

# 琉球大学学術リポジトリ

## 沖縄島に生育するヒルギ科のマングローブ3種のフ ェノロジーとリターフォール

メタデータ	言語: 出版者: 琉球大学 公開日: 2014-04-30 キーワード (Ja): キーワード (En): 作成者: Kamruzzaman, Md., カムルジャマン, エムディ メールアドレス: 所属:
URL	<a href="http://hdl.handle.net/20.500.12000/28595">http://hdl.handle.net/20.500.12000/28595</a>

**Doctoral Thesis of Science**

**Phenology and Litterfall of Three Mangrove Species in  
the Family Rhizophoraceae on Okinawa Island, Japan**

September 2013

by

**Md. Kamruzzaman**

A dissertation submitted to the Graduate School of Engineering and  
Science, University of the Ryukyus, in partial fulfillment of the  
requirements for the degree of

**Doctor of Science**

**Plant Ecophysiology**

**Marine and Environmental Sciences**

**Graduate School of Engineering and Science**

**University of the Ryukyus**

**Supervisor: Prof. Akio Hagihara**

## **CERTIFICATION**

**We, the undersigned, hereby, declare that we have read this thesis and we have attended the thesis defense and evaluation meeting. Therefore, we certify that, to the best of our knowledge this thesis is satisfactory to the scope and quality as a thesis for the degree of Doctor of Science in Plant Ecophysiology under Marine and Environmental Science, Graduate School of Engineering and Science, University of the Ryukyus.**

## **THESIS REVIEW & EVALUATION COMMITTEE MEMBERS**

---

**(Chairman) Prof. Akio Hagihara**

---

**(Committee) Prof. Makoto Tsuchiya**

---

**(Committee) Prof. Masako Izawa**

## ABSTRACT

Mangroves in the subtropical area of Japan are growing in their northern limits, yet little is known of their phenology. This study was conducted to understand vegetative phenology, reproductive phenology, as well as to evaluate and compare the litterfall dynamics of three mangrove species in the family Rhizophoraceae, *Bruguiera gymnorhiza*, *Kandelia obovata*, and *Rhizophora stylosa* at Manko Wetland, Okinawa Island, Japan. Leaf and stipule litterfall of *B. gymnorhiza* occurred throughout the year, with distinct seasonal patterns. Kendall's coefficient of concordance,  $W$ , revealed that the monthly changes in leaf and stipule litterfall of *B. gymnorhiza* were strongly and significantly concordant among years. Leaf litterfall was linked to monthly maximum wind speed and monthly day length, and stipule litterfall to monthly mean air temperature, monthly maximum wind speed, and monthly rainfall. Branch litterfall showed no clear monthly pattern, but tended to vary with monthly maximum wind speed. Branch litterfall of *B. gymnorhiza* increased exponentially with increasing monthly maximum wind speed. Mean leaf longevity of *B. gymnorhiza* was 19 month. Mean total litterfall was  $10.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ , with the largest component being vegetative organs (62 %). Flower and propagule litterfall of *B. gymnorhiza* were highest in autumn and summer, respectively, and lowest in winter. The  $W$  values revealed that, of the reproductive organs, only flower litterfall had a significant monthly trend. Flower litterfall was correlated with monthly mean air temperature, monthly air relative humidity, and monthly rainfall. The conversion rate of flowers to propagules was 9.8 % in *B. gymnorhiza*. The average development periods from flower buds to flowers and from flowers to mature propagules were approximately one and eight months, respectively. It took nine months to produce mature propagules from flower buds. Except for branches, all vegetative and reproductive litterfall components of *B. gymnorhiza* had clear annual cycles.

In case of *K. obovata*, the leaf and stipule litterfalls continued with a clear monthly pattern throughout the years. New leaf production and leaf fall peaked in summer, immediately after propagules fell. Leaf litterfall was linked to monthly mean air temperature, monthly maximum wind speed, and monthly rainfall, and stipule litterfall was linked to monthly day length and monthly maximum wind speed, respectively. Branch litterfall of *K. obovata* increased exponentially with increasing

monthly maximum wind speed. *Kandelia obovata* had a distinct flowering period, with the flowering phenophase starting in spring and continuing into summer. Fruit initiation started at the end of summer and continued into autumn, whereas propagule production occurred during winter and spring. Flowering of *K. obovata* was influenced by monthly mean air temperature, whereas fruit and propagule litterfall were significantly correlated with monthly day length and monthly mean air temperature, respectively. The present results showed that a small portion (6.1 %) of flowers developed into propagules. The average development period from flower buds to mature propagules was approximately 11 months. Kendall's consistency coefficient suggested that the monthly trends in vegetative and reproductive litterfall components, except branch, did not change significantly among years.

Leaf and stipule litterfall of *R. stylosa* occurred throughout the year, with distinct seasonal patterns. Kendall's coefficient of concordance,  $W$ , revealed that the monthly changes in leaf and stipule litterfall were strongly and significantly concordant among years. Leaf litterfall was significantly correlated with monthly maximum wind speed and monthly day length, and stipule litterfall was significantly correlated with monthly mean air temperature and monthly mean air relative humidity. Branch litterfall showed no clear monthly pattern and correlated well with monthly maximum wind speed. Branch litterfall of *R. stylosa* increased exponentially with increasing monthly maximum wind speed. Mean total litterfall was  $12.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ , with the largest component being vegetative organs (78.5 %). Flower, fruit, and propagule litterfall of *R. stylosa* were all highest in summer and lowest in winter. The  $W$  values revealed that most reproductive organs in litterfall had significant monthly trends. Flower and fruit litterfall were significantly correlated with monthly day length and monthly mean air temperature, respectively. The conversion rate of flowers to propagules was 2.2 % in *R. stylosa*. The average development periods from flower buds to flowers, fruits, and mature propagules were approximately 2–3 months, 4–5 months, and 11–12 months, respectively. Except for branches, all vegetative and reproductive litterfall components of *R. stylosa* had approximately one-year cycles.

Over three years, these species showed highest litterfall of leaves and stipules in summer and the lowest litterfall in winter. Litterfall of flowers and fruits peaked in July for *R. stylosa*, and in August and again in October–November for *K. obovata*.

Litterfall of flower buds, flowers, and propagules occurred throughout the year for *B. gymnorrhiza*, but was highest in summer. Litterfall of propagules was highest in September and May for *R. stylosa* and *K. obovata*, respectively. Kendall's coefficient of concordance revealed that the monthly changes for leaf, stipule, flower, and fruit litterfalls of all the species were strongly and significantly concordant among the years. Total annual litterfall in *R. stylosa* was significantly different from *K. obovata* and *B. gymnorrhiza*, however, the later two species had no significant differences. Leaves contributed the most to the total litterfall of all the three species, and represented 58.4, 54.0, and 50.4 % of the total litterfall for *R. stylosa*, *K. obovata*, and *B. gymnorrhiza*, respectively. Except for branches and flower bud primordia, all other components of litterfall had clear annual cycles for all three species. *R. stylosa* and *K. obovata* showed a negative correlation between leaf production and reproductive organ production, but *B. gymnorrhiza* tended to increase leaf production with increasing reproductive organ production.

This study evaluated the litterfall dynamics of the mangrove *B. gymnorrhiza* along the Okukubi River, Okinawa Island, Japan. Leaf and stipule litterfall occurred throughout the year, with respective distinct monthly patterns, and could be governed by monthly maximum wind speed and monthly day length, and monthly mean air temperature, respectively. Branch litterfall depended on monthly maximum wind speed and increased exponentially with increasing monthly maximum wind speed. Mean leaf litterfall of *B. gymnorrhiza* was  $774.8 \pm 95.8 \text{ g m}^{-2} \text{ yr}^{-1}$ , which contributed the most to total litterfall and represented 65.8 % of total litterfall. Flower litterfall might be influenced by monthly mean air temperature. Annual leaf litterfall per plot was almost constant regardless of the tree density of the plot. *Bruguiera gymnorrhiza* showed a positive correlation between leaf production and reproductive organ production.

## PUBLICATION LIST

1. **Kamruzzaman M**, Sharma S, Hoque ATMR, Hagihara A (2012) Litterfall of three subtropical mangrove species in the family Rhizophoraceae. *Journal of Oceanography*. 68:841–850
2. **Kamruzzaman M**, Sharma S, Kamara M, Hagihara A (2013) Vegetative and reproductive phenology of the mangrove *Bruguiera gymnorhiza* (L.) Lam. on Okinawa Island, Japan. *Trees-Structure and Function*. 27:619–628
3. **Kamruzzaman M**, Sharma S, Hagihara A (2013) Vegetative and reproductive phenology of the mangrove *Kandelia obovata*. *Plant Species Biology*. 28:118–129
4. **Kamruzzaman M**, Sharma S, Kamara M, Hagihara A (2013) Phenological traits of the mangrove *Rhizophora stylosa* Griff. at the northern limit of its biogeographical distribution. *Wetlands Ecology and Management*. 21:277–288

## **ACKNOWLEDGEMENTS**

In the name of Allah, the most Gracious and the most Merciful

Alhamdulillah, all praises to Allah for the strengths and His blessing in completing this thesis.

I am entirely grateful to my supervisor Prof. Akio Hagihara, for the absolute support of this research. His invaluable help of constructive comments and suggestions throughout the experimental and thesis works have contributed to the success of this research. I am grateful to my referees Profs. Makato Tsuchiya and Masako Izawa for their helpful critics and suggestions that make this thesis satisfactory. I am also very grateful to Dr. Shigeta Mori, Researcher, Forestry and Forest Products Research Institute, Tsukuba, Japan, for his encouragement and helpful suggestions during my doctoral research.

I deeply thank to Drs. Sahadev Sharma and Rashila Deshar for cordial help and valuable suggestions during my research. I thank to Mr. Kamara Mouctar for help and support during my field work. I appreciate the supports and helps I received from all my friends and well-wishers here in Okinawa.

I really thank to the Ministry of Education, Culture, Sports, Science and Technology (MEXT) for funding my study in Japan and the Faculty of Science, University of the Ryukyus for the fulfillment of my study. I would like to thank the staffs of the Faculty of Science and Biology office for their cooperation and valuable advice.

Finally, but not last, my deepest gratitude goes to my beloved parents, as well as my relatives and well wishers for their endless love, prayers, and encouragement. Most importantly, I am more than grateful to my beautiful family, Tahmid, Mahira, and Mitu for their love for me in every way. Without a doubt, I also dedicate the success of this work to you guys for being part of me and for giving me the most valuable teachings of all, the way of life.

