site 5 and 7 where increments were 1.53 ± 0.54 and 1.71 ± 0.31 mm month⁻¹ 121 122 respectively. At Site 1 the average stem growth rates varied in the range of 1.01 ± 0.30 mm month⁻¹. This range was 123 slightly lower comparing to that on sample trees at Site 4 of 1.05 ± 0.15 mm month⁻¹, Site 6 of 1.07 ± 0.19 mm month⁻¹ and Site 11 of 1.05 ± 0.42 mm month⁻¹. Slightly lower stem growth rates were measured on trees at Site 3, 12, 2, and Site 8 124 of 0.83 ± 0.27 , 0.84 ± 0.25 , 0.90 ± 0.39 , 0.92 ± 0.31 mm month⁻¹ respectively. Trees at Site 9 and 10 had average stem 125 growth rates which were comparable, measured at 1.24 ± 0.24 and 1.20 ± 0.53 mm month⁻¹ respectively. 126





Commented [W12]: move after the results on sites 5 and 7, the results are sorted from the highest to lowest sites

128 129

Figure 2. Average stem growth rates of tagged trees at various sites over 59 months. Error bars are standard deviations representing variability over 59 months
 132

Differing conditions at the study sites resulted in different growth rates of mangrove species. Results from this study 133 134 indicate that higher growth rates were measured at Site 5 and 7 (low intertidal environment) where soil water salinity was at intermediate level (14.0 \pm 0.02 µg L⁻¹ and 18.0 \pm 0.00 µg L⁻¹, respectively), and a relatively lower growth rate was 135 recorded for trees growing at Site 2 and 3 (high intertidal environment) where soil water salinity was relatively higher (19.5 \pm 0.00 µg L⁻¹ and 19.0 \pm 0.00 µg L⁻¹, respectively). The effect of soil water salinity on growth rate might be 136 137 138 inconsistent considering a relative lower growth rate at Site 8 and 12 where soil water salinity was at intermediate level 139 $(17.5 \pm 0.21$ and $13.3 \pm 0.47 \,\mu g \, L^{-1})$. This inconsistency was probably due to the existence of micro-topography in form of 140 the river levee at Site 8 and transgressed bedrock coast at Site 12. These micro-topography variations according to Thom 141 (1982) can cause varying physiological responses in different species and there may be more or less favourable plant 142 growth in a specific habitat due to the response of species to stress conditions.

Although soil water salinity was relatively higher ($19.7 \pm 1.25 \,\mu g \, L^{-1}$) at Site 10, growth rates of trees at this site were 143 measured at medium growth rate. This rate of growth was probably affected by tidal inundation frequency of this site that 144 145 was measured at 30 to 45% compared to 13 to 30% at Site 2 and 3. How trees of B. gymnorrhiza and R. apiculata respond 146 to specific conditions at Site 10 needs further investigation. The effect of salinity on mangrove growth has been reported 147 by various studies (e.g. Robert et al. 2009; Menesez et al. 2003; Nasim et al. 2013; Noor et al. 2015). In Pakistan, for example, Nasim et al. (2013) reported that the maximum growth rate of A. marina was presumably due to low salinity and 148 149 the minimum growth rate was related to higher salinity. Similar pattern was reported by Menesez et al. (2003) in the 150 mangroves from Braganca Peninsula, North Brazil. In mangrove forests, conditions of high salinity can cause osmotic 151 stress and reduce the availability of water, resulting in stomatal closure and reduced supply of carbon dioxide (Li et al. 152 2008). Furthermore, membrane disorganisation and disturbance of nutrient balance may be induced by salt stress 153 (Hasegawa et al. 2000).

154

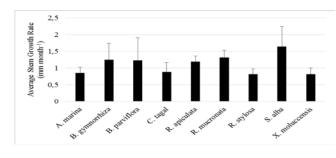
Commented [W13]: not in the library

Commented [W14]: how is the explanation for sites 1 (low Tidal Inundation Frequency) and 11 (low Soil Water Salinity)?

Commented [W15]: does this affect species diversity in a location?

