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Mangroves and Crabs as Ecosystem Engineers in Zanzibar

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ABSTRACT

Primary productivity within mangroves results from detrital and coprophagous interactions on the forest floor. The feeding behaviors of Sesarmid crabs (Decapoda:Brachyura) alter the structural and chemical composition of benthic sediment through the consumption and incorporation of mangrove leaf-litter. In doing so they create habitats for organisms that in turn provide an additional food source for herbivorous crabs. Species specific herbivory was observed in order to understand the implications of Sesarmid activity on sediment composition. The study was conducted at two contrasting mangrove forest sites, one in a protected area at Jozani and the other in a disturbed area at Pete in Zanzibar, Tanzania. Equal quantities of leaves from three tree species (*Rhizophora mucronata*, *Bruguiera gymnorrhiza* and *Ceriops tagal*) were added to experimental plots. The level of herbivory for each leaf was observed and compared in order to assess the presence of dietary preference in Sesarmid crabs. Results indicate that crab herbivory is lower in community used Pete mangroves than at the protected site. Green leaves were fed upon more than senescent yellow leaves. There was a clear preference of crabs for mature green *R. mucronata* leaves. The results of preferential herbivory are then applied to the larger framework of mangrove restoration. The implications of leaf preference may be an invaluable component for future reforestation projects that aim to replant trees and restore ecosystem functionality as well.

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1.0 INTRODUCTION

Mangroves are intertidal tropical and subtropical forests composed of specially adapted facultative halophytes. With over 60 species worldwide (Macnae, 1968), mangroves provide essential habitats for both terrestrial and aquatic organisms. In addition to numerous socio-economic benefits, the ecosystem services mangroves provide make them among the most important coastal environments. The structural complexity of mangrove forests assists in shoreline stabilization (Bosire et al., 2003). In coastal communities timber is used for fuel, boats, and home construction. Mangroves contribute to the subsistence of local fisheries by acting as either a direct or indirect food sources and as a nursery for future catch. A number of studies have attempted to place a monetary value on coastal forests. For instance, Walton (2006) found that replanted Philippine mangroves provided 578-25678 kg ha⁻¹ yr⁻¹ (US\$463-2215 ha⁻¹ yr⁻¹) in fish catch. Increased awareness of mangrove influence has in recent years prompted escalated conservation efforts. Throughout the world, numerous rehabilitation studies have occurred with varying degrees of success (Kaly & Jones, 1998; Bosire et al., 2003, 2008; Kirui et al., 2007). While most researchers recognize that it is unrealistic for restoration to exact natural conditions, an approximation of the original system may be possible. Of utmost concern is the return of major ecosystem processes.

1.1 Conceptual Framework

Mangrove forest ecosystems cover an estimated 14.7 million ha of the world's tropical shorelines (Bosire et al. 2008), representing a decline from the reported 19.8 million ha in 1980. Anthropogenic factors are the leading cause for reductions in mangrove area. In response to the widespread degradation of the world's mangroves the number of studies focusing on these complex ecosystems has been steadily increasing for decades. Based in Florida, the classic works of Odum and Heald (Odum, 1971; Odum and Heald, 1974) focused on the influence of abiotic factors (tidal inundation, salinity, and sediment characteristics) as the primary drivers of ecosystem function. More recent work in the Western Indian Ocean (WIO) has encouraged a shift towards viewing benthic fauna as integral to forest structuring processes. Burrowing crabs of families Grapsidae and Ocypodidae (Decapoda: Brachyura) are the most widely researched mangrove macrofauna. Through the incorporation of leaves by burrowing and consumption, these crabs affect: nutrient retention, litter decomposition, mangrove colonization and zonation,

soil chemistry, and food web dynamics (Robertson and Daniel, 1989; Smith, 1991; Alongi, 1994; Woitchik et al., 1997; Lee, 1998; Skov and Hartnoll, 2002; Krauss et al., 2007).

Although some arboreal climbing species actively forage on tree leaves, the majority of herbivorous crabs rely on mangrove litter. In the WIO the main agents of continuous litter turnover are Sesarimid crabs (Graspididae) (Lee 1998). Most Sesarminae are either grazers or shredder detritivores dependent on mangrove biomass. Crabs forage continually on fallen leaves; either feeding directly or transporting them to burrows for later consumption. Studies throughout the Indo-Pacific region have documented varying, but usually substantial rates of litter removal by mangrove crabs (Steinke et al., 1993; Robertson and Daniels, 1989; Skov, 2001; Olafsson et al., 2002). Research from a variety of mangrove environments have shown that crabs are responsible for removing 30-90% of annual litter fall (Kristensen, 2008).

The assimilation of mangrove organic material by crabs is very low (<50 %) and most material consumed is egested as faecal matter (Lee, 1993; Nordhaus and Wolff, 2007). In his review of the Sesarminae, Lee (1998) recognized that through their involvement with detrital and coprophagous food chains, in conjunction with differential propagule consumption and bioturbation, Sesarimids can affect the growth and production of mangrove trees. The extensive contributions of mangrove crabs have led to their distinction as ecosystem engineers (Kristensen 2008). Jones et al. (1997) defines organisms as ecosystem engineers when they 'directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain, and/or create habitats.'

Mangrove crabs are *allogenic engineers* in that they are able to change the environment by transforming living material from one state to another via mechanical and other actions. Their active incorporation of leaf-litter ensures the retention of mangrove productivity within the ecosystem. Leaf incorporation maintains a rich and biogeochemically heterogenous sediment. By macerating and burrowing, crabs accelerate the microbial decay of leaves. Following consumption, egested fecal matter promotes bacterial and algal populations. Their burrows physically affect sediment topography and chemistry. Crab bioturbation significantly decreases ammonium and sulphide concentrations in mangrove soil, positively benefiting mangrove productivity (Nordhaus and Wolff, 2007). Burrows provide opportunities for the mixing of groundwater and overlying water resulting in the removal of salt from around roots and the

exchange of soil nutrients. Through their comprehensive involvement with ecosystem functioning burrowing crabs are a fundamental component of mangrove forests in the WIO.

1.2 Status of Mangrove Restoration Projects

Kirui et al. (2007) recognized that mangrove reforestation projects often suffer from low sapling survival, especially after transplanting saplings from nurseries to reforestation areas. This may be due to the sediment conditions at the target site, the planting strategy, or failure to reestablish ecosystem functions. Bosire et al. (2008) defines functionality as the ability of restored mangroves to process nutrients and organic matter, trap sediments, provide food and habitat for animals, protect shorelines, provide plant products and a scenic environment, in a similar fashion to natural mangrove forests. Considering the direct and indirect forces Sesamid crabs are capable of exerting, it is apparent that their role must be incorporated into future restoration efforts. An increased understanding of mangrove crab feeding ecology will assist in devising natural reforestation regimes.

In the present study, working in an East African mangrove ecosystem, I attempted to evaluate the potential impacts of species-specific foraging by Sesamid crabs and the effects of litter retention and incorporation on generating favorable sediment. This study intended to determine:

- (i) the existence of preferential feeding within the leaf litter layer
- (ii) the mangrove characteristics that may influence dietary specialization
- (iii) the implications that leaf predilection may have for reestablishing functional mangrove ecosystems.

2.0 STUDY AREA

The Zanzibar archipelago is situated 40 km off the coast of Tanzania about 6° south of the equator. According to the 2002 national census 984,625 people live on Zanzibar's two small islands Unguja and Pemba (1,666 km² and 988 km² respectively). Zanzibar is characterized by a tropical climate with 1500 mm annual rainfall on average and temperature extremes from 24° to 28° C (Silima et al., 2009).



Mangrove forests comprise 197 km² (7.4%) of Zanzibar's 2650 km², with the largest mangrove ecosystem found around Chwaka, Makoba and Menai Bay in the Pete region of Unguja and in the Northeast coast of Pemba (Francis and Bryccesson, 2001). Of the reported 20,000 ha of mangrove forest on Zanzibar, approximately 14,000 hectares (70%) are found on Pemba and 6,000 hectares (30%) on Unguja. They make up the second largest forest ecosystem after coral rag.

Both study sites, Jozani and Pete, are found near the Menai Bay in Unguja (Appendix 1). Located about 40 km south east of Zanzibar Town the area is part of the Pete-Jozani shehia. In their terrestrial survey Leskinen et al. (1997) identified nine species of mangrove in Zanzibar: *R. mucronata*, *B. gymnorrhiza*, *C. tagal*, *X. granatum*, *H. littoralis*, *A. marina*, *L. racemosa* and *S. alba*. In the Menai Bay the most common species are *R. mucronata* (20% relative dominance), *B. gymnorrhiza* (29% relative dominance), *C. tagal* (42% relative dominance) (Othman, 2005). The local communities of Pete have traditionally relied on subsistence agriculture and the harvesting of natural resources, especially timber from nearby terrestrial ecosystem for fuel and construction materials.

In terms of the faunal composition, the crabs are the most conspicuous invertebrates of the mangroves of Tanzania. The upper zone is often inhabited by marsh crabs (*Sesarma*). In the Ceriops and Bruguiera zone, *Uca spp* (the fiddler crabs) are the most dominant. The creeks are inhabited by *Uca* and *Scylla serrata*. On sandy portions soldier crabs (*Dotilla spp*) are common and *Dotilla fenestrata* is reported to be restricted to the East African coast (Semesi, 1992).