# TABLE OF CONTENTS

<b>Topic</b>	<b>Page no</b>
Certification.....	ii
Abstract.....	iii
Publication List.....	vi
Acknowledgements.....	vii
Table of Contents.....	viii
List of Tables.....	xii
List of Figures.....	xiv
<b>CHAPTER – I</b>	
<b>General Introduction</b>	
1.1. Introduction.....	1
1.1.1. Litterfall production.....	1
1.1.2. Vegetative and reproductive phenology.....	2
1.1.3. Leaf longevity .....	4
1.1.4. Typhoon effects.....	4
1.1.5. Successful conversion from flowers to propagules.....	5
1.1.6. Development phase of reproductive organs.....	5
1.1.7. Coordination between leaf development and reproductive cycles.....	6
References.....	6
<b>CHAPTER – II</b>	
<b>Vegetative and Reproductive Phenology of the Mangrove <i>Bruguiera gymnorrhiza</i> (L.) Lamk.</b>	
2.1. Introduction.....	13
2.2. Materials and methods.....	14
2.2.1. Study site.....	14
2.2.2. Forest structure.....	14
2.2.3. Climate data.....	14

2.2.4. Litterfall collection.....	15
2.2.5. Leaf longevity.....	15
2.2.6. Statistical analysis.....	16
2.3. Results.....	17
2.3.1. Vegetative phenology.....	17
2.3.2. Reproductive phenology.....	18
2.4. Discussion.....	19
2.5. Conclusion.....	22
References.....	23

### CHAPTER – III

#### Vegetative and Reproductive Phenology of the Mangrove *Kandelia obovata*

(S., L.) Yong

3.1. Introduction.....	37
3.2. Materials and methods.....	38
3.2.1. Study site.....	38
3.2.2. Climate data.....	39
3.2.3. Litterfall collection.....	39
3.2.4. Statistical analysis.....	40
3.3. Results.....	41
3.3.1. Vegetative phenology.....	41
3.3.2. Reproductive phenology.....	42
3.4. Discussion.....	44
3.4.1. Vegetative phenology.....	44
3.4.2. Reproductive phenology.....	45
3.5. Conclusion.....	47
References.....	47

### CHAPTER – IV

#### Phenological Traits of the Mangrove *Rhizophora stylosa* Griff.

4.1. Introduction.....	62
4.2. Materials and methods.....	63

4.2.1. Study site.....	63
4.2.2. Forest structure.....	63
4.2.3. Climate data.....	63
4.2.4. Litterfall collection.....	64
4.2.5. Statistical analysis.....	64
4.3. Results.....	65
4.3.1. Vegetative phenology.....	65
4.3.2. Reproductive phenology.....	66
4.4. Discussion.....	68
4.5. Conclusion.....	70
References.....	71

## CHAPTER – V

### Litterfall of Three Subtropical Mangrove Species in the Family Rhizophoraceae

5.1. Introduction.....	85
5.2. Materials and methods.....	86
5.2.1. Study site.....	86
5.2.2. Forest structure.....	86
5.2.3. Litterfall collection.....	87
5.2.4. Statistical analysis.....	87
5.3. Results.....	88
5.4. Discussion.....	91
5.5. Conclusion.....	93
References.....	94

## CHAPTER – VI

### Temporal Variation in Litterfall Production of *Bruguiera gymnorrhiza* Stands along the Okukubi River

6.1. Introduction.....	106
6.2. Materials and methods.....	107
6.2.1. Study site.....	107

<b>6.2.2. Climate data.....</b>	<b>107</b>
<b>6.2.3. Litterfall collection.....</b>	<b>108</b>
<b>6.2.4. Leaf longevity.....</b>	<b>108</b>
<b>6.2.5. Statistical analysis.....</b>	<b>108</b>
<b>6.3. Results.....</b>	<b>110</b>
<b>6.4. Discussion.....</b>	<b>112</b>
<b>6.5. Conclusion.....</b>	<b>116</b>
<b>References.....</b>	<b>117</b>

## **CHAPTER – VII**

### **General Discussion and Conclusion**

<b>7.1. Discussion.....</b>	<b>133</b>
<b>7.2. Conclusion.....</b>	<b>139</b>
<b>References.....</b>	<b>140</b>

## LIST OF TABLES

Topic	Page no
<b>Table 2-1.</b> Kendall's coefficient of concordance, $W$ , showing agreement in the monthly changes in litterfall components of <i>Bruguiera gymnorrhiza</i> among five years of this study.	26
<b>Table 2-2.</b> Adjusted $R^2$ values from stepwise multiple regression analysis of vegetative and reproductive litterfall components of <i>Bruguiera gymnorrhiza</i> in relation to environmental factors. Significant probabilities of the coefficient value are indicated by * ( $p \leq 0.05$ ), ** ( $p \leq 0.01$ ), or *** ( $p \leq 0.001$ ).	27
<b>Table 2-3.</b> Annual amounts of vegetative and reproductive litterfall components of <i>Bruguiera gymnorrhiza</i> during the study period.	28
<b>Table 2-4.</b> Mean numbers of reproductive organs ( $m^{-2} yr^{-1} \pm SE$ ) of <i>Bruguiera gymnorrhiza</i> and their conversion rates ( $\% \pm SE$ ) during the study period.	29
<b>Table 3-1.</b> Annual amounts of vegetative and reproductive litterfall components of <i>Kandelia obovata</i> during the study period.	51
<b>Table 3-2.</b> Kendall's consistency coefficient, $W$ , showing agreement in the monthly changes in litterfall components of <i>Kandelia obovata</i> among five years of this study.	52
<b>Table 3-3.</b> Adjusted $R^2$ values from stepwise method of multiple regression analysis of vegetative and reproductive litterfall components of <i>Kandelia obovata</i> in relation to environmental factors. Significant probabilities of the coefficient value are indicated by * ( $p \leq 0.05$ ), ** ( $p \leq 0.01$ ), or *** ( $p \leq 0.001$ ).	53
<b>Table 3-4.</b> Mean numbers of reproductive organs ( $m^{-2} yr^{-1} \pm SE$ ) of <i>Kandelia obovata</i> and their conversion rates ( $\% \pm SE$ ) during the study period.	54
<b>Table 4-1.</b> Kendall's coefficient of concordance, $W$ , showing agreement in the monthly changes in litterfall components of <i>Rhizophora stylosa</i> among five years of this study.	74
<b>Table 4-2.</b> Adjusted $R^2$ values from the stepwise multiple regression analysis of vegetative and reproductive litterfall components from <i>Rhizophora stylosa</i> in relation to environmental factors. Significant probabilities are indicated by * ( $p \leq 0.05$ ), ** ( $p \leq 0.01$ ), or *** ( $p \leq 0.001$ ).	75

<b>Table 4-3.</b> Annual amounts of vegetative and reproductive litterfall components of <i>Rhizophora stylosa</i> during the study period.	<b>76</b>
<b>Table 4-4.</b> Mean numbers of reproductive organs ( $\text{m}^{-2} \text{yr}^{-1} \pm \text{SE}$ ) of <i>Rhizophora stylosa</i> and their conversion rates ( $\% \pm \text{SE}$ ) during the study period.	<b>77</b>
<b>Table 5-1.</b> Kendall's coefficient of concordance $W$ showing the degree of similarity in the monthly changes for the litterfall components of <i>Rhizophora stylosa</i> , <i>Kandelia obovata</i> , and <i>Bruguiera gymnorhiza</i> among the years during the study period.	<b>98</b>
<b>Table 5-2.</b> Mean number of flowers, fruits, and propagules ( $\text{m}^{-2} \text{year}^{-1}$ ) of the three species during the study period.	<b>99</b>
<b>Table 5-3.</b> Mean conversion rates ( $\% \pm \text{SE}$ ) of fertilized flowers into fruits and propagules of the three species during the study period.	<b>100</b>
<b>Table 5-4.</b> Mean annual mass ( $\text{g m}^{-2} \text{year}^{-1} \pm \text{SE}$ ) of litterfall components of the three species during the study period.	<b>101</b>
<b>Table 6-1.</b> Adjusted $R^2$ values from the stepwise multiple regression analysis of vegetative and reproductive litterfall components in relation to environmental factors. Significant probabilities are indicated by * ( $p \leq 0.05$ ), ** ( $p \leq 0.01$ ), and *** ( $p \leq 0.001$ ).	<b>121</b>
<b>Table 6-2.</b> Annual amounts ( $\text{g m}^{-2} \text{yr}^{-1} \pm \text{SE}$ ) of vegetative and reproductive litterfall components during the study period.	<b>122</b>
<b>Table 6-3.</b> Mean numbers of reproductive organs ( $\text{m}^{-2} \text{yr}^{-1} \pm \text{SE}$ ) and their conversion rates ( $\% \pm \text{SE}$ ) during the study period.	<b>123</b>
<b>Table 7-1.</b> Adjusted $R^2$ values from the stepwise multiple regression analysis of vegetative and reproductive litterfall components of <i>B. gymnorhiza</i> , <i>K. obovata</i> , and <i>R. stylosa</i> in relation to environmental factors. Significant probabilities are indicated by * ( $p \leq 0.05$ ), ** ( $p \leq 0.01$ ), and *** ( $p \leq 0.001$ ). Numerals in parentheses are tolerances of the coefficients of the multiple regression for a component.	<b>145</b>

## LIST OF FIGURES

Topic	Page no
Fig. 2-1. Location of the study area. The hatched zone indicates the mangrove area. Arrow indicates the plot area ( <i>filled square</i> ).	30
Fig. 2-2. Phenograms of the litterfall of the vegetative components of <i>B. gymnorrhiza</i> in Manko Wetland. Vertical bars represent standard errors of the means, $n = 5$ .	31
Fig. 2-3. Correlograms of vegetative litterfall of <i>B. gymnorrhiza</i> in Manko Wetland.	32
Fig. 2-4. Exponential relationship between monthly branch litterfall of <i>B. gymnorrhiza</i> and monthly maximum wind speed ( $R^2 = 0.81$ ). ●: 1st year; ○: 2nd year; ■: 3rd year; ◆: 4th year; ▼: 5th year.	33
Fig. 2-5. Phenograms of the litterfall of the reproductive components of <i>B. gymnorrhiza</i> in Manko Wetland. Vertical bars represent standard errors of the means, $n = 5$ .	34
Fig. 2-6. Correlograms of reproductive litterfall of <i>B. gymnorrhiza</i> in Manko Wetland.	35
Fig. 2-7. Crosscorrelation coefficients between pairs of the reproductive components of <i>B. gymnorrhiza</i> in Manko Wetland.	36
Fig. 3-1. Location of the study area. The hatched zone indicates the mangrove area. Arrow indicates the plot area ( <i>bold line</i> ).	55
Fig. 3-2. Climatic diagram of the four climatic factors examined (temperature, sunshine, humidity, and rainfall). Data were obtained from the Okinawa Meteorological Observatory, Naha, Okinawa.	56
Fig. 3-3. Phenograms of the litterfall of the vegetative components of <i>K. obovata</i> in Manko Wetland.	57
Fig. 3-4. Exponential relationship between monthly branch litterfall of <i>K. obovata</i> and monthly maximum wind speed ( $R^2 = 0.83$ ). ●: 1st year; ○: 2nd year; ■: 3rd year; ◆: 4th year; ▼: 5th year.	58
Fig. 3-5. Phenograms of the litterfall of the vegetative and reproductive components and the total litterfall of <i>K. obovata</i> in Manko Wetland.	59
Fig. 3-6. Phenograms of the litterfall of the reproductive components of <i>K. obovata</i> in Manko Wetland.	60