155 Variation between species

Figure 3 shows the stem growth rate for nine species. The result from the ANOVA statistical test indicated that average 156 157 stem growth rate was significantly different between species (F(8,243) = 7.063, p-value = 0.00, < 0.05). A relatively highest growth was measured on S. alba (1.65 \pm 0.69 mm month⁻¹) and a relatively lowest growth on R. stylosa, X. 158 159 *moluccensis, A. marina, C. tagal*, measured at 0.82 ± 0.16 , 0.82 ± 0.18 , 0.85 ± 0.18 , 0.88 ± 0.28 mm month⁻¹ respectively. 160 A relatively medium growth rate was measured on R. apiculata, B. parviflora, B. gymnorrhiza, R. mucronata, measured at 161 1.19 ± 0.16 , 1.22 ± 0.69 , 1.25 ± 0.49 , 1.31 ± 0.22 mm month⁻¹, respectively. When the growth rates were expressed as a 162 percentage of the initial girth of each tagged tree, there was apparently higher stem growth rates on tagged trees of B. 163 gymnorrhiza, C. tagal and R. mucronata with an initial girth of more than 50 cm compared to trees with an initial girth of 164 less than 50 cm. Conversely, there was a relatively slower growth rate on tagged trees of R. apiculata and S. alba with an 165 original girth of more than 50 cm compared to trees with an initial girth of less than 50 cm. For other species, comparison 166 of growth rates between trees with an initial girth more than 50 cm and less than 50 cm was not evaluated because the 167 absence of comparable data.



168

Figure 3. Average stem growth rate of nine species over 59 months; error bars (Standard Deviations) represented variability over 59 months
 months

Table 2. Average stem growth rate (girth increment and as percentage of initial girth measured for nine species over 59 months); error
 bars (Standard Deviations) represented variability over 59 months, n represented number of tagged tree

Species	Stem Growth Rate as Percent Initial Girth in mm/month (mean ± SD)		
	< 50 cm	> 50 cm	
A. marina	-	$0.85 \pm 0.58 \ (n = 7)$	
B. gymnorrhiza	0.83 ± 0.55 (n = 1)	$1.33 \pm 1.05 \ (n = 5)$	
B. parviflora	1.22 ± 0.81 (n = 1)	-	
C. tagal	0.80 ± 0.59 (n = 8)	$1.21 \pm 0.76 \ (n = 2)$	
R. apiculata	1.37 ± 0.59 (n = 6)	0.96 ± 0.58 (n = 5)	
R. mucronata	$0.47 \pm 0.56 \ (n = 4)$	0.69 ± 0.59 (n = 1)	
R. stylosa	-	$0.85 \pm 0.48 \ (n = 2)$	
S. alba	$1.73 \pm 0.89 \ (n = 2)$	1.60 ± 0.92 (n = 3)	
X. moluccensis	-	0.82 ± 0.41 (n = 1)	

177

178 Results from this study confirmed that the nine mangrove species had different growth rate, and the growth rate 179 recorded in this study is different compared to those conducted elsewhere. For example, the annual diameter increment of 180 R. apiculata was 0.32 cm year⁻¹ in mature mangrove forests in Malaysia (Putz and Chan 1986) and 0.25 cm year⁻¹ in the mangrove forests in Micronesia (Devoe and Cole 1998) which were lower than the average growth rate by this species in 181 182 this study (0.45 cm/year). For *B. gymnorrhiza*, the annual growth increments were reported 0.35 cm year⁻¹ in Micronesia 183 which were relatively lower compared to the growth rate of this species in this study ($0.48 \text{ cm year}^{-1}$). The annual diameter 184 increments of S. alba were reported 0.49 cm year⁻¹ in the mangrove forests in Micronesia (Devoe and Cole 1998) which 185 were relatively lower compared to the growth rates of these species measured in this study (0.60 cm year⁻¹). Differences in 186 growth rate of similar species from different places explained the important role of local environment and climatic 187 condition to growth of mangrove species.

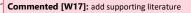
In this study, large trees of *B. gymnorrhiza*, *C. tagal*, *R. mucronata* grew faster than small trees. The case for trees of *B. gymnorrhiza* and *R. mucronata* might explain that trees of these species remained at vigorous growth. Meanwhile, the case for trees of *C. tagal* might be different. Small trees of this species were found dominant at site 2 and 3 where salinity is usually higher, and that trees are growing stunted at this condition. Sample of large trees of this species were found at Site

Commented [W16]: try to search data from previous research as a comparison?