2.1 JCBNP Protected Mangrove

The Jozani Chwaka Bay National Park (JCBNP) is the first and only national park in Zanzibar, Tanzania. Covering over 50 km², the forest is home to a number of plant and animal species. Following the revision of the forest policy in 1995 a proportion of the land traditionally used by Pete residents was transferred into a conservation area and tourism site. Adjacent to the parks entrance, a 1 km road leads to the JCBNP managed mangrove forest. A large stream passes through the woods and at spring high tides the entire area is entirely submerged. The sediment is a neutral dark black mud (pH 7.06) containing fine particulates and, upon close inspection, an abundance of petiole remnants. A single boardwalk passes through the dense woods. As it is one of the parks major attractions for ecotourism, this patch of mangrove forest is protected from any form of timber harvest, fishing or other form of extraction. As a result the area is host to an array of fish, bird, and mangrove species. Numerous mature trees of *C. tagal*, *B. gymnorhiza*, and *R. mucronata* are found in relatively equal distributions. Conservation efforts at Jozani have helped maintain what is becoming a rare example of an undisturbed mangrove forest.

2.2 Pete Disturbed Mangrove

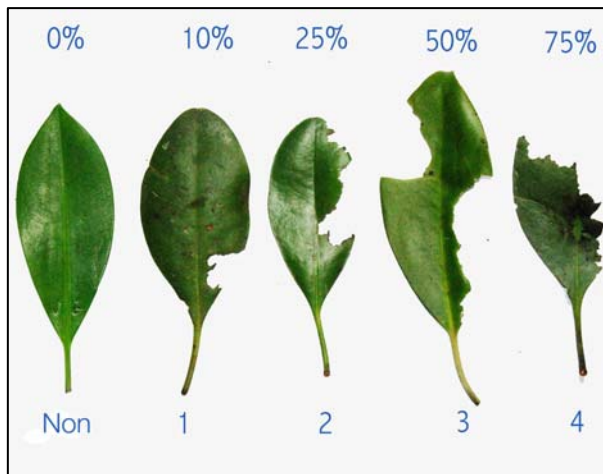
The second site is an area of intense deforestation. Outside the JCBNP protected area more than 80% of the Pete mangroves shows signs of overharvesting, with stump densities averaging 2241 per ha (Othman, 2005). The second experimental area is situated near the Jozani mangrove but varies considerably in its ecological composition due to intense deforestation. The area is dominated almost exclusively by young *R. mucronata* trees about 4-5 m tall. There are numerous stumps and no mature adult trees. Around the periphery of the forest exist few young *B. gymnorhiza* and *C. tagal* trees and seedlings. Snaking through this young woods are numerous shallow tidal streams. The sediment is a neutral silty mud (pH 6.82) with a hard base of clay ~8 cm beneath the surface. There are *C. tagal* reforestation efforts interspersed within the forest. Small grids of 15-25 seedlings <1 m tall recently planted by local community members. *Cerriops tagal* is frequently utilized for its hard wood and quality charcoal. This may explain the cause for its removal and subsequent replanting.

3.0 METHODS

3.1 Study System

Selective herbivory was observed at both sites. At the undisturbed JCBNP mangrove two 50 m transects were founded 25 m from the visitor boardwalk. The transects were spaced 25 m apart and oriented perpendicular to the coast (120° Magnetic N). Along each, five 1 m² quadrats were established every 10 m. An additional observational transect with ten 1 m² quadrats every 5 m was laid out (oriented 40° N) to record burrow frequencies and sesarmid behavior. An identical experimental system was constructed at the disturbed Pete mangrove. Approximately 25 m from the habitat edge the first 50 m transect was founded with the second ~10 m away. In accordance with the JCBNP site, both transects at Pete were oriented to 120° N with five quadrats every 10 m along their length. Again a 50 m observational transect was established.

To record incidences of preferential feeding specific quantities of leaves from three mangrove species were added along the trial transects. Prior to trial periods all previous litter fall was removed. To each quadrat 10 new leaves (half senescent yellow leaves and half mature green leaves) of *B. gymnorrhiza*, *C. tagal*, and *R. mucronata* were introduced. After four hours the extent of herbivory was scored for each group of 30 leaves. Based on previously collected



leaf samples, I devised the following scale: None to immeasurable consumption: Non; 10% or less consumed: Level I; 25% consumed: Level II; 50% consumed: Level III; 75% consumed: Level IV. Leaves in which only the petiole remains or are completely absent (assumed burial): Level V. The percent of herbivory was photographed for individual leaves to allow post trial comparisons.

3.2 Feeding Trials

To understand behavioral characteristics of resident crab populations 15 minute observational surveys were conducted. The number of burrows was recorded for each plot. Ten

minutes were allowed for disturbed crabs to reemerge from their burrows. The activities of present crabs were recorded. Following field observations crabs were identified taxonomically.

Feeding experiments started 6 November 2009. Sesarmid crabs retreat to their burrows during tidal inundation thus leaf removal does not occur at high tide; all work was therefore conducted at low tide. Trials at JCBNP protected mangrove occurred from 7-11 November 2009. During high neap tides (8-14 November) the forest floor remained above water. Trials at the Pete disturbed mangrove occurred from 13-17 November 2009. Some quadrats were located on streambeds that remained flooded during high spring tides (15-21 November); measurements of herbivory were unavailable for these plots. Preceding the experimental periods all cordon and ribbon was removed from study areas.

The results for over 2500 leaves were compiled and assessed for indications of preferential herbivory.

4.0 RESULTS

4.1 Field Observations

Crabs had carapace widths ranging from <10 mm to ~ 50 mm. Based on eye position, cheliped morphology and coloration observed members of the sub-family Sesarminae (Grapsidae) were identified as *Sesarma guttatum* (A. Milne Edwards). Sesarmids were distinguishable by their dark purple to brown claws in which both the immobile part (propodus) and mobile part (dactylus) had ridges (tubercles) and were colored bright red-orange. Ocyopodids were easily identifiable as *Uca* spp. (fiddler crabs) by the prominent, brightly-colored cheliped of sexually dimorphic males. Both crab families were omnipresent in the study areas but occupied different habitats. Sesarmids are common in wet and muddy areas with sufficient canopy cover. The Ocyopodids are often observed in areas with little canopy cover and firm, dry sandy or clay soil. Fiddler crabs are not involved in leaf litter consumption; most time is spent reinforcing territorial boundaries through characteristic displays (Bisang, 2009 unpub. dat.).

The feeding ecology of Sesarmid crabs was observed. Most time was spent foraging on microfauna within the sediment. As crabs moved throughout territories they would continually glean organic material from the soil surface with their chelae. Leaf herbivory was observed

within the experimental plots. Crabs would typically approach the leaf near the petiole. One cheliped would grasp the leaf while the other was used to tear off <1 mm sections of the leaf. This motion was repeated with the grasping claw and feeding claw alternating. Leaves were also the subjects of territoriality. Smaller crabs were usually deterred if the encroaching crab was larger in size. In some instances Sesarmids would pick the leaves up and carry them to their burrows to avoid confrontational encounters.

4.2 Assessing Preferential Feeding by Leaf Damage

Sampling from across species showed that exactly 12% (n =334) of 2790 added leaves had quantities of consumption ranging from level I (10% herbivory) to level V (leaf absent). No leaves exhibited 100% herbivory; Level V leaves were absent from experimental plots due to crab activity or other abiotic factors.

Leaves with observable quantities of consumption (n =252) were recorded. Incidences of herbivory in both sites were greatest for mature green *R. mucronata* (RM) leaves (n =145). Senescent leaf herbivory was greatest with *B. gymnorrhiza* leaves (n =32). Senescent leaves from *C. tagal* exhibited no herbivory (Table 1).

Table 1. Comparative number of consumed leaves for each species at the two study sites of Jozani and Pete, Zanzibar, Tanzania.

Site	Species					
	<i>C. tagal</i>		<i>R. mucronata</i>		<i>B. gymnorrhiza</i>	
	Green	Senescent	Green	Senescent	Green	Senescent
Jozani	16	0	121	9	33	28
Pete	4	0	24	7	6	4
TOTAL	20	0	145	16	39	32

The general herbivory (senescent and mature) was assessed for both study sites (Figure 1). At the Jozani study site 94% of added *C. tagal* leaves, 70% of added *R. mucronata* leaves and 83% of added *B. gymnorrhiza* leaves exhibited no signs of herbivory. At the Pete site 98% of added *C. tagal* leaves, 91% of added *R. mucronata* leaves and 95% of added *B. gymnorrhiza* leaves exhibited no signs of herbivory. Percentage of leaves with no herbivory was less at Jozani.

Observable herbivory was greatest at level I. At Jozani 2% of added *C. tagal* leaves, 17% of added *R. mucronata* leaves and 9% of added *B. gymnorrhiza* leaves exhibited levels of herbivory in which 10% of their area was lost. At Pete Level I was also the most represented herbivory level, albeit with lower percentages; 1% of added *C. tagal* leaves, 6% of added *R. mucronata* leaves and 2% of added *B. gymnorrhiza* leaves exhibited levels of herbivory in which 10% of their area was lost.

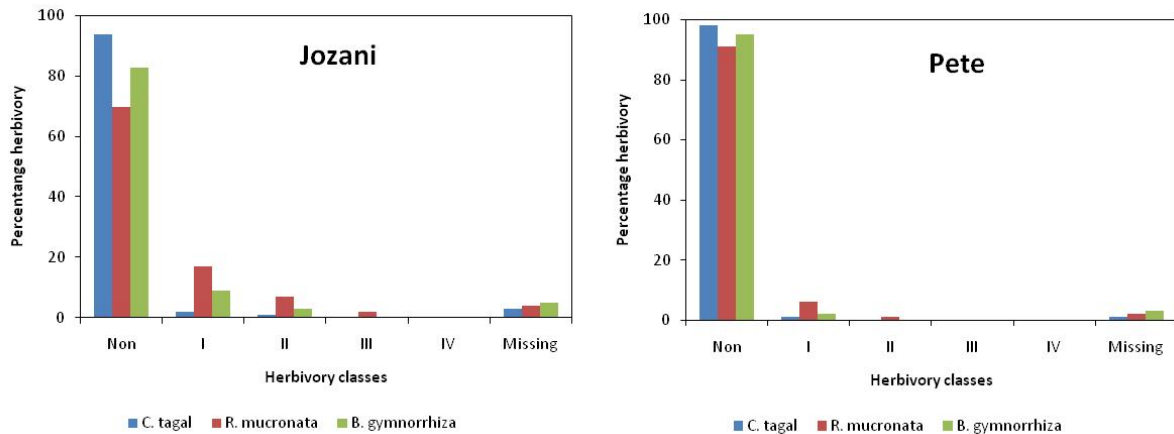


Figure 1. Overall percentage levels of mangrove leaf herbivory by crabs at the two sites of Jozani and Pete, Zanzibar, Tanzania. Roman numbers I – IV, non and missing categories represent herbivory classes as described in the methods (para 2).