<b>Fig. 3-7.</b> Crosscorrelation coefficient between pairs of the reproductive components of <i>K. obovata</i> in Manko Wetland.	<b>61</b>
<b>Fig. 4-1.</b> Location of the study area. The hatched zone indicates the mangrove area. Arrow indicates the plot area ( <i>filled square</i> ).	<b>78</b>
<b>Fig. 4-2.</b> Phenograms of the litterfall of the vegetative components of <i>R. stylosa</i> in Manko Wetland. Vertical bars represent standard errors of the means, $n = 5$ .	<b>79</b>
<b>Fig. 4-3.</b> Correlograms of vegetative litterfall of <i>R. stylosa</i> in Manko Wetland.	<b>80</b>
<b>Fig. 4-4.</b> Exponential relationship between monthly branch litterfall of <i>R. stylosa</i> and monthly maximum wind speed ( $R^2 = 0.95$ ). ●: 1st year; ○: 2nd year; ■: 3rd year; ◆: 4th year; ▼: 5th year.	<b>81</b>
<b>Fig. 4-5.</b> Phenograms of the litterfall of the reproductive components of <i>R. stylosa</i> in Manko Wetland. Vertical bars represent standard errors of the means, $n = 5$ .	<b>82</b>
<b>Fig. 4-6.</b> Correlograms of reproductive litterfall of <i>R. stylosa</i> in Manko Wetland.	<b>83</b>
<b>Fig. 4-7.</b> Crosscorrelation coefficients between pairs of reproductive components of <i>R. stylosa</i> in Manko Wetland. Arrows indicate maturation periods.	<b>84</b>
<b>Fig. 5-1.</b> Location of the study area. The hatched zone indicates the mangrove area. Arrows indicate the plot area.	<b>102</b>
<b>Fig. 5-2.</b> Monthly patterns of litterfall of vegetative and reproductive components, and total litterfall, of <i>R. stylosa</i> ( <i>filled columns</i> ), <i>K. obovata</i> ( <i>open columns</i> ), and <i>B. gymnorhiza</i> ( <i>hatched columns</i> ). Vertical bars represent the standard error of the mean.	<b>103</b>
<b>Fig. 5-3.</b> Correlograms of monthly vegetative and reproductive litterfall components of <i>R. stylosa</i> ( <i>filled circles</i> ), <i>K. obovata</i> ( <i>hatched square</i> ), and <i>B. gymnorhiza</i> ( <i>open circles</i> ).	<b>104</b>
<b>Fig. 5-4.</b> Relationships between stipule litterfall and reproductive litterfall for <i>R. stylosa</i> ( $r = -0.675, p = 0.005$ ) (a), <i>K. obovata</i> ( $r = -0.332, p = 0.003$ ) (b), and <i>B. gymnorhiza</i> ( $r = 0.367, p = 0.178$ ) (c).	<b>105</b>
<b>Fig. 6-1.</b> Location of the study area. A non-continuous (215 m long, 5 m wide) belt-transect along the river was established and divided it into 43 plots.	<b>124</b>

<b>Fig. 6-2.</b> Phenograms of vegetative litterfall. Vertical bars represent the standard errors of means ( $n = 43$ ).	125
<b>Fig. 6-3.</b> Correlograms of vegetative litterfall components. Arrows indicate a 1-year cycle. **, Kendall's $W$ value with the significant probability of 0.01.	126
<b>Fig. 6-4.</b> Phenograms of reproductive litterfall. Vertical bars represent the standard errors of means ( $n = 43$ ).	127
<b>Fig. 6-5.</b> Correlograms of reproductive litterfall components. Arrows indicate a 1-year cycle. *, Kendall's $W$ value with the significant probability of 0.05.	128
<b>Fig. 6-6.</b> Crosscorrelation coefficients between pairs of reproductive components. Arrows indicate maturation periods.	129
<b>Fig. 6-7.</b> Exponential relationship between monthly branch litterfall of <i>B. gymnorhiza</i> and monthly maximum wind speed. ●: 1st year; ○: 2nd year; ■: 3rd year.	130
<b>Fig. 6-8.</b> Relationship between leaf litterfall per tree ( $l$ ) and population density ( $\rho$ ) on a log-log scale. The straight line is fit with $l = 745.2\rho^{-0.9774}$ . ●: 1st year; ○: 2nd year; ◆: 3rd year.	131
<b>Fig. 6-9.</b> Relationship between stipule litterfall and reproductive litterfall ( $r = 0.80, p < 0.001$ ). ●: 1st yr; ○: 2nd yr; ◆: 3rd yr.	132
<b>Fig. 7-1.</b> Relationship between leaf litterfall per tree ( $l$ ) and tree density ( $\rho$ ) of <i>B. gymnorhiza</i> at Manko Wetland and along the Okukubi River on log-log coordinates. The straight line is fit with $l = 701.48\rho^{-0.9905}$ ( $R^2 = 0.87$ ). ▲: 1st year-Manko; ▼: 2nd year-Manko; ◇: 3rd year-Manko; ■: 4th year-Manko; ●: 5th year-Manko. ●: 1st year- Okukubi; ○: 2nd year-Okukubi; ◆: 3rd year-Okukubi.	146
<b>Fig. 7-2.</b> Relationship between leaf litterfall per tree ( $l$ ) and tree density ( $\rho$ ) of <i>K. obovata</i> at Manko Wetland on log-log coordinates. The straight line is fit with $l = 484.71\rho^{-0.9099}$ ( $R^2 = 0.54$ ). ▲: 1st year; ▼: 2nd year; ◇: 3rd year; ■: 4th year; ●: 5th year.	147
<b>Fig. 7-3.</b> Relationship between leaf litterfall per tree ( $l$ ) and tree density ( $\rho$ ) of <i>R. stylosa</i> at Manko Wetland on log-log coordinates. The straight line is fit with $l = 850.91\rho^{-1.2813}$ ( $R^2 = 0.40$ ). ▲: 1st year; ▼: 2nd year; ◇: 3rd year; ■: 4th year; ●: 5th year.	148
<b>Fig. 7-4.</b> Phenology of reproductive organs of <i>B. gymnorhiza</i> .	149

- Fig. 7-5.** Phenology of reproductive organs of *K. obovata*. **150**
- Fig. 7-6.** Phenology of reproductive organs of *R. stylosa*. **151**
- Fig. 7-7.** Relationships between stipule litterfall and reproductive litterfall for *B. gymnorrhiza* ( $r = 0.007, p = 0.972$ ) (a), *K. obovata* ( $r = -0.42, p = 1.2 \times 10^{-06}$ ) (b), and *R. stylosa* ( $r = -0.22, p = 0.286$ ) (c) at Manko Wetland. ▲: 1st year; ▼: 2nd year; ◇: 3rd year; ■: 4th year; ■: 5th year. **152**
- Fig. 7-8.** Relationship between stipule litterfall and reproductive litterfall for *B. gymnorrhiza* at Manko Wetland and along the Okukubi River ( $r = 0.27, p = 0.0006$ ). ▲: 1st year- Manko; ▼: 2nd year- Manko; ◇: 3rd year- Manko; ■: 4th year- Manko; ■: 5th year- Manko; ●: 1st year- Okukubi; ○: 2nd year- Okukubi; ◆: 3rd year- Okukubi. **153**

# CHAPTER I

## General Introduction

---

### 1.1. Introduction

Mangroves are assemblages of trees and shrubs that dominate the intertidal zone along coastlines, estuaries and islands in tropical and subtropical regions of the world (Middleton and Mckee 2001). Mangrove forests are an important natural resource for coastal communities in tropical countries (Tomlinson 1994), but they are under threat due to widespread degradation and enormous pressures to use the land to support other economic activities, such as aquaculture (Fortes 1988; Adeel and Pomeroy 2002). Mangroves are often important contributors to the primary production of near-shore environments, providing a food source for a range of organisms (Lugo and Snedaker 1974; Odum and Heald 1975; Robertson et al. 1992; Coupland et al. 2005). The sustainable use of mangrove forest requires thorough understanding of the ecological processes by which mangrove forests are affected, and recover from both natural and man-associated disturbances (Padilla et al. 2004).

#### 1.1.1. *Litterfall production*

Mangrove vegetation supports food web through its litterfall production. The study of quantitative aspects of litterfall is an important part of forest ecology, dealing with a major pathway for both energy and nutrient transfer in this type of ecosystem (Bray and Gorham 1964). In order to fully understand the biological processes of energy and nutrient cycles, the quantity and composition of litterfall and its seasonal pattern of fall throughout the year must be pursued (Hagihara et al. 1978). Much of the leaf material produced by mangroves directly enters the detrital food web, with comparatively little consumed by herbivores (Robertson and Duke 1987; Farnsworth and Ellison 1991; Coupland 2002; Coupland et al. 2005). In contrast, mangrove flowers and propagules are often a valuable food source for a host of animals, including insects and crabs (Robertson et al. 1990; Clarke 1992; Minchinton and Dalby-Ball 2001; Clark and Kerrigan 2002; Coupland et al. 2005). Patterns in the production of leaves and timing of flowering and fruiting have been linked to seasonal variation in environmental

conditions, including temperature and rainfall in tropical and subtropical mangrove communities (Fernandes 1999; Gwada et al. 2000; Ochieng and Erftemeijer 2002; Coupland et al. 2005). Consequently, it has been suggested that plant phenologies develop that are synchronized to local or regional environmental conditions (Fernandes 1999). Manko Wetland, Okinawa Island, Japan, contains some of the most diverse mangrove communities such as *Bruguiera gymnorhiza* (L.) Lamk., *Kandelia obovata* (S., L.) Yong, and *Rhizophora stylosa* Griff., all in the family Rhizophoraceae, the most important family of true mangroves, which consists of 22 mangrove species and numerous hybrids found in tropical and subtropical areas of the world. However, very few studies have documented litter production (Hardiwinoto et al. 1989; Mokolensang and Tokuyama 1998) or leaf phenology and litterfall production (Gwada et al. 2000; Khan et al. 2009; Analuddin et al. 2009; Sharma et al. 2011, 2012) of these three species in the subtropics. Therefore, this study focuses on investigation of phenological changes and compares litterfall production among *B. gymnorhiza*, *R. stylosa*, and *K. obovata*. This study also describes the temporal variation of litterfall production of mangrove *B. gymnorhiza* along the Okukubi River, Okinawa Island, Japan, over three years.