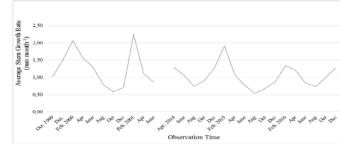
192	11 where soil water salinity was lower. Thus, in the case of	of C. tagal,	, differences in growth rate between small and large
193	trees were due to primarily soil water salinity.	-	

195 Seasonal variation

Figure 4 shows average stem growth rates of 48 tagged trees selected from 12 different sites. This figure shows that average stem growth rate started to increase in August or October over a year. This trend reached a maximum value in February at different levels with the highest level of 2.24 mm month⁻¹ in February 2001 and the lowest level of 1.33 mm month⁻¹ in February 2016. From February, stem growth rate decreased and reached minimum value around August and October at different levels ranging from 0.53 mm month⁻¹ in August 2015 to 0.74 mm month⁻¹ in August 2014. Between April 2015 and February 2016 there was abnormality in stem growth rate, During this period rates of average stem growth rates were apparently low.

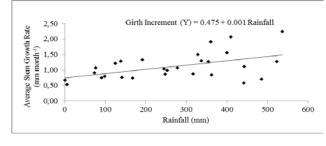


Commented [W18]: why was there a disconnection between June and April 2014



5 Figure 4. Temporal average stem growth rate over 59 months

A seasonal pattern in stem growth rates is very clear from data in Figure 4 and this is supported by the result from regression analyses, multiple and simple analyses. When two variables of rainfall and temperature were involved in the analysis the result confirmed that the regression model was significant (p-value < 0.05). Similar result was confirmed from simple regression with single variable of rainfall and temperature (p-value < 0.05). Figure 5 shows relationship between rainfall and stem growth rate. It is clear from this figure that rainfall positively correlated with stem growth. On the contrary, temperature negatively correlated with stem growth as shown in Figure 6.



18 Figure 5. Relation between rainfall and stem growth rate

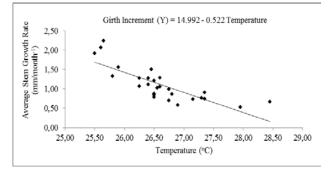


Figure 6. Relation between rainfall and stem growth rate

Previous studies indicated that growth rate in mangroves is seasonal (e.g. Jintana et al. 1985; Day 1990; Krauss et al. 2006). Field measurements indicated that growth rate is seasonal in study sites and this correlates positively with rainfall and negatively with temperature. Duke et al. (1981) also found that the growth of the tropical mangrove trees Diospyros was related to rainfall, producing 0.272 mm² growth increment per millimetre rain. This positive correlation between rainfall and growth rate was reported for Bruguiera and Rhizophora species in Thailand (Jintana et al. 1985) and for the mangroves in Laguna de Terminos, Mexico (Day 1990).

230 The effect of rainfall and temperature on intertidal environment where mangroves grew may be related to two factors; water availability and soil water salinity. Between these two factors, soil water salinity is assigned as the major seasonal variable causing wood anatomical changes and hence growth rings (Robert et al. 2009). In addition, Robert et al. (2011) in their study of the mangrove forest of Gazi Bay at the Kenyan coast confirmed that climatic conditions that result in a range of soil water salinity experienced over the year were a prerequisite for the formation of growth rings. The low growth rate 235 that was recorded between April 2015 and February 2016 corresponds with a dry season. The effect of the 2015/2016 El 236 Nino-Southern Oscillation (ENSO) resulted in reduced rainfall in the region with only 450.3 mm rainfall in total for eight months from March to October 2015. The most severe drought condition lasted for four months from July to October 2015 with only 13 mm rainfall in total.

239 Although, the volume of rainfall returned to normal by November 2015 measured at 337 mm month⁻¹, the effect of the 240 drought on low growth rate continued until February 2016. Drexler and Ewel (2001) studied the effect of the 1997-1998 241 ENSO related drought on hydrology and salinity in a Micronesian Wetland Complex. They found that mean salinity during 242 low tide was approximately twice as high during the drought, and short-term climate perturbations such as ENSO can 243 disrupt important coastal processes. Over repeated drought cycles, such perturbations have the potential to affect the 244 structure and function of mangrove forests. The effect of drought on mangroves can be related to the decrease of carbon 245 assimilation rate (Sobrado 1999), decrease of net photosynthetic rate and low water use efficiency (Sobrado 2006).