The amount of selective herbivory (either mature or yellow) was assessed for both study sites (Table 2). In both study sites green leaves experienced more herbivory than senescent leaves. Approximately 81% of green leaves showed no signs of crab activity. Whereas, 96% of senescent leaves showed no signs of herbivory. The highest percentage of herbivory was observed in *R. mucronata* leaves at Jozani; more than half the leaves showed signs of crab activity. There were no instances of observable herbivory on the senescent leaves of *C. tagal* in either study site. Again, the most the observed leaves had 10% of their area lost (Level I).

Table 2. Comparative percentages of selective herbivory on leaves of three mangrove species at the two sites of Jozani and Pete, Zanzibar Tanzania. Roman numbers I – IV, non and missing categories represent herbivory classes as described in the methods (para 2).

Site	Leaf type	Species	Percentage herbivory					
			non	I	II	III	IV	Missing
Jozani	green	<i>C. tagal</i>	90	5	1	0	0	4
		<i>R. mucronata</i>	44	32	12	3	2	7
		<i>B. gymnorrhiza</i>	82	9	4	0	0	5
	senescent	<i>C. tagal</i>	98	0	0	0	0	2
		<i>R. mucronata</i>	95	2	2	0	0	1
		<i>B. gymnorrhiza</i>	85	8	3	0	0	4
Pete	green	<i>C. tagal</i>	96	2	0	0	0	2
		<i>R. mucronata</i>	86	9	1	0	0	4
		<i>B. gymnorrhiza</i>	93	3	0	0	0	4
	senescent	<i>C. tagal</i>	100	0	0	0	0	0
		<i>R. mucronata</i>	97	3	0	0	0	0
		<i>B. gymnorrhiza</i>	96	2	0	0	0	2

The total levels of consumption were added for each study site. Incidences of herbivory were greatest for mature green *R. mucronata* leaves. All levels of consumption were observed, with 10% herbivory most frequently represented (68%, n =98), followed by 25% herbivory (24%, n =35), 50% herbivory (5%, n =7), and 75% herbivory (3%, n =5). Incidences of herbivory in both sites for mature *B. gymnorrhiza* leaves were less (n = 39). All levels of consumption were observed, with 10% herbivory most frequently represented (66%, n =26), followed by 25% herbivory (26%, n =10), 50% herbivory (5%, n =2), and 75% herbivory (3%, n =1). The fewest incidences of herbivory were observed on green *C. tagal* leaves (n =20). Consumption levels of 10% (75%, n =15), 25 % (20%, n =4) and 75% (5%, n =1) were observed.

5.0 DISCUSSION

5.1 Differences in Herbivory Between Sites

Consumption levels were lower at the disturbed Pete forest (Table 1 & Figure 1). Approximately 95% of all experimentally added leaves, both senescent and mature, showed no signs of herbivory. The Pete trials took place during neap tides. Some plots remained inundated for the entire trial period and were thus devoid of foraging. The inundation of the study area may

also have affected the timing of crab emergence, resulting in less time for litter foraging. The ecological composition of the disturbed mangrove likely also influenced feeding activity. One of the most evident differences between study sites was the prevalence of canopy gaps in the disturbed forest. Insolation, exposure to the sun's rays, has been shown to alter soil chemistry and faunal composition (Kirui et al. 2007). Half of the experimental plots fell within these unshaded gap areas. The gaps at Pete tended to have more sandy soil and were dominated by *Uca* spp. By contrast, those areas with dense stands of young *R. mucronata* trees possessed dark mud and Sesarmid populations. However, due to the altered environmental conditions Sesarmid densities were much lower at Pete (Bisang, 2009, unpub. dat.). Impoverished crab densities due to altered forest conditions offer an explanation for reduced level of consumption.

Although, fewer leaves were consumed at Pete *R. mucronata* was still preferred over *C. tagal* and *B. gymnorrhiza*. Previous studies believed that herbivore preference may be influenced by the most abundant trees species. The species dominance hypothesis has shown not to be in effect in mangroves (Lee, 1998). There are other reasons explaining observed preferential feeding.

5.2 Preferential Herbivory

The reasons for leaf herbivory have remained the subject of much study (Skov & Hartnoll, 2002; Erickson et al., 2003; Thongtham & Kristensen, 2005; Nordhaus & Wolff, 2007; Chen & Ye, 2008; Ya et al., 2008; Thongtham et al., 2007; Imgraben & Dittman, 2008). Although mangrove biomass is a major component of Sesarmid diets, it has relatively low nutritional value. The leaves of many species have concentrations of polyphenolic compounds such as tannins and high C:N ratios, up to ~100 in some species. In order for an invertebrate to maintain growth, carbon to nitrogen ratios of consumed materials must not exceed the Russel-Hunter index of 17:1 (Russel-Hunter, 1970). Leaf palatability is also age dependent, mature green leaves usually contain more nitrogen than senescent yellow leaves. Thongtham and Kristensen (2005) determined that *Neosemartium versicolor* crabs fed discriminately on leaves at different stages of decomposition. They found that senescent *Rhizophora apiculata* leaves (C:N =123) had the lowest levels of consumption. The nitrogen rich green leaves (C:N =50) were consumed less than brown decaying leaves (C:N =83) but more than yellow leaves. Yellow leaves just fallen from trees are poor in nitrogen and rich in tannins. The higher palatability of

brown leaves compared with green and, in particular, yellow leaves probably results from improved nutritional value and removal of inhibitory compounds by the aging process. Although decomposed leaves were not used in the present study, green leaves exhibited greater herbivory than yellow leaves (Table 2). Approximately 96% of senescent leaves added to both study areas showed no signs of herbivory. In both study areas senescent leaves of *C. tagal* were never observed with consumption damage. By contrast, green *R. mucronata* leaves had the highest percentage of leaves with observable herbivory.

Senescent *B. gymnorrhiza* leaves experienced more incidences of herbivory than senescent leaves of the other two study species (Table 1, 2). Skov and Hartnoll (2002) found that senescent *B. gymnorrhiza*, *R. mucronata*, and *C. tagal* leaves had C:N ratios of 74, 109, and 184 respectively. In the present study incidences of senescent consumption parallel these C:N values. More senescent *B. gymnorrhiza* leaves were eaten than any other senescent leaf species. The carbon content for *C. tagal* leaves are more than 10x greater than the Russel-Hunter value, this may explain why herbivory on these leaves was completely absent. They are not nutritionally justifiable.

Nitrogen content is not the only component determining leaf palatability. Chen & Ye (2008) found that other factors influencing leaf palatability include: tannins, crude fibers, and water content. In their study the authors found that, in addition to C:N ratios, crude fiber content was negatively correlated with species specific feeding of mature green leaves. The high herbivory rates for aged leaves are ascribed to decreased tannin content and increased water content. Similarly, Emmerson and Ndeze (2007) found that water content may explain differential consumption rates in their species preference experiments. The arboreal sesarimid *Parasesarma leptosoma* grazed extensively on *R. mucronata*, marginally on *B. gymnorrhiza* and not at all on *A. marina*. The water content of grazed species was higher than in *A. marina*. These authors identified differences in leaf physiology as possible factors determining leaf palatability. Both *R. mucronata* and *B. gymnorrhiza* are salt excluders and release salt through their roots. *Avicennia marina* is a salt secretor and regulates internal sodium levels by expelling salt through pores in the leaves. The leaves of the salt excluders were also found to be thicker and more succulent, whereas *A. marina* leaves are small and tough.

These findings may help elucidate the reasons behind preferential herbivory observed in the present study. The mangroves leaves used to examine herbivory are analogous to the species

of Emmerson and Ndeze (2007). Not only are *C. tagal* leaves small and leathery, but like *A. marina*, it is a salt secretor as well. Low water content and high salinity may explain the lack of herbivory observed in the leaves of *C. tagal*. Moreover, tree-climbing crabs were found grazing more often on *R. mucronata* than *B. gymnorrhiza* trees. This may be explained by higher total nitrogen for *R. mucronata* (3.1% per leaf) than *B. gymnorrhiza* (2.95% per leaf) (Emmerson & Ndeze, 2007). Erickson et al. (2003) found that the *Rhizophora* congener *R. mangle* was preferred over *Avicennia germinans*, and *Laguncularia racemosa* in American mangrove forests. The corresponding results from Pete and JCBNP mangroves fit previous studies in which *Rhizophora* spp. were found to be subjects of selective consumption. Green *R. mucronata* leaves were fed upon more than any other leaf category (Figure 1; Table 1, 2). Almost half (49%) of the experimentally added green *R. mucronata* leaves at Jozani showed signs of crab herbivory. Amount of consumed material is also greater for *R. mucronata* (Table 2). Data from both sites shows that 13% of added leaves experienced Level II consumption (Figure 1). Even though crab activity was less at Pete, 10% of green *R. mucronata* leaves observed had visible crab damage.