### **1.1.2. Vegetative and reproductive phenology**

Litterfall production is the shedding of vegetative or reproductive plant structures (Siddiqui and Qasim 1990). Litterfall collection is a standard non-destructive technique for assessing the productivity, phenology, and turnover of biomass in a forest (Newbould 1967). Phenological events can be assessed directly by observation but also through indirect evidence, e.g., from litterfall data, if the possible time lag between formation and shedding of plant organs is known. For example in Rhizophoraceae, occurrence of stipules in litterfall is of special interest as stipules protect the shoot's terminal bud and are shed when a new pair of leaves unfolds. They are therefore a reliable indicator for leaf formation (Mehlig 2006). Many studies have documented mangrove litterfall to assess mangrove productivity; however, fewer studies have documented mangrove phenology, particularly vegetative and reproductive phenology using litterfall data. Knowledge of mangrove phenology is important for understanding both mangrove contribution to near-shore productivity and the plant-animal interactions within the community itself.

Phenology is the study of the seasonal occurrence of developmental or life cycle events, such as budbreak, flowering, or autumn leaf drop (Rathcke and Lacey 1985). The timing of these events is known to be sensitive to short-and long-term variability in climate, and is thus a robust indicator of the effects of climate change, especially observed rising temperatures (Richardson et al. 2006). The diversity and complexity of phenological patterns is greater in tropical than in temperate forest ecosystems (Borchert 1983). In tropical and subtropical forest ecosystems, the phenological rhythms may be very variable among years, mainly for flowering and fruiting (Engel and Martines 2005).

Plants that produce new organs when irradiance is maximal will realize two advantages. First, assimilation is greatest for a crop of new leaves before herbivory and senescence reduce leaf area and photosynthetic potential (Larcher 1973; Field 1987). Second, it is most efficient to transfer assimilates directly into growing organs rather than store them in different tissues first and mobilize and translocate them later (Chapin et al. 1990). Light limited trees are predicted to produce new leaves and flowers during the season of maximal irradiance. Phenological selection requires predictable temporal variation in a limiting environmental factor (Wright and Schaik 1994).

As mangroves in Okinawa thrive in a distinctly seasonal climate, they have to cope with substantial seasonal changes in environmental factors, both at macro- and micro-scale levels. Therefore, it can be expected that several climatically-related environmental factors that influence their growth and production, such as water status (acting through rainfall or fresh-water supply), insolation and temperature, intertidal salinity, soil aeration and redox potential are to be expected to concomitantly vary with seasonality (Gwada et al. 2000).

Mangrove species of the family Rhizophoraceae are characterized by vivipary, where the embryo develops into a seedling while still forming part of the fruit attached to the parent tree (Tomlinson 1994). According to Newstrom et al. (1994), at least a five-year period is needed to recognize and describe the great diversity of reproductive phenological patterns in tropical trees, due to many differences in frequency and regularity within time series between species. In spite of this, long term phenological studies are scarce in the literature, the majority of them referring to a period of up to 1 to 2 years. Detailed site-specific phenological studies have been documented for members

of the family Avicenniaceae, for instances, the genus *Avicennia* (Wium-Andersen and Christensen 1978; Lopez-Portillo and Ezcurra 1985; Duke 1990). Good detailed reports also available for the family Rhizophoraceae, for instance, the genera *Bruguiera* (Steinke and Charles 1984), *Rhizophora* (Gill and Tomlinson 1971; Duke et al. 1984; Christensen and Wium-Andersen 1977; Wium-Andersen 1981, Coupland et al. 2005, 2006; Akmar and Juliana 2012; Wilson and Saintilan 2012), and *Ceriops* (Slim et al. 1996). *Kandelia* has not received sufficient attraction with respect to these topics. No previous studies have examined the vegetative and reproductive phenology of *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* growing at the northern limit of their biogeographical distribution. Therefore, the aim of this study is to describe the phenorhythms and phenological patterns of the major tree species at Manko Wetland, during a five-year period, in relation to climatic factors. The current study also describes the phenology of *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* at Manko Wetland and relates it to environmental factors.

### **1.1.3. Leaf longevity**

Leaf longevity is defined as the time period from emergence to fall of a leaf. The leaf life span is related to the balance between costs and benefits associated with leaf construction and maintenance (Chabot and Hicks 1982; Harper 1989; Kikuzawa 1991; Reich et al. 1991). Thus, leaf longevity may be considered as a balance between lifetime carbon gain of a leaf and its construction and maintenance costs (Chabot and Hicks 1982). Leaf phenology is assumed to change with the climatic change. Phenological observations, such as leaf fall and new leaf production, on the vegetative growth of mangroves allow for estimates of leaf longevity (Wium-Andersen 1981; Duke et al. 1984). Therefore, this study focuses on the estimation of leaf longevity of *B. gymnorrhiza* at Manko Wetland and compare favorably with those of other studies.

### **1.1.4. Typhoon effects**

Mangroves are important wetland ecosystems throughout the tropical and subtropical coastal areas of the world (Mitsch and Gosselink 2000), providing a variety of ecosystem services such as sources of food (fishes, crabs, etc.), wood, and protection from extreme events such as cyclones and tsunamis (Giesn et al. 2006). Tropical

cyclones (typhoons) affect ecosystem structure in tropical coastal ecosystems in many islands of the western Pacific (Kauffman and Cole 2010). The effects of typhoons are not limited to structural damage including uprooting of trees to form forest gaps. Strong winds, particularly in combination with salt stress, can make forests largely defoliate (Xu et al. 2004). Disturbances, such as wind, can greatly affect annual or monthly litterfall rates (Lodge et al. 1991; Vitousek et al. 1995). Tropical cyclones in Central America (hurricanes) and East Asia (typhoons) impact forests with varying frequencies, from annually in Taiwan (Mabry et al. 1998), to once a century in New England (Boose et al. 1994). When these storms impact a forest they often cause large amounts of litterfall (Lodge et al. 1991; Lu et al. 1988; Horng et al. 1995; Lin 1998; Lin et al. 2003). In Japan, the areas most frequently affected by typhoons are the southern part of the main islands and the subtropical southern islands. Despite the fact that typhoons are major, natural disturbances in the western Pacific (Schneider 1967), few studies have focused on the ecological and physical effects of typhoons on Pacific islands. Only a few studies have examined the effects of typhoons on litterfall of subtropical forest of Japan (Xu et al. 2004; Sato 2004) and only a few previous studies have examined the effects of typhoon on the mangroves of Okinawa Island, Japan (Hardiwinoto et al. 1989; Sharma et al. 2012). Therefore, this study focuses on the effects of typhoon on the mangroves of Okinawa Island dominated by *B. gymnorrhiza*, *K. obovata*, and *R. stylosa*.

#### **1.1.5. Successful conversion from flowers to propagules**

The reproductive biology of mangroves has often been regarded with interest due to the unusual breeding mechanisms, including vivipary, exhibited by many of these plants (Tomlinson 1994). Surprisingly little is known of mangrove pollination biology, with limited emphasis on the process and success rate of propagule production (Gill and Tomlinson 1971; Primack et al. 1981; Duke et al. 1984; Duke 1990; Hogarth 1999; Tyagi 2003; Coupland et al. 2005, 2006). The aim of this study is to investigate the reproductive biology; specifically, the relative success rate of fruit and propagule production from flower of three mangrove species *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* at Manko Wetland.

#### **1.1.6. Development phase of reproductive organs**

Most mangrove species share two common characters: i) fruit/propagule/seed dispersal in water and ii) vivipary (Macnae 1968; Tomlinson 1994). In viviparous plants the offspring grows continuously while still attached to the mother tree. When there is no dormancy at all and seed even germinates before abscission, this is called true vivipary. In case of mangroves, true vivipary exists in all species of the genera *Bruguiera*, *Kandelia*, *Rhizophora*, and *Ceriops* all belonging to the family Rhizophoraceae (Tomlinson 1994). Phenological data are essential for prediction of the tree's ability to adapt growth and propagation strategies to ambient conditions (Mehlig 2006). Vegetative propagation in mangroves of the Rhizophoraceae family has been unsuccessful (Rabinowitz 1978). So, sexual reproduction remains the main mode of plant production for the costal rehabilitation program for mangrove restoration (Tyagi 2003). Understanding the flowering, fruiting, and propagule production pattern as well as development phase of each reproductive organ are important to know the propagation strategies at the northern limit of their biogeographical distribution. Therefore, this study describes the flowering pattern and development phase of each reproductive organ in *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* at Manko Wetland.

#### **1.1.7. Coordination between leaf development and reproductive cycles**

In mangroves, there is some coordination between vegetative and floral phenology (Wium-Andersen and Christensen 1978). Coordination may be an indication of resource partitioning within plants as suggested by Duke et al. (1984). Some mangrove species showed clear depression in leafing rates when the production of flowers and fruits had a maximum (Gill and Tomlinson 1971; Wium-Andersen and Christensen 1978; Duke et al. 1984; Coupland et al. 2005). Understanding of the coordination between vegetative and reproductive organs production are important to know the resource partitioning strategies of mangrove *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* growing at the northern limit of their biogeographical distribution. Therefore, this study describes the correlations between leafing and reproductive organs production in *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* on Okinawa Island.

## **References**

Adeel Z, Pomeroy R (2002) Assessment and management of mangrove ecosystems in

- developing countries. *Trees* 16:235–238
- Akmar NZ, Juliana WAW (2012) Reproductive phenology of two *Rhizophora* species in Sungai Pulai Forest Reserve, Johor, Malaysia. *Malays Appl Biol* 41:11–21
- Analuddin K, Sharma S, Suwa R, Hagihara A (2009) Crown foliage dynamics of mangrove *Kandelia obovata* in Manko Wetland, Okinawa Island, Japan. *J Oceanogr* 65:121–127
- Boose ER, Foster DR, Fluet M (1994) Hurricanes and landscape-level disturbance in tropical and temperate forests. *Ecol Monogr* 64:369–400
- Borchert R (1983) Phenological and control of flowering in tropical trees. *Biotropica* 15:81–89
- Bray JR, Gorham E (1964) Litter production in forests of the world. *Adv Ecol Res* 2:101–157
- Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. *Annu Rev. Ecol Syst* 13:229–259
- Chapin FS, Schulze ED III, Money HA (1990) The ecology and economics of storage in plants. *Annu Rev Ecol Evol Syst* 21:423–447
- Christensen B, Wium-Andersen S (1977) Seasonal growth of mangrove trees in southern Thailand. I. The phenology of *Rhizophora apiculata* BL. *Aquat Bot* 3:281–286
- Clark PJ (1992) Predispersal mortality and fecundity in the grey mangrove (*Avicennia marina*) in southeastern Australia. *Aust J Ecol* 17:161–168
- Clark PJ, Kerrigan R (2002) The effects of seed predators on the recruitment of mangroves. *J Ecol* 90:728–736
- Coupland GT (2002) The ecological interaction between insects and mangroves in Darwin Harbour, Australia. PhD Thesis, Northern Territory University, Darwin
- Coupland GT, Paling EI, McGuinness KA (2005) Vegetative and reproductive phenologies of four mangrove species from northern Australia. *Aust J Bot* 53:109–117
- Coupland GT, Paling EI, McGuinness KA (2006) Floral abortion and pollination in four species of tropical mangroves from northern Australia. *Aquat Bot* 84:151–157
- Duke NC, Bunt JS, Williams WT (1984) Observations on the floral and vegetative phenologies of north-eastern Australian mangroves. *Aust J Bot* 32:87–99