246 In conclusion, stem growth rates in mangrove trees growing at different habitats varied considerably, and the factor of 247 soil water salinity seemed to be the major cause of this variation at high intertidal environment. The higher stem growth 248 rate was measured on mangrove trees growing at low intertidal environment with low to medium soil water salinity and 249 higher tidal inundation frequency. Soil water salinity and growth rates relationship may not be significant in the existence 250 of micro-topography such as river levee and transgressed bedrock coast, and in the case at the middle intertidal 251 environment where trees of B. gymnorrhiza and R. apiculata were dominant in the canopy. The stem growth rates were 252 significantly different between the ten species observed with a relatively higher growth rate on S. alba, a medium growth 253 rate on R. apiculata, B. parviflora, B. gymnorrhiza, R. mucronata, and a low growth rate on R. stylosa, X. molucensis, A. 254 marina, C. tagal. Growth rates on trees with an original girth of more than 50 cm were higher on B. gymnorrhiza, C. tagal 255 and R. mucronata, but these were higher on trees with an original girth of less than 50 cm on R. apiculata and S. alba. 256 Growth rate patterns in observed mangroves were seasonal, and this pattern correlated positively to rainfall and negatively 257 to temperature. The effect of the 2015-2016 El Nino on reduced growth rates was significant on mangroves in the study 258 site

259

220 221 222

223 224

225

226

227

228 229

231

232 233

234

237 238

ACKNOWLEDGMENTS

This research was supported in part by Ausaid-ADS Program. It is a pleasure to thank Brama Djabar for site map 260 preparation, Kelola's staffs, Im and Mubin for field assistance, Professor Eugene Moll, Associate Professor David Lamb, 261 Jim Davie, Norm Duke for supervision of the early work. I also thank Kate Night for helpful edits and comments. 262

Commented [W19]: temperature

Commented [W20]: add literature about the effect of temperature on growth

Commented [W21]: ten or nine

REFERENCES

318 319

263

Clough BF. 1979. Mangrove ecosystem in Australia: structure, function and management. Proceedings of the Australian National Mangrove Workshop. Australian Institute of Marine Science, Cape Ferguson, 18-20 April 1979. Day RH. 1990. Growth rates of three species of mangroves bordering Laguna de Terminos, Campeche, Mexico. [Thesis]. The University of Texas,

Texas. Devoe NN, Cole TG. 1998. Growth and yield in mangrove forests of the Federal States of Micronesia. Forest Ecol Manag 103:33-48.

Ding Hou. 1958. Rhizophoraceae. Flora Malesiana, I(5):429-93.

Djamaluddin R. 2004. The dynamics of margrove forest in relation to die-back and human use in Bunaken National Park, North Sulawesi, Indonesia. [Dissertation]. University of Queensland, Brisbane.

Djamaluddin R. 2018. The mangrove flora and their physical habitat characteristics in Bunaken National Park, North Sulawesi, Indonesia. Biodiversitas 19(4):1303-1312

Drexler JZ, Ewel KC. 2001. Effect of the 1997-1998 ENSO-related drought on hydrology and salinity in a Micronesian Wetland Complex. Estuaries 24(3):347-356.

Duke NC, Botto MC, Ellison JC. 1998. Factors influencing biodiversity and distributional gradients in mangroves. Global. Ecol Biogeogr 7:27-47. Duke NC, 1992. Mangrove floristics and biogeography. In: Robertson AI, Alongi DM (eds). Coastal and Estuarine Studies. American Geophysical Union, Washington.

Duke NC, Birch WR, Williams WT. 1981. Growth rings and rainfall correlations in a mangrove tree of the genus Diospyros (Ebenaceae). Aust J Bot 29.135-142 Giesen W, Wulffraat S, Zieren M, Scholten L. 2006. Mangrove guide book for Southeast Asia. FAO and Wetlands International.