5.3 Alternative Sources of Sustenance

The research on mangrove crab feeding ecology is unequivocal; the litter layer is a major food source for many Sesarmids and Ocypodids. Yet most studies have concluded that mangrove leaves are of low nutritive value due to a disproportionately high C:N ratio. Crabs do not rely completely on leaf litter as a food source. In the present study observed crabs spent more time foraging on unseen particles in the sediment than consuming experimentally added leaves. Field studies in Zanzibar report that in 76% of *Neosemartium meinerti* observations and in 66% of *S. guttatum* observations crabs were engaged in sediment feeding activities (Skov and Hartnoll, 2002). Similarly, Ya et al. (2008) found that in Singapore *Perisesarma eumolpe* and *P. indiarum* spent more time grazing than feeding on mangrove leaves. Crabs egest only 60% of consumed leaf litter and faeces tend to have lower C:N ratios than leaves. It was therefore hypothesized that crabs may feed on mud enriched by decaying mangrove faecal matter (Lee, 1993). Instead, research has shown that in order to fulfill nitrogen requirements crabs likely feed on meiofauna found within the sediment. Bacteria, microalgae, epifauna and animal remains scraped from the top few millimeters of sediment likely provide supplemental nitrogen for Mangrove crabs (Lee, 1998). Gut analyses of Sesarmid crabs have found remnants of small

microinvertebrates (I.E. planktonic organisms, larvae, amphipods), parts of fish and other crustaceans (Erickson et al., 2003; Thongtham & Kristensen, 2005). At the JCBNP site a dark green covering of algae was often seen covering piles of crab pellets. Algae has 10x higher nitrogen content (C:N 7-10) than mangrove litter (C:N 30-100) and therefore may make up a major source of N for mangrove ecosystems (Nordhaus & Wolff, 2007; Kristensen, 2008). The digestion processes of crabs can change the physical and chemical conditions of mangrove leaf litter. These changes enhance the nutritional qualities of faecal matter and promote coprophagous benthic invertebrates and microphytobenthos (Cannicci et al, 2007). Though faeces may not contribute directly to crab nutrition, the continuous egestion of leaf matter promotes coprophagous food chains and habitats within the sediment that may supply mangrove crabs with other sources of sustenance.

5.4 Sediment Composition and Sesarmid Crabs

Mangrove sediment is at once the provider and product of crab consumption. Through the retention and integration of leaf litter a structurally heterogenous sediment is generated that is both habitat and source of trophic interaction. Bacteria populations are ~70x more abundant in sediments with crab faecal matter (Cannicci et al., 2007). These bacteria are primarily responsible for the degradation of leaf litter. The brown decaying leaves preferred by mangrove crabs are the product of such microbial decomposition. Haphazard litter handling, resulting in microscopic leaf fragments, provides an ideal substrate for additional microbial colonization. In the present study 24% of consumed leaves were absent. Leaf burial ensures the incorporation of nutrients into mangrove soil and as the leaf ages microbial activity is promoted. Crab burrows also influence sediment quality by assisting in gas and solute exchange. The burrows of Sesarmids are labyrinthine cavities capable of increasing soil surface area by 150-380% (Kristensen, 2008). Excavated soil has increased aeration and allows water to percolate through the sediment thus permitting chemical exchange. Litter consumption contributes to the formation of soil habitats that, through detrital trophic processes and bioturbation, sustain the source of litter productivity. Moreover, mangrove crabs create a structurally and chemically heterogenous habitat by making leaf material available to benthic organisms through maceration, digestion, and burial.

5.5 Implications for Reforestation Regimes

The ecosystem effects of Sesarmids must not be overlooked when considering mangrove conservation. In Tanzania, over 20% of the population lives within the coastal regions (Silima et al., 2008). The mangrove ecosystems in these areas are subject to increasing pressure from human activities. The indiscriminate cutting of mangroves for fuel, timber and other uses has decimated natural stands surrounding many coastal communities. Mangrove extraction can result in physical and biological changes to a site, such as increased sediment salinity, high insolation, loss of nutrients and disruption of critical species interactions. An objective driving mangrove reforestation efforts is wood production for timber, poles, and fuel. Most mangrove reforestation projects have involved planting single species that are of higher cash-crop value, culturally significant and/or are easier to plant (Kirui et al., 2007). Restoration efforts tend to focus on silviculture, that is the processes of establishing and growing of trees, and overlook the implications of disrupted species interactions. As a result replanted forests often suffer from incomplete ecosystem functioning.

In the Pete region *Ceriops tagal* are the most cut species comprising 48.2% of all observed stumps (Othman, 2005). Throughout Zanzibar this species is targeted for harvesting because of its strong wood and good fuel production. At the Pete study site, replanting *C. tagal* was happening on a minor scale. Most seedlings were found on silty-clay mud in open areas; and none measured more than 1 m in height. Although this species is socio-economically important, in light of the present findings concerning selective litter herbivory and the related soil generating processes *C. tagal* may not be the most appropriate candidate for replanting if restoring ecosystem functionality is intended.

The findings of the present study may aid in the construction of holistic reforestation regimes. The majority of biological activity in mangroves occurs at the benthic level. The detritivory of Sesarmids, and those organisms supported by crab activity, drive the formation of a highly productive sediment. Establishing these fundamental species interactions is therefore necessary for the creation of a viable soil capable of supporting both trees and attendant organisms. Incorporating an understanding of preferential feeding ecology into restoration projects may assist in promoting the succession of absent Sesarmids and the return of contingent ecosystem functions.

By planting preferred mangrove species it may be possible to reinforce Sesarmid

recolonization. Stands of *R. mucronata* are likely to engender healthy crab populations for a number of reasons. Literature has shown that *Rhizophora* spp. are palatable due to their water content, lack of crude fiber, and, relative to *C. tagal* and *B. gymnorrhiza*, superior total C:N content. Possibly of greater significance when considering palatability is the decreased salt levels found in *R. mucronata* leaves. This factor may also play an important role in sediment generation. Preferential feeding would entail greater incorporation, and therefore higher proportion of *R. mucronata* material in the soil. Kirui et al. (2007) found that in Kenya soil salinity was negatively correlated with sapling establishment and survival. If leaves of the salt excluder *R. mucronata* are the primary component of the benthic substrate, as opposed to a salt rich *C. tagal* leaves, propagule succession may be favored. Additionally, *R. mucronata* leaves not subject to any crab herbivory may contribute to the formation of soil more than other sampled species. Woitchik et al. (1997) found that over decomposition periods of 50 days during the rainy season in Kenya *R. mucronata* leaves lost 98% of their mass, whereas *C. tagal* lost 69% mass. Even without the modifying influence of Sesarmids, *R. mucronata* detritus will aid in the recovery of functional sediment.

The contributions of *B. gymnorrhiza* litter should not be overlooked. Within the senescent leaves observed, these leaves were fed on more than the other two test species. Much of the litter in the Jozani study site was senescent *B. gymnorrhiza* leaves. It should be noted that young trees and seedlings are likely produce less senescent leaves, and so their ability to supply matter for soil generation will not occur until later in their life cycle. Nevertheless, *R. mucronata* and *B. gymnorrhiza* are the candidate species best suited to produce litter material that is selectively fed upon and therefore prone to the formation of favorable benthic conditions. Utilizing the findings on selective feeding offered here it becomes possible to construct reforestation schemes that promote the recolonization of crabs, and the subsequent reinstatement of their engineering effects.

6.0 CONCLUSION

This study has shown that crab activity, as measured by their herbivory on leaves, is less in the disturbed mangroves of Pete. The amount of leaf material consumed was dependent on the leaf age and leaf species. Crabs fed less on senescent yellow leaves than green leaves. There is an apparent preference of Sesarmid crabs for the green leaves of *R. mucronata*. Future

reforestation efforts may want to consider this species as a primary candidate for reinforcing crab populations. The predilection of Sesarmids for *R. mucronata* leaves may be exploited to accelerate the generation of favorable sediment capable of supporting benthic communities and corresponding mangrove species. Together these elements may facilitate the approach of this vital ecosystem to natural conditions.

7.0 RECOMMENDATIONS

It may be interesting to focus directly on soil characteristics within the mangrove. Comparing the carbon and nitrogen quotients in areas with different levels of disturbance may shed light on litter processing dynamics. By comparing carbon signatures of the different leaves it may be possible to determine which mangroves species contribute more to sediment composition and quality. Doing laboratory experiments that show decreased salinity levels in *R. mucronata* or *B. gymnorrhiza* (the excluders) based soil versus *C. tagal* and *A. marina* (the secretors) based soil would elucidate the affects specific trees have on their sediment. Certainly more work could be done on the feeding ecology of Sesarmid crabs. Although not statistically significant, crabs seemed to eat more during spring tides. This may be due to daily tidal flow creating a feeding impetus. However, during field observations I noticed that during neap tides, when the Jozani area did not become inundated, sediment algal cover became more noticeable. Whether or not there was more due to long exposure, I don't know. But a surfeit of algae may affect how heavily crabs feed on the litter layer. Based on the findings presented here and the voluminous literature on mangrove ecology it may be possible to develop site-specific reforestation regimes. Before even considering replanting trees with feeding preference in mind it is first necessary to evaluate the site. Considerations of tidal regimes, salinity, zonation and coastal activity will all play vital roles in determining proper areas for reforestation. Then one can worry about which trees to plant to reinforce crab populations. Further work evaluating optimal sites for reinstating crab-based ecosystems would be ideal.