- Duke NC (1990) Phenological trends with latitude in the mangrove tree *Avicennia marina*. *J Ecol* 78:113–133
- Engel VL, Martins FR (2005) Reproductive phenology of Atlantic forest tree species in Brazil: an eleven year study. *Trop Ecol* 46:1–16
- Fernandes MEB (1999) Phenological patterns of *Rhizophora* L., *Avicennia* L. and *Laguncularia* Gaertn. f. in Amazonian mangrove swamps. *Hydrobiologia* 413:53–62
- Field C (1987) Leaf-age effects on stomatal conductance. In: Zeiger E, Farquhar GD, Cowan IR (eds) *Stomatal function*. Stanford University Press, Stanford, Calif, pp 367–384
- Fortes MD (1988) Mangrove and seagrass beds of East Asia: habitats under stress. *Ambio* 17:207–213
- Farnsworth EJ, Ellison AM (1991) Patterns of herbivory in a Belizean mangrove swamp. *Biotropica* 23:555–567
- Giesen W, Wulffraat S, Zieren M, Scholten L (2006) *Mangrove guidebook for Southeast Asia*. FAO and Wetlands International. Dharmasarn Co., Ltd, Bangkok
- Gill AM, Tomlinson PB (1971) Studies on the growth of red mangrove (*Rhizophora mangle* L.). 3. Phenology of the shoot. *Biotropica* 3:109–124
- Gwada P, Makoto T, Uezu Y (2000) Leaf phenological traits in the mangrove *Kandelia candel* (L.) Druce. *Aquat Bot* 68:1–14
- Hagihara A, Suzuki M, Hozumi K (1978) Seasonal fluctuations of litterfall in a *Chamaecyparis obtuse* plantation. *J Jap For Soc* 60:397–404
- Hardiwinoto S, Nakasuga T, Igarashi T (1989) Litter production and decomposition of a mangrove forest at Ohura Bay, Okinawa. *Res Bull Coll Exp For, Hokkaido Univ* 46:577–594
- Harper JL (1989) The value of a leaf. *Oecologia* 80:53–58
- Hornig FW, YU HM, Ma FC (1995) Typhoons of 1994 doubled the annual litterfall of the Fu-shan mixed hardwood forest ecosystem in northeastern Taiwan. *Bull Taiwan For Res Inst New Ser* 10:485–491
- Kauffman JB, Cole TG (2010) Micronesian mangrove forest structure and tree responses to a severe typhoon. *Wetlands* 30:1077–1084
- Khan MNI, Suwa R, Hagihara A (2009) Biomass and aboveground net primary

- production in a subtropical mangrove stand of *Kandelia obovata* (S., L.) Yong at Manko Wetland, Okinawa, Japan. *Wetlands Ecol Manage* 17:585–599
- Kikuzawa K (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *Amer Naturalist* 138:1250–1263
- Larcher W (1973) *Ökologie der planzen*. Ulmer, Stuttgart
- Lopez-Portillo J, Ezcurra E (1985) Litterfall of *Avicennia germinans* L. in a one year cycle in a mudflat at the Laguna de Mecoanacan, Tabasco, Mexico. *Biotropica* 17:186–190
- Lin KC, Hamburg SP, Tang S, Hsia Y, Lin T (2003) Typhoon effects on litterfall in a subtropical forest. *Can J For Res* 33:2184–2192
- Lin ST (1998) Dry matter dynamics and the nutrient contents of litterfall in the Chi-lan Shan hardwoods of northeastern Taiwan. *Q J Chin For* 31:115–130
- Lodge DJ, Scatena FN, Asbury CE, Sánchez MJ (1991) Fine litterfall and related nutrient inputs resulting from hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico. *Biotropica* 23:336–342
- Lu SY, Chi SC, Lu HS (1988) Physical and hydrologic characteristics of forest floor at five different stands in central Taiwan. *Bull Taiwan For Res Inst. New Ser* 3:407–413
- Lugo AE, Snedaker SC (1974) The ecology of mangroves. *Ann Rev Ecol Evol Syst* 5:39–64
- Mabry CM, Hamburg SP, Lin TC, Horng FW, King HB, Hsia YJ (1998) Typhoon disturbance and stand-level damage patterns at a subtropical forest in Taiwan. *Biotropica* 30:238–250
- Macnae W (1968) A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific region. *Adv Mar Biol* 6:73–270
- Mehlig U (2006) Phenology of the red mangrove, *Rhizophora mangle* L., in the Caeté Estuary, Pará, equatorial Brazil. *Aquat Bot* 84:158–164
- Middleton BA, Mckee KL (2001) Degradation of mangrove tissues and implications for peat formation in Belizean island forests. *J Ecol* 89:818–828
- Minchinton TE, Dalby-Ball M (2001) Frugivory by insects on mangrove propagules: effects on the early life history of *Avicennia marina*. *Oecologia* 129:243–252
- Mitsch WJ, Gosselink JG (2000) *Wetlands*, 3rd edn. Wiley, New York

- Mokolensang JF, Tokuyama A (1998) Litter production of mangrove forest at the Gesashi River. *Bull Coll Sci, Univ of Ryukyus* 65:73–79
- Newbould PJ (1967) Methods for estimating the primary production of forests. IBP Handbook No.2. Blackwell Scientific Publications, Oxford
- Newstrom LE, Frankie GW, Baker HG (1994) A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica* 2:141–159
- Ochieng CA, Erftemeijer PLA (2002) Phenology, litterfall and nutrient resorption in *Avicennia marina* (Forssk.) Vierh in Gazi Bay, Kenya. *Trees* 16:167–171
- Odum WE, Heald EJ (1975) The detritus-based food web of an estuarine mangrove community. In: Cronin LE (ed) *Estuarine research*. Academic press, New york, pp. 265–286
- Padilla C, Fortes MD, Duarte CM, Terrados J, Kamp-Nielsen L (2004) Recruitment, mortality and growth of mangrove (*Rhizophora* sp.) seedlings in Ulugan Bay, Palawan, Philippines. *Trees* 18:589–595
- Rabinowitz D (1978) Dispersal properties of mangrove propagules. *Biotropica* 10:47–57
- Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. *Annu Rev Ecol Evol Syst* 16:179–214
- Reich PB, Uhl C, Walters MB, Ellsworth DS (1991) Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species. *Oecologia* 86:16–24
- Richardson AD, Bailey AS, Denny EG, Martin CW, Keefes J (2006) Phenology of a northern hardwood forest canopy. *Glob Change Biol* 12:1174–1188
- Robertson AI, Duke NC (1987) Insect herbivory on mangrove leaves in North Queensland. *Aust J Ecol* 12:1–7
- Robertson AI, Giddins R, Smith TJ (1990) Seed predation by insects in tropical mangrove forest: extent and effects on seed viability and the growth of seedlings. *Oecologia* 83:213–219
- Robertson AI, Alongi DM, Boto KG (1992) Food chains and carbon fluxes. In: Robertson AI, Alongi DM (eds) *Tropical mangrove ecosystems*, American Geophysical Union, Washington, DC, pp. 293–329
- Sato T (2004) Litterfall dynamics after a typhoon disturbance in a *Castanopsis*

- cuspidata* coppice, southwestern Japan. *Ann For Sci* 61:431–438
- Schneider DM (1967) Typhoons on Yap. *Human organization* 16:10–14
- Sharma S, Kamruzzaman M, Hoque ATMR, Analuddin K, Hagihara A (2011) Vegetative and reproductive phenology, and litterfall production of *Rhizophora stylosa* in Okinawa Island, Japan. *Int J Environ* 1:20–26
- Sharma S, Hoque ATMR, Analuddin K, Hagihara A (2012) Litterfall dynamics in an overcrowded mangrove *Kandelia obovata* (S.,L.) Yong stand over five years. *Estuar Coast Shelf Sci* 98:31–41
- Siddiqui PJ, Qasim (1990) Litter production and physico-chemical conditions in mangrove, *Avicennia marina* (Forsk.) Vierh., swamps at Karachi back waters and Bakran Creek. *J Islam Acad Sci* 3:15–21
- Slim FJ, Gwada P, Hemminga MA (1996) Biomass and litterfall of *C. tagal* and *R. mucronata* in the mangrove forest of Gazi bay, Kenya. *Mar Freshwater Res* 47:999–1007
- Steinke TD, Charles LM (1984) Productivity and phenology *Avicennia marina* (Forsk.) Vierh. and *Bruguiera gymnorhiza* (L.) Lamk. in Mgeni estuary, South Africa. In: Teas HJ (ed.) *Physiology and management of mangroves*. Junk, The Hague, pp.25–36
- Tomlinson PB (1994) *The botany of mangroves*. Cambridge University Press, Cambridge
- Tyagi AP (2003) Location and interseasonal variation in flowering, propagule setting and propagule size in mangroves species of the family Rhizophoraceae. *Wetlands Ecol Manage* 11:167–174
- Vitousek PM, Gerrish G, Turner DR, Walker LR, Mueller-Dombois D (1995) Litterfall and nutrient cycling in four Hawaiian montane rainforests. *J Trop Ecol* 11:189–203
- Wilson NC, Saintilan N (2012) Growth of the mangrove species *Rhizophora stylosa* Griff. at its southern latitudinal limit in eastern Australia. *Aquat Bot* 101:8–17
- Wium-Andersen S (1981) Seasonal growth of mangrove trees in Southern Thailand. III. Phenology of *Rhizophora mucronata* Lamk. and *Scyphiphora hydrophyllacea* Gaertn. *Aquat Bot* 10:371–376

- Wium-Andersen S, Christensen B (1978) Seasonal growth of mangrove trees in southern Thailand. II. Phenology of *Bruguiera cylindrica*, *Ceriops tagal*, *Lumnitzera littorea* and *Avicennia marina*. *Aquat Bot* 5:383–390
- Wright JS, Schaik CPV (1994) Light and the phenology of tropical trees. *Amer Naturalist* 143:192–199
- Xu X, Hirata E, Shibata H (2004) Effect of typhoon disturbance on fine litterfall and related nutrient input in a subtropical forest on Okinawa Island, Japan. *Basic Appl Ecol* 5:271–282

## CHAPTER II

### Vegetative and Reproductive Phenology of the Mangrove

#### *Bruguiera gymnorhiza* (L.) Lamk.

---

##### 2.1. Introduction

Mangroves are important contributors of nutrients to coastal ecosystems. Their litterfall is a valuable indicator of their productivity and input of materials and energy into subtidal systems (Mackey and Smail 1995). Litterfall also indicates phenological events for mangrove species (Leach and Burgin 1985; Duke 1990; Clark 1994) when the time lag between the formation and shedding of plant organs is known (Mehlig 2006). Mangrove phenology is important for understanding both the contribution of mangroves to near-shore productivity and plant–animal interactions within the community itself (Coupland et al. 2005). Phenological observations, such as leaf fall and new leaf production, on the vegetative growth of mangroves allow for estimates of leaf longevity (Wium-Andersen 1981, Duke et al. 1984). In addition to fallen leaves, mangrove reproductive organs are often a valuable food source for a wide variety of animals, including insects and crabs (Robertson et al. 1992). Phenological events in mangrove communities have been suggested to be influenced by local or regional environmental conditions, particularly day length, air temperature, rainfall, and water status (Saenger and Moverley 1985, Naido 1989; Duke 1990; Fernandes 1999). Many studies have documented mangrove litterfall to assess mangrove productivity; however, fewer studies have documented mangrove phenology, particularly reproductive phenology.