Gill AM. 1971. Endogenous control of growth ring development in Avicennia. For Sci 17:462–465. Hamilton SE, Casey D. 2016. Creation of a high spatio-temporal resolution global database of contin (CGMFC-21). Global Ecol. Biogeogr 25(6):729-738. is mangrove forest cover for the 21st century

Geord C. J., Global Bogeog 20(0):197130.
Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ. 2000. Plant cellular and molecular responses to high salinity. Ann Rev Plant Phys 51:463–499.
Jintana V, Komiyama A, Moriya H, Ogino K. 1985. Forest ecological studies of mangrove ecosystem in Ranong, Southern Thailand - 4. Diameter growth measurement by dendrometry. In: Studies on the mangrove ecosystem. Nodai Research Institute (ed), Tokyo University of Agriculture,

Kairo JG. 2001. Ecology and restoration of mangrove systems in Kenya. Ph.D Thesis, Vrije Universiteit Brussel, Belgium. Kathiresan K, Bingham BL. 2001. Biology of mangrove and mangrove ecosystem. Adv Mar Biol 40:81-251. Krauss KW, Keeland BD, Allen JA, Ewell KC, Johnson DJ. 2006. Effects of season, rainfall, and hydrogeomorphic setting on mangrove tree growth in

Micronesia, Biotropica 39(2):161-170.

Li N, Chen S, Zhou Z, Xy, Li C, Shao J, Wang R, Fritz E, Huttermann A, Polle A. 2008. Effect of NaCl on photo synthesis, salt accumulation and ion compartmentation in two mangrove species, *Kandelia candel* and *Bruguiera gymorrhiza*. Aquat Bot 88:303–310. Maxwell GS. 2015. Gaps in mangrove science. ISME/GLOMIS 13(5):18-38. Menezes M, Berger U, Worbes M. 2003. Annual growth rings and long-term growth patterns of mangrove trees from the Bragança peninsula, North

Brazil, Wetl Ecol Mang 11:33-242.

Nazim K, Ahmed M, Shaukat SS, Khani MU, Ali QM. 2013. Age and growth rate estimation of grey mangrove Avicennia Marina (Forsk.) Vier from Pakistan. Pakistan Journal Botany Pakistan J. Bot. 45(2):535-542.

Noor T, Batool N, Mazhar R, Ilyas N. 2015. Effects of siltation, temperature and salinity on mangrove plants. European Academic Research II(11):14172-14179. Noor YR, Khazali M, Suryadiputra INN. 2006. Mangrove introduction guide. Ditjen PPHKA-Wetland International, Bogor. [Indonesian]

Putz FE, Chan HT. 1986. Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. Forest Ecol Mana 17:211-230. Rajkaran A, Adams JB. 2008. The effect of sediment conditions on the growth rate of mangroves. S Afr J Bot 74(2):375-376.

Robert EMR, Schmitz N, Okello JA, Boeren I, Beechman H, Koedam N. 2011. Mangrove growth rings: fact or fiction. Trees 25:49-58. Robert EMR, Schmitz N, Kirauni HA, Koedam N. 2009. Salinity fluctuations in the mangrove forest of Gazi Bay, Kenya: lessons to take for future research. Nature and Fauna 24:89-95.

Sobrado MA. 1999. Drought effects on photosynthesis of the mangrove, Avicennia germinans, under contrasting salinities. Trees 13(3):125-130.

Sobrado MA. 2006. Deferential gas exchange responses to salinity and drought in the mangrove tree Avicennia germinans (Avicenniaceae). International Journal Tropical Biology 54(2):371-375.
Spalding MD, Blasco F, Field CD. 1997. World Mangrove Atlas. International Society for Mangrove Ecosystems, Okinawa.

Srikanth S, Lum SKY, and Chen Z. 2015. Mangrove root: adaptations and ecological importance. Tress 30(2):451-465. Suarez N, Sobrado MA, Medina E. 1998. Salinity effects on the leaf water relations components and ion accumulation patterns in Avicennia germinans (L.) seedlings. Oecologia 114:299-304.

Charles Decoupy and Constraints and Constra

Verheyden A, Kairo JT, Beeckman H, Koedam N. 2004. Growth rings, growth ring formation and age of mangrove *Rhizophora mucronata*. Ann Bot 94:59-66.

Commented [W22]: not in the script