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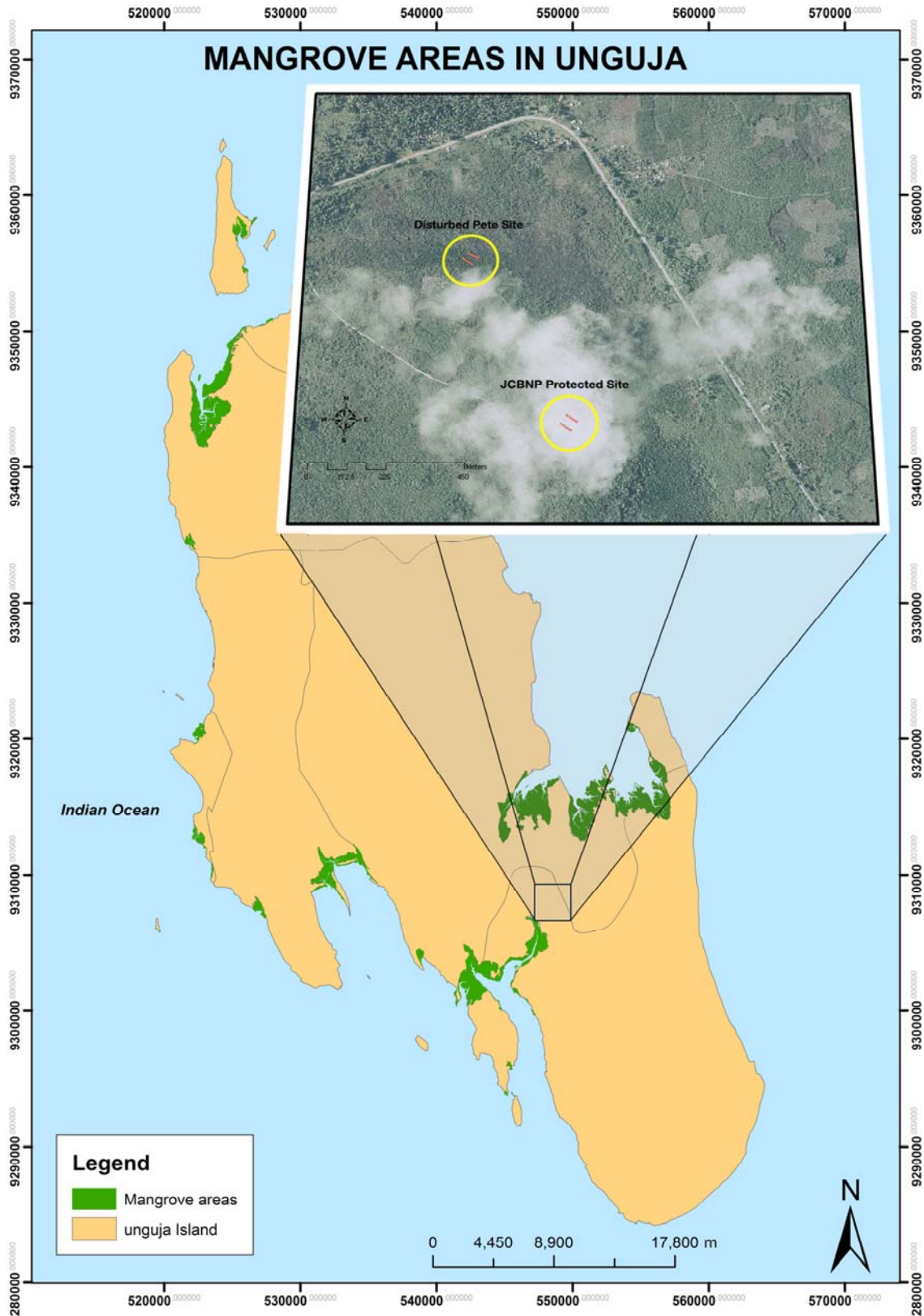
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APPENDICES

Appendix 1. Map of Unguja Island showing mangrove areas and study sites



Appendix 2a. Jozani site herbivory counts for *C. tagal*

JOZANI	TRANSECT	Plot	Leaves	0	1	2	3	4	5	
7/11/2009	1	A	CT (g)	5						
			CT (y)	5						
		B	CT (g)	4						1
			CT (y)	5						
		C	CT (g)	5						
			CT (y)	5						
		D	CT (g)	4			1			
			CT (y)	5						
		E	CT (g)	5						
			CT (y)	5						
	2	A	CT (g)	5						
			CT (y)	3						2
		B	CT (g)	5						
			CT (y)	5						
		C	CT (g)	5						
			CT (y)	5						
		D	CT (g)	5						
			CT (y)	5						
		E	CT (g)	5						
			CT (y)	5						
Sum				96	0	1	0	0	3	
Mean				4.8	###	1	###	##	1.5	
%				96	0	1	0	0	3	
Sum(g)				48	0	1	0	0	1	
Sum(y)				48	0	0	0	0	2	
Mean(g)				4.8	###	1	###	##	1	
Mean(y)				4.8	###	###	###	##	2	
% (g)				96	0	2	0	0	2	
% (y)				96	0	0	0	0	4	
8/11/2009	1	A	CT (g)	5						
			CT (y)	5						
		B	CT (g)	4	1					
			CT (y)	5						
		C	CT (g)	3	1				1	
			CT (y)	5						
		D	CT (g)	3	2					
			CT (y)	5						
		E	CT (g)	3	2					
			CT (y)	5						
	2	A	CT (g)	3	1	1				
			CT (y)	5						
		B	CT (g)	5						
			CT (y)	5						
		C	CT (g)	5						
			CT (y)	5						
		D	CT (g)	5						
			CT (y)	5						

		E	CT (g)	5						
			CT (y)	5						
			Sum	91	7	1	0	0		1
			Mean	4.55	1.4	1	###	##		1
			%	91	7	1	0	0		1
			Sum(g)	41	7	1	0	0		1
			Sum(y)	50	0	0	0	0		0
			Mean(g)	4.1	1.4	1	###	##		1
			Mean(y)	5	###	###	###	##		###
			%(g)	82	14	2	0	0		2
			%(y)	100	0	0	0	0		0
9/11/2009	1	A	CT (g)	5						
			CT (y)	5						
		B	CT (g)	2	1					2
			CT (y)	5						
		C	CT (g)	5						
			CT (y)	5						
		D	CT (g)	4		1				
			CT (y)	5						
		E	CT (g)	5						
			CT (y)	5						
	2	A	CT (g)	5						
			CT (y)	5						
		B	CT (g)	5						
			CT (y)	5						
		C	CT (g)	5						
			CT (y)	5						
		D	CT (g)	5						
			CT (y)	5						
		E	CT (g)	5						
			CT (y)	5						
			Sum	96	1	1	0	0		2
			Mean	4.8	1	1	###	##		2
			%	96	1	1	0	0		2
			Sum(g)	46	1	1	0	0		2
			Sum(y)	50	0	0	0	0		0
			Mean(g)	4.6	1	1	###	##		2
			Mean(y)	5	###	###	###	##		###
			%(g)	92	2	2	0	0		4
			%(y)	100	0	0	0	0		0
10-11-09	1	A	CT (g)	5						
			CT (y)	5						
		B	CT (g)	4	1					
			CT (y)	4						1
		C	CT (g)	5						
			CT (y)	5						
		D	CT (g)	3	1					1
			CT (y)	5						

		E	CT (g)	4						1
			CT (y)	5						
	2	A	CT (g)	5						
			CT (y)	5						
		B	CT (g)	5						
			CT (y)	5						
		C	CT (g)	4	1					
			CT (y)	5						
		D	CT (g)	2						3
			CT (y)	5						
		E	CT (g)	5						
			CT (y)	5						
			Sum	91	3	0	0	0		6
			Mean	4.55	1	###	###	##		1.5
			%	91	3	0	0	0		6
			Sum(g)	42	3	0	0	0		5
			Sum(y)	49	0	0	0	0		1
			Mean(g)	4.2	1	###	###	##		1.67
			Mean(y)	4.9	###	###	###	##		1
			%(g)	84	6	0	0	0		10
			%(y)	98	0	0	0	0		2
11/11/2009										
	1	A	CT (g)	5						
			CT (y)	5						
		B	CT (g)	5						
			CT (y)	5						
		C	CT (g)	5						
			CT (y)	5						
		D	CT (g)	5						
			CT (y)	4						1
		E	CT (g)	4	1					
			CT (y)	4						1
	2	A	CT (g)	5						
			CT (y)	4						1
		B	CT (g)	5						
			CT (y)	5						
		C	CT (g)	5						
			CT (y)	5						
		D	CT (g)	5						
			CT (y)	5						
		E	CT (g)	4					1	
			CT (y)	5						
			Sum	95	1	0	0	1		3
			Mean	4.75	1	###	###	1		1
			%	95	1	0	0	1		3
			Sum(g)	48	1	0	0	1		0
			Sum(y)	47	0	0	0	0		3
			Mean(g)	4.8	1	###	###	1	###	
			Mean(y)	4.7	###	###	###	##		1
			%(g)	96	2	0	0	2		0

%(y)	94	0	0	0	0	6
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Overall							
Means	Sum	469	12	3	0	1	15
	Mean	4.69	###	###	###	##	1.4
	%	93.8	2.4	0.6	0	0.2	3
	Sum(g)	225	12	3	0	1	9
	Sum(y)	244	0	0	0	0	6
	Mean(g)	4.5	###	###	###	##	###
	Mean(y)	4.88	###	###	###	##	###
	%(g)	90	4.8	1.2	0	0.4	3.6
	%(y)	97.6	0	0	0	0	2.4