*Bruguiera gymnorhiza* (L.) Lamk is widely distributed from the southeastern coast of Africa through Asia to subtropical Australia and the southwestern Pacific (Allen and Duke 2006). The present study was conducted at Manko Wetland, Okinawa Island, Japan, which is occupied by *B. gymnorhiza* and other species of the family Rhizophoraceae. Because Okinawa has a distinct seasonal climate, its mangroves must cope with substantial seasonal changes in environmental factors. No previous studies have examined the vegetative and reproductive phenology of *B. gymnorhiza* growing at the northern limit of its biogeographical distribution, though a few studies have investigated litterfall production (Hardiwinoto et al. 1989; Mokolensang and Tokuyama

1998). Therefore, the aims of the present study were to investigate the vegetative and reproductive phenology of *B. gymnorhiza* growing in a subtropical region, determine the development period of each reproductive organ, and to identify how climatic factors affect *B. gymnorhiza* phenology.

## 2.2. Materials and methods

### 2.2.1. Study site

The study was conducted at Manko Wetland, Okinawa Island, Japan (26°11'N, 127°40'E) (Fig. 2-1), over 4 years from April 2008 to March 2013. This wetland is an important area for migratory birds and has been registered on the Ramsar List of Wetlands of International Importance (a Ramsar site) since 1999. The study area is a brackish tidal flat covering an extensive area at low tide; the average tidal range varies from 3–212 mm, that is, a minimum low of 3 mm to maximum height of 212 mm. The mangroves grow in a mud flat area mainly composed of clay (RIS 1999). The area is subtropical, as determined by a warmth index (i.e., a cumulative value of mean monthly temperatures  $> 5^{\circ}\text{C}$ ) of  $219.8 \pm 15.4$  (SE)  $^{\circ}\text{C}$  month from 2000–2009 (Okinawa Meteorological Observatory, Naha, Japan), within the range of 180–240 $^{\circ}\text{C}$  month for subtropical regions (Kira 1991).

### 2.2.2. Forest structure

Four mangrove species grow at the study site; three belong to the family Rhizophoraceae: *Bruguiera gymnorhiza* (L.) Lamk., *Kandelia obovata* Sheue, Liu and Yong, and *Rhizophora stylosa* Griff. The fourth species, *Excoecaria agallocha* L., is in the family Euphorbiaceae. We established five plots (4 m  $\times$  4 m each) in a *B. gymnorhiza* stand to represent the full tidal range at which the species occurred. The number of plots was based on the availability of the pure stands of the species. All trees in the study plots were numbered, and height ( $H$ ) and stem diameter at  $H/10$  ( $D_{0.1H}$ ) were measured in April 2010 and 2012. Tree density, mean  $H$ , and mean  $D_{0.1H}$  of *B. gymnorhiza* were 1.8  $\text{m}^{-2}$ ,  $3.2 \pm 0.1$  m, and  $5.1 \pm 0.2$  cm, respectively as of 2012.

### 2.2.3. Climate data

Meteorological data were obtained from the Okinawa Meteorological Observatory,

Naha, Japan, from April 2008 to March 2013 (i.e., over the time period during which the field work was conducted). Observation station is responsible for weather services in Okinawa region. It is 2.8 km far from the study area. During the study period, the temperature fluctuated approximately 15°C from the coldest month to the hottest, and mean annual air temperature was  $23.2 \pm 0.2^\circ\text{C}$ . Mean annual day length was  $4362.7 \pm 2.5 \text{ h yr}^{-1}$ . Rainfall varied throughout the year but exceeded  $100 \text{ mm month}^{-1}$  in most months. The monthly rainfall during the study period ranged from  $20 \text{ mm month}^{-1}$  in December 2008 to  $674 \text{ mm month}^{-1}$  in August 2012 with an annual mean of  $2224.5 \pm 247.0 \text{ mm yr}^{-1}$ . The mean monthly air relative humidity was  $73.5 \pm 0.8 \%$ . Monthly maximum wind speed varied from the lowest  $10.6 \text{ m s}^{-1}$  in February 2013 to the highest  $35 \text{ m s}^{-1}$  in May 2011.

#### **2.2.4. Litterfall collection**

Litterfall was collected using 1-mm mesh litter traps with collection area of  $0.2 \text{ m}^2$ . Two litter traps were placed in each plot  $> 1 \text{ m}$  high from the ground to avoid tidal water. The litter traps were emptied monthly; the collected litterfall was kept in a cotton bag and carried to the laboratory where it was separated into leaves, stipules, branches, flower bud primordia, flower buds, flowers, and propagules. Individual components of the litterfall were dried at  $80^\circ\text{C}$  for 48 h, desiccated at room temperature, and then weighed using a digital balance (EK-600H, A & D Co., Ltd., Tokyo, Japan). The numbers of reproductive components, such as flowers and propagules, were counted to estimate the success of propagule sets. Following Duke (1990), the conversion rates from flower to propagule was calculated as  $(\text{propagules}) / (\text{flowers} + \text{propagules})$ .

#### **2.2.5. Leaf longevity**

Leaf mass of the standing trees,  $w_L$ , (kg) was estimated using the allometric equation for *B. gymnorhiza* (Deshar et al. 2012) as follows:

$$w_L = 0.01349(D_{0.1H}^2 \cdot H)^{0.7779} \quad (2-1)$$

where  $H$  is the tree height (m) and  $D_{0.1H}$  is the stem diameter at  $H/10$  (cm).

In a stand undergoing self-thinning leaf biomass stabilizes when annual leaf production is balanced by annual leaf litterfall (Waring and Running 1998; Deshar et al. 2012; Sharma et al. 2012). Leaf biomass of the stand was estimated by applying Eq.

(2-1) to the census data of each plot in 2010 and 2012. The ratio of leaf biomass,  $B$ , ( $\text{kg m}^{-2}$ ) to annual leaf litterfall,  $F$ , ( $\text{kg m}^{-2} \text{ yr}^{-1}$ ) provides an estimate of mean leaf longevity,  $L$ , (yr) for trees in the stand:

$$L = \frac{B}{F} \quad (2-2)$$

### 2.2.6. Statistical analysis

Kendall's coefficient of concordance,  $W$ , was used to evaluate the degree of similarity in monthly change among years for each litterfall component. Litterfall data were ranked by monthly mass for every year, and  $W$  was calculated for monthly litterfall. When  $W = 1.0$ , the monthly changes in litterfall are concordant among years, while when  $W = 0.0$ , the monthly changes are completely different among years. The  $\chi^2$  test was used to determine the significance of the  $W$  value (Saito et al. 2003).

We performed a stepwise multiple regression analysis to determine the effects of five environmental factors — temperature, day length, rainfall, humidity, and maximum wind speed — on litterfall of leaves, stipules, branches, flower buds, flowers, and propagules, using MA-MACRO/MRA software (ver. 3.0, Practical Business Education Institute, Tokyo, Japan). The stepwise multiple regression was continued until the adjusted  $R^2$  value showed a decreasing trend. A criterion of  $F$  value  $> 2.0$  was set to determine the minimum significance of a variable to be included in the equation. Multiple regression analysis of environmental factors on mangrove litterfall is difficult because the environmental factors often co-vary. A criterion of tolerance  $> 0.1$  was selected to avoid multicollinearity among the variables (Shiga et al. 2004).

The autocorrelation coefficient  $r_{xx}(k)$  was calculated for each litterfall component to evaluate its yearly cycle:

$$r_{xx}(k) = \frac{\sum_{j=1}^{N-k} (X_j - \bar{X}_{1, N-k})(X_{j+k} - \bar{X}_{1+k, N})}{\sqrt{\sum_{j=1}^{N-k} (X_j - \bar{X}_{1, N-k})^2 \sum_{j=1}^{N-k} (X_{j+k} - \bar{X}_{1+k, N})^2}}, \text{ where } k (= 0, 1, 2, \dots) \text{ is the}$$

time lag in months;  $N (= 48)$  is the total number of months in the time series;  $X_j$  and  $X_{j+k}$  are litterfall components of the  $j^{\text{th}}$  month and  $(j+k)^{\text{th}}$  month, respectively; and  $\bar{X}_{1, N-k}$  and  $\bar{X}_{1+k, N}$  are the mean values of the components from the first to the  $(N-k)^{\text{th}}$  month and from the  $(1+k)^{\text{th}}$  to the  $N^{\text{th}}$  month, respectively.

The crosscorrelation coefficient  $r_{xy}(l)$  was calculated to identify the lag,  $l$ , in

maturation time between reproductive organs using their time series data:

$$r_{xy}(l) = \frac{\sum_{j=1}^{N-l} (X_j - \bar{X}_{1, N-l})(Y_{j+l} - \bar{Y}_{1+l, N})}{\sqrt{\sum_{j=1}^{N-l} (X_j - \bar{X}_{1, N-l})^2 \sum_{j=1}^{N-l} (Y_{j+l} - \bar{Y}_{1+l, N})^2}}, \text{ where } l (= 0, 1, 2, \dots) \text{ is the time lag}$$

in months;  $N (= 48)$  is the total number of months in the time series;  $X_j$  and  $Y_{j+l}$  are the reproductive components, respectively, of the  $j^{\text{th}}$  month and  $(j+l)^{\text{th}}$  month;  $\bar{X}_{1, N-l}$  is the mean value of an element from the first to the  $(N-l)^{\text{th}}$  month; and  $\bar{Y}_{1+l, N}$  is the mean value of the other element from the  $(1+l)^{\text{th}}$  to the  $N^{\text{th}}$  month.