Appendix 2b. Jozani site herbivory counts for *R. mucronata*

JOZANI	TRANSECT	Plot		0	1	2	3	4	5	
7/11/2009	1	A	RM (g)	1	3					
			RM (y)	4			1			
		B	RM (g)	2						3
			RM (y)	5						
		C	RM (g)	1	1	2				1
			RM (y)	5						
		D	RM (g)	1	2	2				
			RM (y)	5						
		E	RM (g)	1	3				1	
			RM (y)	3	2					
	2	A	RM (g)	1	2				1	1
			RM (y)	5						
		B	RM (g)	1	3	1				
			RM (y)	5						
		C	RM (g)		2	3				
			RM (y)	5						
		D	RM (g)	1	2	2				
			RM (y)	4	1					
		E	RM (g)		2			1	1	1
			RM (y)	5						
	Sum			55	23	10	2	3	7	
	Mean			3.056	2.09	2	1	1	1.4	
	%			55	23	10	2	3	7	
Sum(g)			9	20	10	1	3	7		
Sum(y)			46	3	0	1	0	0		
Mean(g)			1.125	2.22	2	1	1	1.4		
Mean(y)			4.6	1.5	###	1	##	##		
% (g)			18	40	20	2	6	14		
% (y)			92	6	0	2	0	0		
8/11/2009	1	A	RM (g)		3	2				
			RM (y)	5						
		B	RM (g)	4		1				
			RM (y)	5						
		C	RM (g)		3	2				
			RM (y)	4		1				
		D	RM (g)	2	1		1		1	
			RM (y)	5						
		E	RM (g)	2	3					
			RM (y)	5						
	2	A	RM (g)	3	2					
			RM (y)	5						
		B	RM (g)	3	2					
			RM (y)	5						
		C	RM (g)	4	1					
			RM (y)	4	1					
		D	RM (g)	1	1	1	1		1	
			RM (y)	5						

		E	RM (g)		1	3	1		
			RM (y)	5					
			Sum	67	18	10	3	0	2
			Mean	3.941	1.8	1.7	1	##	1
			%	67	18	10	3	0	2
			Sum(g)	19	17	9	3	0	2
			Sum(y)	48	1	1	0	0	0
			Mean(g)	2.714	1.89	1.8	1	##	1
			Mean(y)	4.8	1	1	###	##	##
			%(g)	38	34	18	6	0	4
			%(y)	96	2	2	0	0	0
9/11/2009	1	A	RM (g)	4	1				
			RM (y)	5					
		B	RM (g)	5					
			RM (y)	5					
		C	RM (g)	3	1	1			
			RM (y)	5					
		D	RM (g)	3	1				1
			RM (y)	2		2			1
		E	RM (g)	1	4				
			RM (y)	4	1				
	2	A	RM (g)	3	1	1			
			RM (y)	5					
		B	RM (g)	3	2				
			RM (y)	5					
		C	RM (g)	3	1	1			
			RM (y)	5					
		D	RM (g)			1	1		3
			RM (y)	5					
		E	RM (g)	2	2	1			
			RM (y)	5					
			Sum	73	14	7	1	0	5
			Mean	3.842	1.56	1.2	1	##	1.7
			%	73	14	7	1	0	5
			Sum(g)	27	13	5	1	0	4
			Sum(y)	46	1	2	0	0	1
			Mean(g)	3	1.63	1	1	##	2
			Mean(y)	4.6	1	2	###	##	1
			%(g)	54	26	10	2	0	8
			%(y)	92	2	4	0	0	2
10-11-09	1	A	RM (g)	2	3				
			RM (y)	5					
		B	RM (g)	2	3				
			RM (y)	5					
		C	RM (g)	2	2	1			
			RM (y)	5					
		D	RM (g)	3	2				
			RM (y)	5					

		E	RM (g)	1	2	2				
			RM (y)	5						
	2	A	RM (g)	2	1	2				
			RM (y)	5						
		B	RM (g)	3	1					1
			RM (y)	5						
		C	RM (g)	2	2	1				
			RM (y)	5						
		D	RM (g)	2	1	1				1
			RM (y)	5						
		E	RM (g)		1		1	1	1	2
			RM (y)	5						
			Sum	69	18	7	1	1	4	
			Mean	3.632	1.8	1.4	1	1	1.3	
			%	69	18	7	1	1	4	
			Sum(g)	19	18	7	1	1	4	
			Sum(y)	50	0	0	0	0	0	
			Mean(g)	2.111	1.8	1.4	1	1	1.3	
			Mean(y)	5	###	###	###	##	##	
			%(g)	38	36	14	2	2	8	
			%(y)	100	0	0	0	0	0	
11/11/2009	1	A	RM (g)	5						
			RM (y)	5						
		B	RM (g)	4	1					
			RM (y)	5						
		C	RM (g)	4	1					
			RM (y)	5						
		D	RM (g)	4	1					
			RM (y)	5						
		E	RM (g)	2	2		1			
			RM (y)	3						2
	2	A	RM (g)	4	1					
			RM (y)	5						
		B	RM (g)	4						1
			RM (y)	5						
		C	RM (g)	5						
			RM (y)	5						
		D	RM (g)	2	3					
			RM (y)	5						
		E	RM (g)	2	2					1
			RM (y)	5						
			Sum	84	11	0	1	0	4	
			Mean	4.2	1.57	###	1	##	1.3	
			%	84	11	0	1	0	4	
			Sum(g)	36	11	0	1	0	2	
			Sum(y)	48	0	0	0	0	2	
			Mean(g)	3.6	1.57	###	1	##	1	
			Mean(y)	4.8	###	###	###	##	2	
			%(g)	72	22	0	2	0	4	

%(y) 96 0 0 0 0 4

Overall Means		Sum	348	84	34	8	4	22
	Mean	3.734	1.76	###	1	##	1.3	
	%	69.6	16.8	6.8	1.6	0.8	4.4	
	Sum(g)	110	79	31	7	4	19	
	Sum(y)	238	5	3	1	0	3	
	Mean(g)	2.51	1.82	###	1	##	1.3	
	Mean(y)	4.76	###	###	###	##	##	
	%(g)	44	31.6	12	2.8	1.6	7.6	
	%(y)	95.2	2	1.2	0.4	0	1.2	

Appendix 2c. Jozani site herbivory counts for *B. gymnorrhiza*

JOZANI	TRANSECT	Plot		0	1	2	3	4	5		
7/11/2009	1	A	BG (g)	4		1					
			BG (Y)	3	1	1					
		B	BG (g)	1	1	2				1	
			BG (Y)	5							
		C	BG (g)	4		1					
			BG (Y)	3	1	1					
		D	BG (g)	4						1	
			BG (Y)	5							
		E	BG (g)	3	1	1					
			BG (Y)	3	1		1				
	2	A	A	BG (g)	4	1					
				BG (Y)	5						
			B	BG (g)	2	2	1				
				BG (Y)	5						
			C	BG (g)	1	2	1	1			
				BG (Y)	5						
			D	BG (g)	3						2
				BG (Y)	3	1					1
			E	BG (g)	4	1					
				BG (Y)	4						1
		Sum		71	12	9	2	0	6		
		Mean		3.6	1.2	1.1	1	##	1.2		
		%		71	12	9	2	0	6		
		Sum(g)		30	8	7	1	0	4		
		Sum(y)		41	4	2	1	0	2		
		Mean(g)		2.7	1.1	1	0.5	0	1		
		Mean(y)		3.7	0.8	0.7	0.5	0	0.7		
%(g)		60	16	14	2	0	8				
%(y)		82	8	4	2	0	4				
8/11/2009	1	A	BG (g)	4		1					
			BG (Y)	5							
		B	BG (g)	4	1						
			BG (Y)	5							
		C	BG (g)	3	1	1					
			BG (Y)	5							
		D	BG (g)	5							
			BG (Y)	5							
		E	BG (g)	5							
			BG (Y)	3	1	1					
	2	A	BG (g)	2	3						
			BG (Y)	4	1						
		B	BG (g)	5							
			BG (Y)	4		1					
		C	BG (g)	5							
			BG (Y)	5							
		D	BG (g)	5							
			BG (Y)	4						1	

		E	BG (g)	3	2						
			BG (Y)	4	1						
			Sum	85	10	4	0	0		1	
			Mean	4.3	1.4	1	##	##		1	
			%	85	10	4	0	0		1	
			Sum(g)	41	7	2	0	0		0	
			Sum(y)	44	3	2	0	0		1	
			Mean(g)	3.7	1.4	0.7	0	0		0	
			Mean(y)	4	0.8	0.7	0	0		0.5	
			%(g)	82	14	4	0	0		0	
			%(y)	88	6	4	0	0		2	
9/11/2009	1	A	BG (g)	5							
			BG (Y)	4	1						
		B	BG (g)	5							
			BG (Y)	4		1					
		C	BG (g)	5							
			BG (Y)	3					1	1	
		D	BG (g)	5							
			BG (Y)	3	2						
		E	BG (g)	4							1
			BG (Y)	2	1						2
	2	A	BG (g)	5							
			BG (Y)	5							
		B	BG (g)	5							
			BG (Y)	5							
		C	BG (g)	5							
			BG (Y)	5							
		D	BG (g)	5							
			BG (Y)	3	1						1
		E	BG (g)	3							2
			BG (Y)	4	1						
			Sum	85	6	1	0	1		7	
			Mean	4.3	1.2	1	##	1		1.4	
			%	85	6	1	0	1		7	
			Sum(g)	47	0	0	0	0		3	
			Sum(y)	38	6	1	0	1		4	
			Mean(g)	4.3	0	0	0	0		1	
			Mean(y)	3.5	1	0.5	0	1		1	
			%(g)	94	0	0	0	0		6	
			%(y)	76	12	2	0	2		8	
10-11-09	1	A	BG (g)	5							
			BG (Y)	4							1
		B	BG (g)	5							
			BG (Y)	4	1						
		C	BG (g)	5							
			BG (Y)	5							
		D	BG (g)	5							
			BG (Y)	5							

		E	BG (g)	5									
			BG (Y)	3	2								
	2	A	BG (g)	4	1								
			BG (Y)	5									
		B	BG (g)	4								1	
			BG (Y)	5									
		C	BG (g)	4	1								
			BG (Y)	5									
		D	BG (g)	4								1	
			BG (Y)	4	1								
		E	BG (g)	3								2	
			BG (Y)	5									
			Sum	89	6	0	0	0	0	0	0	5	
			Mean	4.5	1.2	##	##	##	##	##	##	1.3	
			%	89	6	0	0	0	0	0	0	5	
			Sum(g)	44	2	0	0	0	0	0	0	4	
			Sum(y)	45	4	0	0	0	0	0	0	1	
			Mean(g)	4	0.7	0	0	0	0	0	0	1	
			Mean(y)	4.1	1	0	0	0	0	0	0	0.5	
			%(g)	88	4	0	0	0	0	0	0	8	
			%(y)	90	8	0	0	0	0	0	0	2	
11/11/2009	1	A	BG (g)	4	1								
			BG (Y)	4	1								
		B	BG (g)	5									
			BG (Y)	4		1							
		C	BG (g)	5									
			BG (Y)	5									
		D	BG (g)	5									
			BG (Y)	4	1								
		E	BG (g)	5									
			BG (Y)	5									
	2	A	BG (g)	4	1								
			BG (Y)	4								1	
		B	BG (g)	4	1								
			BG (Y)	4	1								
		C	BG (g)	4		1							
			BG (Y)	5									
		D	BG (g)	3	2								
			BG (Y)	5									
		E	BG (g)	4								1	
			BG (Y)	3								2	
			Sum	86	8	2	0	0	0	0	0	4	
			Mean	4.3	1.1	1	##	##	##	##	##	1.3	
			%	86	8	2	0	0	0	0	0	4	
			Sum(g)	43	5	1	0	0	0	0	0	1	
			Sum(y)	43	3	1	0	0	0	0	0	3	
			Mean(g)	3.9	1	0.5	0	0	0	0	0	0.5	
			Mean(y)	3.9	0.8	0.5	0	0	0	0	0	1	
			%(g)	86	10	2	0	0	0	0	0	2	

%(y) 86 6 2 0 0 6

Overall							
Means	Sum	416	42	16	2	1	23
	Mean	4.2	1.2	##	##	##	1.2
	%	83	8.4	3.2	0.4	0	4.6
	Sum(g)	205	22	10	1	0	12
	Sum(y)	211	20	6	1	1	11
	Mean(g)	3.7	0.8	0.4	0.1	0	0.7
	Mean(y)	3.8	0.9	0.5	0.1	0	0.7
	%(g)	82	8.8	4	0.4	0	4.8
	%(y)	84	8	2.4	0.4	0	4.4

Appendix 3a. Pete site herbivory counts for *C. tagal*

PETE	TRANSECT	Plot	Leaves	0	1	2	3	4	5
13-11-09	1	A	CT (g)	5					
			CT (y)	5					
		B	CT (g)	5					
			CT (y)	5					
		C	CT (g)	5					
			CT (y)	5					
		D	CT (g)	5					
			CT (y)	5					
		E	CT (g)	5					
			CT (y)	5					
	2	A	CT (g)	5					
			CT (y)	5					
		B	CT (g)	5					
			CT (y)	5					
		C	CT (g)	5					
			CT (y)	5					
		D	CT (g)	5					
			CT (y)	5					
		E	CT (g)	5					
			CT (y)	5					
			Sum	100	0	0	0	0	0
			Mean	5	##	##	##	##	##
			%	100	0	0	0	0	0
			Sum(g)	50	0	0	0	0	0
			Sum(y)	50	0	0	0	0	0
			Mean(g)	5	##	##	##	##	##
			Mean(y)	5	##	##	##	##	##
		%(g)	100	0	0	0	0	0	
		%(y)	100	0	0	0	0	0	
14-11-09	1	A	CT (g)	5					
			CT (y)	5					
		B	CT (g)	3	2				
			CT (y)	5					
		C	CT (g)	5					
			CT (y)	5					
		D	CT (g)	5					
			CT (y)	5					
		E	CT (g)	5					
			CT (y)	5					
	2	A	CT (g)	5					
			CT (y)	5					
		B	CT (g)	5					
			CT (y)	5					
		C	CT (g)	5					
			CT (y)	5					
		D	CT (g)	5					
			CT (y)	5					

		E	CT (g)	5					
			CT (y)	5					
			Sum	98	2	0	0	0	0
			Mean	4.9	2	##	##	##	##
			%	98	2	0	0	0	0
			Sum(g)	48	2	0	0	0	0
			Sum(y)	50	0	0	0	0	0
			Mean(g)	4.8	2	##	##	##	##
			Mean(y)	5	##	##	##	##	##
			%(g)	96	4	0	0	0	0
			%(y)	100	0	0	0	0	0
15-11-09	1	A	CT (g)	5					
			CT (y)	5					
		B	CT (g)	5					
			CT (y)	5					
		C	CT (g)	5					
			CT (y)	5					
		D	CT (g)	4	1				
			CT (y)	5					
		E	CT (g)	5					
			CT (y)	5					
	2	A	CT (g)	5					
			CT (y)	5					
		B	CT (g)	5					
			CT (y)	5					
		C	CT (g)	5					
			CT (y)	5					
		D	CT (g)	5					
			CT (y)	5					
		E	CT (g)	5					
			CT (y)	5					
			Sum	99	1	0	0	0	0
			Mean	5	1	##	##	##	##
			%	99	1	0	0	0	0
			Sum(g)	49	1	0	0	0	0
			Sum(y)	50	0	0	0	0	0
			Mean(g)	4.9	1	##	##	##	##
			Mean(y)	5	##	##	##	##	##
			%(g)	98	2	0	0	0	0
			%(y)	100	0	0	0	0	0
16-11-09	1	A	CT (g)	5					
			CT (y)	5					
		B	CT (g)	5					
			CT (y)	5					
		C	CT (g)	5					
			CT (y)	5					
		D	CT (g)	5					
			CT (y)	5					

		E	CT (g)	5						
			CT (y)	5						
	2	A	CT (g)	5						
			CT (y)	5						
		B	CT (g)	3						2
			CT (y)	5						
		C	CT (g)	5						
			CT (y)	5						
		D	CT (g)	5						
			CT (y)	5						
		E	CT (g)	4	1					
			CT (y)	5						
			Sum	97	1	0	0	0	0	2
			Mean	4.9	1	##	##	##	##	2
			%	97	1	0	0	0	0	2
			Sum(g)	47	1	0	0	0	0	2
			Sum(y)	50	0	0	0	0	0	0
			Mean(g)	4.7	1	##	##	##	##	2
			Mean(y)	5	##	##	##	##	##	##
			%(g)	94	2	0	0	0	0	4
			%(y)	100	0	0	0	0	0	0
17-11-09										
	1	A	CT (g)	5						
			CT (y)	5						
		B	CT (g)	5						
			CT (y)	5						
		C	CT (g)	2						3
			CT (y)	5						
		D	CT (g)	5						
			CT (y)	5						
		E	CT (g)	5						
			CT (y)	5						
	2	A	CT (g)	5						
			CT (y)	5						
		B	CT (g)	5						
			CT (y)	5						
		C	CT (g)	5						
			CT (y)	5						
		D	CT (g)	4						1
			CT (y)	5						
		E	CT (g)	5						
			CT (y)	5						
			Sum	96	0	0	0	0	0	4
			Mean	4.8	##	##	##	##	##	2
			%	96	0	0	0	0	0	4
			Sum(g)	46	0	0	0	0	0	4
			Sum(y)	50	0	0	0	0	0	0
			Mean(g)	4.6	##	##	##	##	##	2
			Mean(y)	5	##	##	##	##	##	##
			%(g)	92	0	0	0	0	0	8

%(y) 100 0 0 0 0 0

Overall Means		Sum	490	4	0	0	0	0	6
		Mean	4.9	##	##	##	##	##	##
		%	98	0.8	0	0	0	0	1.2
		Sum(g)	240	4	0	0	0	0	6
		Sum(y)	250	0	0	0	0	0	0
		Mean(g)	4.8	##	##	##	##	##	##
		Mean(y)	5	##	##	##	##	##	##
		%(g)	96	1.6	0	0	0	0	2.4
		%(y)	100	0	0	0	0	0	0

Appendix 3b. Pete site herbivory counts for *R. mucronata*

PETE	TRANSECT	Plot	Leaves						
13-11-09	1	A	RM (g)	5					
			RM (y)	5					
		B	RM (g)	5					
			RM (y)	5					
		C	RM (g)	5					
			RM (y)	5					
		D	RM (g)	5					
			RM (y)	5					
		E	RM (g)	3	2				
			RM (y)	5					
	2	A	RM (g)	5					
			RM (y)	5					
		B	RM (g)	5					
			RM (y)	5					
		C	RM (g)	4				1	
			RM (y)	5					
		D	RM (g)	5					
			RM (y)	5					
		E	RM (g)	5					
			RM (y)	5					
		Sum	97	2	0	0	0	1	
		Mean	4.9	2	##	##	##	1	
		%	97	2	0	0	0	1	
		Sum(g)	47	2	0	0	0	1	
		Sum(y)	50	0	0	0	0	0	
		Mean(g)	4.7	2	##	##	##	1	
		Mean(y)	5	##	##	##	##	##	
		%(g)	94	4	0	0	0	2	
		%(y)	100	0	0	0	0	0	
14-11-09	1	A	RM (g)	5					
			RM (y)	5					
		B	RM (g)	5					
			RM (y)	4	1				
		C	RM (g)	5					
			RM (y)	5					
	D	RM (g)	2	1	1		1		
		RM (y)	4	1					
	E	RM (g)	2	2	1				
		RM (y)	5						
	2	A	RM (g)	5					
			RM (y)	5					
		B	RM (g)	5					
			RM (y)	5					
		C	RM (g)	5					
			RM (y)	5					
	D	RM (g)	5						
		RM (y)	5						