## 2.3. Results

### 2.3.1. Vegetative phenology

There were distinct differences in vegetative (leaf, stipule, branch) organ litterfall between months in *B. gymnorrhiza* (Fig. 2-2). Leaf litterfall (Fig. 2-2a) and stipule litterfall (Fig. 2-2b) occurred continuously throughout the year, and each showed a clear monthly trend. Leaf litterfall was highest in summer (June–August) and lowest in winter (December–February). In contrast to other years, excessive leaf litterfall occurred in May 2011 due to typhoon. Thereafter, the rates in that year decreased distinctly in June and July (summer). Stipule litterfall, which is an indicator of new leaf production, was also highest in summer months (June–August) and lowest in winter months (December–February). Kendall's coefficient of concordance,  $W$ , revealed that the monthly leaf and stipule litterfall were strongly and significantly concordant among study years (Table 2-1). Autocorrelation coefficient revealed that the leaf (Fig. 2-3a) and stipule (Fig. 2-3b) litterfall showed a 1-year cycle. Branch litterfall, including small twigs, bark, and large branches, showed no clear monthly pattern (Fig. 2-2c, Table 2-1) or annual cycle (Fig. 2-3c). Figure 2-4 depicts the exponential relationship between branch litterfall and monthly maximum wind speed. Branch litterfall increased exponentially with increasing monthly maximum wind speed.

Table 2-2 presents the results of the stepwise multiple regression analyses for vegetative and reproductive (flower bud, flower, propagule) organs litterfall with environmental factors. Leaf litterfall was significantly related to monthly maximum wind speed and monthly day length, whereas stipule litterfall was related to monthly

mean air temperature, monthly maximum wind speed, and monthly rainfall. Branch litterfall varied with monthly maximum wind speed.

The living leaf biomass of this *B. gymnorrhiza* stand was  $660 \pm 82$  and  $766 \pm 96$  g m<sup>-2</sup> for the years 2010 and 2012, respectively, whereas the annual leaf litterfall of the stand was  $386 \pm 5$  and  $539 \pm 12$  g m<sup>-2</sup> yr<sup>-1</sup> for the 2<sup>nd</sup> year (April 2009 to March 2010) and 4<sup>th</sup> year (April 2011 to March 2012), respectively (Table 2-3). Using these values we estimate that leaf longevity was  $1.7 \pm 0.3$  and  $1.4 \pm 0.1$  yr for the 2<sup>nd</sup> year and 4<sup>th</sup> year, respectively.

### **2.3.2. Reproductive phenology**

Reproductive components of *B. gymnorrhiza* were present in litter traps with regular periodicity across years (Table 2-1). Litterfall of flower buds, including both immature and mature buds, was highest in summer (June–August) and lowest in autumn (September–November) (Fig. 2-5a). Kendall's *W* values revealed that the monthly trends in flower bud primordia and flower buds litterfall were not significant among years, though peaks of flower bud litterfall occurred in August of the 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> year (Table 2-1). Flower litterfall was observed throughout the year, but was highest in September and lowest in January (Fig. 2-5b). Unfertilized flowers aborted and fell quickly from trees, and some pollinated flowers also fell. Kendall's *W* values revealed that monthly flower litterfall showed strong and significant concordance among years (Table 2-1). *Bruguiera gymnorrhiza* has no distinct fruiting stage, because propagule development immediately follows fertilization, with a single hypocotyl emerging from an attached mature calyx. Propagule litterfall including both mature and developing ones was found throughout the year, but the abundance of mature propagules was highest in summer and lowest in winter, with the exception of May 2011, when the strong typhoon (Songda) substantially increased propagule litterfall (Fig. 2-5c). Kendall's *W* values also revealed that the propagule litterfall had no significant trend to occur in any particular month of the year (Table 2-1). The autocorrelation coefficient revealed that flower bud (Fig. 2-6a), flower (Fig. 2-6b), and propagule (Fig. 2-6c) litterfall each had clear annual cycles.

Flower bud litterfall was associated with monthly day length, whereas flower litterfall was significantly linked to monthly mean air temperature, monthly air relative

humidity, and monthly rainfall (Table 2-2). Propagule litterfall was related to monthly day length and monthly maximum wind speed. The mean total reproductive organs litterfall was  $377 \pm 58 \text{ g m}^{-2} \text{ yr}^{-1}$ , which contributed 38 % to the total litterfall (Table 2-3). Table 2-4 represents the mean number of reproductive organs and their mean survivorship. The mean conversion percentage of flowers to propagules was  $9.8 \pm 0.6 \%$  for *B. gymnorhiza*.

The development phase from flower buds to flowers took 1 month (Fig. 2-7a). After fertilization is completed, hypocotyls develop from flowers and mature into propagules. Flowers took 8 months to develop into mature propagules (Fig. 2-7b). The developmental phase from flower buds to mature propagules took 9 months (Fig. 2-7c).

## 2.4. Discussion

Both leaf and stipule litterfall of *B. gymnorhiza* were lowest in winter and highest in summer. Similar monthly patterns were found by Hardiwinoto et al. (1989) in Ohura Bay, Okinawa Island, Japan. Our results agree with Allen and Duke (2006), who reported that peak leaf litterfall in *B. gymnorhiza* in the northern hemisphere occurred from April–September and peak stipule litterfall from May–September. Duke et al. (1984) reported marked seasonal periodicity in both leaf and stipule litterfall for *B. gymnorhiza* in northern Australia, with a peak in the summer wet season. In contrast to the present study, Shunula and Whittick (1999) reported that *B. gymnorhiza* on Unguja Island, Zanzibar, Tanzania, produced litterfall throughout the year, with no significant seasonal differences in leaf production. Results similar to ours were observed in southern Thailand in the congeneric species *B. cylindrica* (L.) Blume, which showed unimodal patterns with maximum leafing and shedding rates during the tropical monsoon season, which has high air temperatures and heavy rainfalls (Wium-Andersen and Christensen 1978). Leaf production and leaf litterfall in *B. gymnorhiza* followed the same unimodal pattern found in *K. obovata* in subtropical regions (Sharma et al. 2012). Unimodal leaf and stipule litterfall peaks have been observed in Rhizophoraceae species in subtropical areas (Gill and Tomlinson 1971; Steinke 1988; Wilson and Saintilan 2012), whereas in tropical areas, unimodal, bimodal, and trimodal patterns have been observed in the species of the same family (Wium-Andersen and Christensen 1978; Wium-Andersen 1981; Leach and Burgin 1985).

New leaf production and leaf litterfall of *B. gymnorrhiza* were related to increases in mean air temperature, monthly maximum wind speed and monthly rainfall, and with monthly maximum wind speed and monthly day length, respectively. Similarly, Gill and Tomlinson (1971) found that leaf production of *R. mangle* L. in Florida, USA, was most common in summer when solar radiation and temperature levels were highest. Similar findings were also reported by Gwada et al. (2000), who reported that air temperature was the strongest environmental factor influencing leaf production in other species of Rhizophoraceae at Sashiki on Okinawa Island. Rainfall was also an important factor for new leaf production, which is generally consistent with the findings of Borchert (2012), who reported that heavy rains of the wet season cause bud break and rapid shoot growth in tropical forests. Temperature, day length, and rainfall may be the important external controlling factors of *B. gymnorrhiza* leaf initiation in subtropical regions.

Mangroves at Manko Wetland face frequent typhoons, which disrupt the seasonality of litterfall production and could be the main reason for the higher litterfall, especially the high branch litterfall was observed. High rates of branch litterfall in some months (e.g. September and October, 2010; May and August, 2011; August and September 2012) is attributed to typhoons which have wind speeds that exceed  $17.2 \text{ m s}^{-1}$ . Six strong typhoons (Kompasu, Chaba, Songda, Muifa, Bolaven, and Jelawat) occurred on 1 September and 27 October, 2010, on 28 May and 5 August 2011, and on 26 August and 29 September 2012, respectively. During the typhoons, green leaves were damaged and fell to the ground individually or attached to living broken branches. These green leaves contributed to high levels of leaf litterfall in May and August 2011, and September 2012 (Fig. 2-2a). Vegetative litterfall components were related to monthly maximum wind speed. Similar observations were recorded on Okinawa Island, by Hardiwinoto et al. (1989) and Sharma et al. (2012), who reported that typhoons had strong effects on branch litterfall of *B. gymnorrhiza* and *K. obovata*, respectively.

The mean total litterfall of *B. gymnorrhiza* ( $10.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ) was higher than those recorded on Irimote Island, Okinawa, Japan ( $8.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ; Kishimoto et al. 1987) and in Ohura Bay ( $7.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ; Hardiwinoto et al. 1989). Litterfall was lower than the  $16 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  reported for *B. gymnorrhiza* on Unguja Island, Zanzibar, Tanzania (Shunula and Whittick 1999), and was similar to the  $11.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  of *R.*

*apiculata* Blume and *R. mucronata* Lamk. in the central West Coast of India (Wafar et al. 1997). Similar to the other studies (Wafar et al. 1997; May 1999; Ochieng and Erfteimeijer 2002), leaves of *B. gymnorrhiza* were the major contributors to total litterfall production.

The average leaf longevity of subtropical mangrove *B. gymnorrhiza* was ranged from 17.1 to 21.0 month. This range was longer than those reported for *B. gymnorrhiza* in Fujian Province, China (9–10 month; Wang and Lin 1999) and *B. cylindrica* in southern Thailand (13 month; Wium-Andersen and Christensen 1978), but much shorter than that reported for *B. gymnorrhiza* in north-eastern Australia (2–3 yr; Duke et al. 1984).

All the reproductive components of *B. gymnorrhiza* showed distinct monthly peaks. Flower bud primordia were very difficult to separate from other litterfall components; they were usually confused with segments of inflorescences. Therefore, we were unable to detect any monthly litterfall pattern for flower bud primordia (Table 2-1). The peak periods of flower and propagule litterfall were in summer–autumn and summer, respectively. These data agree generally with the findings of Hardiwinoto et al. (1989) in Ohura Bay. In contrast, flower and propagule production of *B. gymnorrhiza* on Unguja Island, Zanzibar, Tanzania, showed no significant monthly differences (Shunula and Whittick 1999). Flower and propagule litterfall in our study followed the same monthly pattern as in other mangrove species. For example, flowers and propagules of *R. mucronata* in tropical regions had one reproductive peak in summer (Shunula and Whittick 1999).

Flower and propagule litterfall of the subtropical mangrove *B. gymnorrhiza* contributed 38 % to the total litterfall. This is higher than the 13.1 % found by Mokolensang and Tokuyama (1998) for *B. gymnorrhiza* in the estuary of the Geasashi River, Okinawa Island. The proportion of reproductive components to the total litterfall at Manko Wetland was higher than for *R. apiculata* (21.8 %) and *R. mucronata* (23.2 %) on the central West Coast of India (Wafar et al. 1997). The mean conversion rates of flowers to propagules for *B. gymnorrhiza* (9.8 %) was higher than the rate reported for *B. gymnorrhiza* (3.2–4.9 %) in Fiji (Tyagi 2003), but lower than that of *B. gymnorrhiza* (16.8 %) in northeastern Australia (Duke et al. 1984). According to Primack et al. (1981), the high rates of the conversion rates of flowers to propagules in *B. gymnorrhiza*

indicate self-compatibility, as in *Sonneratia alba* J. Simth.