		E	RM (g)	5					
			RM (y)	5					
			Sum	92	5	2	0	0	1
			Mean	4.6	1.3	1	##	##	1
			%	92	5	2	0	0	1
			Sum(g)	44	3	2	0	0	1
			Sum(y)	48	2	0	0	0	0
			Mean(g)	4.4	1.5	1	##	##	1
			Mean(y)	4.8	1	##	##	##	##
			%(g)	88	6	4	0	0	2
			%(y)	96	4	0	0	0	0
15-11-09	1	A	RM (g)	5					
			RM (y)	5					
		B	RM (g)	5					
			RM (y)	5					
		C	RM (g)	2	3				
			RM (y)	5					
		D	RM (g)	1	2	2			
			RM (y)	5					
		E	RM (g)	5					
			RM (y)	5					
	2	A	RM (g)	0	1				4
			RM (y)	5					
		B	RM (g)	5					
			RM (y)	5					
		C	RM (g)	5					
			RM (y)	5					
		D	RM (g)	3	2				
			RM (y)	5					
		E	RM (g)	4	1				
			RM (y)	5					
			Sum	85	9	2	0	0	4
			Mean	4.3	1.8	2	##	##	4
			%	85	9	2	0	0	4
			Sum(g)	35	9	2	0	0	4
			Sum(y)	50	0	0	0	0	0
			Mean(g)	3.5	1.8	2	##	##	4
			Mean(y)	5	##	##	##	##	##
			%(g)	70	18	4	0	0	8
			%(y)	100	0	0	0	0	0
16-11-09	1	A	RM (g)	5					
			RM (y)	5					
		B	RM (g)	5					
			RM (y)	5					
		C	RM (g)	5					
			RM (y)	4	1				
		D	RM (g)	4	1				
			RM (y)	4	1				

		E	RM (g)	5						
			RM (y)	5						
	2	A	RM (g)	2						3
			RM (y)	5						
		B	RM (g)	5						
			RM (y)	5						
		C	RM (g)	5						
			RM (y)	5						
		D	RM (g)	4	1					
			RM (y)	4	1					
		E	RM (g)	3	2					
			RM (y)	5						
			Sum	90	7	0	0	0	0	3
			Mean	4.5	1.2	##	##	##	##	3
			%	90	7	0	0	0	0	3
			Sum(g)	43	4	0	0	0	0	3
			Sum(y)	47	3	0	0	0	0	0
			Mean(g)	4.3	1.3	##	##	##	##	3
			Mean(y)	4.7	1	##	##	##	##	##
			%(g)	86	8	0	0	0	0	6
			%(y)	94	6	0	0	0	0	0
17-11-09										
	1	A	RM (g)	5						
			RM (y)	5						
		B	RM (g)	5						
			RM (y)	5						
		C	RM (g)	2	3					
			RM (y)	4	1					
		D	RM (g)	5						
			RM (y)	5						
		E	RM (g)	5						
			RM (y)	5						
	2	A	RM (g)	5						
			RM (y)	4		1				
		B	RM (g)	4	1					
			RM (y)	5						
		C	RM (g)	5						
			RM (y)	5						
		D	RM (g)	5						
			RM (y)	5						
		E	RM (g)	4						1
			RM (y)	5						
			Sum	93	5	1	0	0	0	1
			Mean	4.7	1.7	1	##	##	##	1
			%	93	5	1	0	0	0	1
			Sum(g)	45	4	0	0	0	0	1
			Sum(y)	48	1	1	0	0	0	0
			Mean(g)	4.5	2	##	##	##	##	1
			Mean(y)	4.8	1	1	##	##	##	##
			%(g)	90	8	0	0	0	0	2

%(y)	96	2	2	0	0	0
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Overall Means		Sum	457	28	5	0	0	10
		Mean	4.6	1.6	##	##	##	2
		%	91	5.6	1	0	0	2
		Sum(g)	214	22	4	0	0	10
		Sum(y)	243	6	1	0	0	0
		Mean(g)	4.3	1.7	##	##	##	2
		Mean(y)	4.9	##	##	##	##	##
		%(g)	86	8.8	1.6	0	0	4
		%(y)	97	2.4	0.4	0	0	0

Appendix 3c. Pete site herbivory counts for *B. gymnorrhiza*

PETE	TRANSECT	Plot		0	1	2	3	4	5	
13-11-09	1	A	BG (g)	5						
			BG (Y)	5						
		B	BG (g)	4						1
			BG (Y)	4	1					
		C	BG (g)	5						
			BG (Y)	5						
		D	BG (g)	5						
			BG (Y)	5						
		E	BG (g)	4	1					
			BG (Y)	5						
	2	A	BG (g)	5						
			BG (Y)	5						
		B	BG (g)	5						
			BG (Y)	5						
		C	BG (g)	5						
			BG (Y)	5						
		D	BG (g)	5						
			BG (Y)	5						
		E	BG (g)	5						
			BG (Y)	5						
			Sum	97	2	0	0	0	1	
			Mean	4.9	1	##	##	##	1	
			%	97	2	0	0	0	1	
			Sum(g)	48	1	0	0	0	1	
			Sum(y)	49	1	0	0	0	0	
			Mean(g)	4.8	1	##	##	##	1	
			Mean(y)	4.9	1	##	##	##	##	
		%(g)	96	2	0	0	0	2		
		%(y)	98	2	0	0	0	0		
14-11-09	1	A	BG (g)	5						
			BG (Y)	5						
		B	BG (g)	5						
			BG (Y)	5						
		C	BG (g)	5						
			BG (Y)	5						
		D	BG (g)	5						
			BG (Y)	5						
		E	BG (g)	5						
			BG (Y)	5						
	2	A	BG (g)	5						
			BG (Y)	5						
		B	BG (g)	5						
			BG (Y)	5						
		C	BG (g)	5						
			BG (Y)	5						
		D	BG (g)	5						
			BG (Y)	4	1					

		E	BG (g)	5					
			BG (Y)	5					
			Sum	99	1	0	0	0	0
			Mean	5	1	##	##	##	##
			%	99	1	0	0	0	0
			Sum(g)	50	0	0	0	0	0
			Sum(y)	49	1	0	0	0	0
			Mean(g)	5	##	##	##	##	##
			Mean(y)	4.9	1	##	##	##	##
			%(g)	100	0	0	0	0	0
			%(y)	98	2	0	0	0	0
15-11-09	1	A	BG (g)	5					
			BG (Y)	5					
		B	BG (g)	5					
			BG (Y)	5					
		C	BG (g)	5					
			BG (Y)	5					
		D	BG (g)	5					
			BG (Y)	5					
		E	BG (g)	5					
			BG (Y)	5					
			RM (g)	0	1				4
			RM (y)	5					
		B	BG (g)	5					
			BG (Y)	5					
		C	BG (g)	5					
			BG (Y)	5					
		D	BG (g)	5					
			BG (Y)	5					
		E	BG (g)	3					2
			BG (Y)	5					
			Sum	93	1	0	0	0	6
			Mean	4.7	1	##	##	##	3
			%	93	1	0	0	0	6
			Sum(g)	43	1	0	0	0	6
			Sum(y)	50	0	0	0	0	0
			Mean(g)	4.3	1	##	##	##	3
			Mean(y)	5	##	##	##	##	##
			%(g)	86	2	0	0	0	12
			%(y)	100	0	0	0	0	0
16-11-09	1	A	BG (g)	4	1				
			BG (Y)	5					
		B	BG (g)	5					
			BG (Y)	5					
		C	BG (g)	5					
			BG (Y)	5					
		D	BG (g)	5					
			BG (Y)	5					

		E	BG (g)	5					
			BG (Y)	5					
	2	A	BG (g)	2					3
			BG (Y)	2					3
		B	BG (g)	5					
			BG (Y)	4					1
		C	BG (g)	5					
			BG (Y)	5					
		D	BG (g)	5					
			BG (Y)	5					
		E	BG (g)	5					
			BG (Y)	5					
			Sum	92	1	0	0	0	7
			Mean	4.6	1	##	##	##	2.3
			%	92	1	0	0	0	7
			Sum(g)	46	1	0	0	0	3
			Sum(y)	46	0	0	0	0	4
			Mean(g)	4.6	1	##	##	##	3
			Mean(y)	4.6	##	##	##	##	2
			%(g)	92	2	0	0	0	6
			%(y)	92	0	0	0	0	8
17-11-09									
	1	A	BG (g)	5					
			BG (Y)	5					
		B	BG (g)	5					
			BG (Y)	5					
		C	BG (g)	3	2				
			BG (Y)	5					
		D	BG (g)	4	1				
			BG (Y)	3	2				
		E	BG (g)	5					
			BG (Y)	5					
	2	A	BG (g)	4	1				
			BG (Y)	5					
		B	BG (g)	5					
			BG (Y)	5					
		C	BG (g)	5					
			BG (Y)	5					
		D	BG (g)	5					
			BG (Y)	5					
		E	BG (g)	4					1
			BG (Y)	4					1
			Sum	92	6	0	0	0	2
			Mean	4.6	1.5	##	##	##	1
			%	92	6	0	0	0	2
			Sum(g)	45	4	0	0	0	1
			Sum(y)	47	2	0	0	0	1
			Mean(g)	4.5	1.3	##	##	##	1
			Mean(y)	4.7	2	##	##	##	1
			%(g)	90	8	0	0	0	2

%(y)	94	4	0	0	0	2
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Overall							
Means	Sum	473	11	0	0	0	16
	Mean	4.7	1.1	##	##	##	##
	%	95	2.2	0	0	0	3.2
	Sum(g)	232	7	0	0	0	11
	Sum(y)	241	4	0	0	0	5
	Mean(g)	4.6	##	##	##	##	##
	Mean(y)	4.8	##	##	##	##	##
	%(g)	93	2.8	0	0	0	4.4
	%(y)	96	1.6	0	0	0	2