At Manko Wetland, reproductive organs were associated with long monthly day length (flower buds) or with monthly mean air temperature, monthly air relative humidity, and monthly rainfall (flowers). Borchert (2012) found that expansion of dormant flower buds may be triggered by increasing exposure to sunlight or the first heavy rains of the wet season. Flowering phenograms of *B. gymnorrhiza* were relatively similar to leaf production phenograms. The timing of newly flushed leaves and flowering phenopahse coincide with each other and both of them were linked with rainfall and relative humidity. In the Caribbean salinity and water balance were observed to regulate flowering and flower bud maturation of *R. mangle* (Sánchez-Núñez and Mancera-Pineda 2011). It may be concluded that air temperature, day length, and rainfall are the environmental clues that control the seasonality of reproductive organ litterfall of *B. gymnorrhiza*.

This is the first study to report the maturation periods of reproductive organs of *B. gymnorrhiza* at the northern limit of its biogeographical distribution. The development of flowers from newly-initiated buds took one month, a time period that is similar to the 35 days reported by Upadhyay and Mishra (2010) for *B. gymnorrhiza* on Orissa coast, India. At Manko Wetland, flowers took eight months to form mature propagules, similarly to the findings of Wium-Andersen and Christensen (1978), who reported that *B. cylindrica* in tropical regions needed 6–8 months from flowers to mature propagules development. In comparison with these reported data of species belonging to the same genus, *B. gymnorrhiza* growing at the northern limit of its biogeographical distribution appears to have a similar maturation period to congeneric species inhabiting tropical regions.

## **2.5. Conclusion**

In summary, the vegetative and reproductive litterfalls of *B. gymnorrhiza* were measured monthly over four years; there was no significant monthly variation among the years in either. The periodicities of leafing and flowering followed unimodal patterns and were governed mainly by air temperature. The annual litterfall production of *B. gymnorrhiza* and its contribution to the Manko Wetland ecosystem was relatively high. The period of reproductive organ development agreed with previous reports for

this species or for congeneric species in tropical regions.

## References

- Allen JA, Duke NC (2006) *Bruguiera gymnorrhiza* (large-leafed mangrove), ver. 2.1. In: Elevitch CR (ed) Species profiles for Pacific Island Agroforestry. Permanent Agriculture Resources (PAR), Holualoa, Hawaii. <http://www.traditionaltree.org>
- Borchert R (2012). The phenology of tropical trees. KU Undergraduate Biology Program, University of Kansas Web. [http://www.biology.ku.edu/tropical\\_tree\\_phenology/](http://www.biology.ku.edu/tropical_tree_phenology/). Accessed 05 October 2012
- Clarke PJ (1994) Baseline studies of temperate mangrove growth and reproduction; demographic and litterfall measures of leafing and flowering. *Aust J Bot* 42:37–48
- Coupland GT, Paling EI, McGuinness KA (2005) Vegetative and reproductive phenologies of four mangrove species from northern Australia. *Aust J Bot* 53:109–117
- Deshar R, Sharma S, Mouctar K, Wu M, Hoque ATMR, Hagihara A (2012) Self-thinning exponents for partial organs in overcrowded mangrove *Bruguiera gymnorrhiza* stands on Okinawa Island, Japan. *For Ecol Manag* 278:146–154
- Duke NC (1990) Phenological trends with latitude in the mangrove tree *Avicennia marina*. *J Ecol* 78:113–133
- Duke NC, Bunt JS, Williams WT (1984) Observations on the floral and vegetative phenologies of north-eastern Australian mangroves. *Aust J Bot* 32:87–99
- Fernandes MEB (1999) Phenological patterns of *Rhizophora* L., *Avicennia* L. and *Laguncularia* Gaertn. f. in Amazonian mangrove swamps. *Hydrobiologia* 413:53–62
- Gill AM, Tomlinson PB (1971) Studies on the growth of red mangrove (*Rhizophora mangle* L.). 3. Phenology of the shoot. *Biotropica* 3:109–124
- Gwada P, Makoto T, Uezu Y (2000) Leaf phenological traits in the mangrove *Kandelia candel* (L.) Druce. *Aquat Bot* 68: 1–14
- Hardiwinoto S, Nakasuga T, Igarashi T (1989) Litter production and decomposition of a mangrove forest at Ohura Bay, Okinawa. *Res Bull Coll Exp For, Hokkaido Univ* 46:577–594
- Kira T (1991) Forest ecosystems of east and southeast Asia in a global perspective. *Ecol Res* 6:185–200

- Kishimoto T, Miyajima H, Nakasuga T, Baba S (1987) Zonation of mangrove forest (III) litterfall and its seasonal change. *Trans Mtg Jpn For Soc* 98:301–302 (in Japanese)
- Leach GJ, Burgin S (1985) Litter production and seasonality of mangroves in Papua New Guinea. *Aquat Bot* 23:215–224
- Mackey AP, Smail G (1995) Spatial and temporal variation in litter fall of *Avicennia marina* (Forssk.) Vierh. in the Brisbane River, Queensland, Australia. *Aquat Bot* 52:133–142
- May JD (1999) Spatial variation in litter production by the mangrove *Avicennia marina* var. *australasica* in Rangaunu Harbor, Northland, New Zealand. *NZ J Mar Freshwat Res* 33:163–172
- Mehlig U (2006) Phenology of the red mangrove, *Rhizophora mangle* L., in the Caeté Estuary, Pará, equatorial Brazil. *Aquat Bot* 84:158–164
- Mokolensang JF, Tokuyama A (1998) Litter production of mangrove forests at the Gaesashi River. *Bull Coll Sci, Univ Ryukyus* 65:73–79
- Naido G (1989) Seasonal plant water relations in a South African mangrove swamp. *Aquat Bot* 33:233–242
- Ochieng CA, Erfemeijer PLA (2002) Phenology, litterfall and nutrient resorption in *Avicennia marina* (Forssk.) Vierh in Gazi Bay, Kenya. *Trees* 16:167–171
- Primack RB, Duke NC, Tomlinson PB (1981) Floral morphology in relation to pollination ecology in five Queensland coastal plants. *Austrobaileya* 4:346–355
- RIS (1999) Information sheet on Ramsar Wetlands (RIS). In: A Directory of Wetlands of International Importance. Ramsar Sites Database. <http://www.org/RSIS/-COP9/Directory/.../2Jp011.html>. Accessed 18 June 2012
- Robertson AI, Alongi DM, Boto KG (1992) Food chains and carbon fluxes. In: Robertson AI, Alongi DM (eds) *Tropical Mangrove Ecosystems*, American Geophysical Union, Washington, DC, pp 239–329
- Saenger P, Moverley J (1985) Vegetative phenology of mangroves along the Queensland coastline. *Proc Ecol Soc Aust* 13:257–265
- Saito K, Okuno T, Asai A, Haga T, Kawai M, Kudo H, Miyamoto K, Masamara M, Osawa Y, Kawamura M, Goto H (2003) Lectures on modern statistics. Practical Business Education Institute, Tokyo (in Japanese)

- Sánchez-Núñez DA, Mancera-Pineda JE (2011) Flowering patterns in three neotropical mangrove species: Evidence from a Caribbean Island. *Aquat Bot* 94:177–182
- Sharma S, Hoque ATMR, Analuddin K, Hagihara A (2012) Litterfall dynamics in an overcrowded mangrove *Kandelia obovata* (S., L.) Yong stand over five years. *Estuar Coast Shelf Sci* 98:31–41
- Shiga T, Okuhara M, Nozawa M (2004) Lectures on multiple regression analysis using Excel. Practical Business Education Institute, Tokyo (in Japanese)
- Shunula JP, Whittick A (1999) Aspects of litter production in mangroves from Unguja Island, Zanzibar, Tanzania. *Estuar Coast Shelf Sci* 49:51–54
- Steinke TD (1988) Vegetative and floral phenology of three mangrove in Mgeni Estuary. *S Afr J Bot* 54:97–102
- Tyagi AP (2003) Location and interseasonal variation in flowering, propagule setting and propagule size in mangroves species of the family Rhizophoraceae. *Wetlands Ecol Manage* 11:167–174
- Upadhyay VP, Mishra PK (2010) Phenology of mangroves tree species on Orissa coast, India. *Trop Ecol* 51:289-295
- Wafar S, Untawale AG, Wafar M (1997) Litter fall and energy flux in a mangrove ecosystem. *Estuar Coast Shelf Sci* 44:111–124
- Wang W, Lin P (1999) Transfer of salt and nutrients in *Bruguiera gymnorrhiza* leaves during development and senescence. *Mangroves Salt Marshes* 3:1–7
- Waring RH, Running SW (1998) Forest ecosystems: analysis at multiple scales. Academic Press, San Diego, California
- Wilson NC, Saintilan N (2012) Growth of the mangrove species *Rhizophora stylosa* Griff. at its southern latitudinal limit in eastern Australia. *Aquat Bot* 101:8–17
- Wium-Andersen S, Christensen B (1978) Seasonal growth of mangrove trees in southern Thailand. II. Phenology of *Bruguiera cylindrica*, *Ceriops tagal*, *Lumnitzera littorea* and *Avicennia marina*. *Aquat Bot* 5:383–390
- Wium-Andersen S (1981) Seasonal growth of mangrove trees in southern Thailand. III. Phenology of *Rhizophora mucronata* Lamk. and *Scyphiphora hydrophyllaceae* Gaertn. *Aquat Bot* 10:371–376

**Table 2-1.** Kendall's coefficient of concordance,  $W$ , showing agreement in the monthly changes in litterfall components of *Bruguiera gymnorhiza* among five years of this study.

Litterfall component	$W$	$\chi^2$ ( $p$ -value)
Leaf	0.6576	36.2 (< 0.001)
Stipule	0.5585	30.7 (< 0.05)
Branch	0.2710	14.9 (0.19)
Sum of vegetative organs	0.6897	37.9 (< 0.001)
Flower bud primordium	0.1242	6.8 (0.81)
Flower bud	0.3194	17.6 (0.09)
Flower	0.5901	32.5 (< 0.001)
Propagule	0.3298	18.1 (0.08)
Sum of reproductive organs	0.5039	27.7 (< 0.05)
Total litterfall	0.6867	37.8 (< 0.001)

**Table 2-2.** Adjusted  $R^2$  values from stepwise multiple regression analysis of vegetative and reproductive litterfall components of *Bruguiera gymnorrhiza* in relation to environmental factors. Significant probabilities of the coefficient value are indicated by \* ( $p \leq 0.05$ ), \*\* ( $p \leq 0.01$ ), or \*\*\* ( $p \leq 0.001$ ).

Component	Monthly mean temperature °C ( $x_1$ )	Monthly day length h month <sup>-1</sup> ( $x_2$ )	Monthly rainfall mm month <sup>-1</sup> ( $x_3$ )	Monthly relative humidity % ( $x_4$ )	mean	Monthly maximum wind speed m s <sup>-1</sup> ( $x_5$ )	Equation
Leaf		0.65 (0.97)				0.57 (0.97)	$y = -146 + 5.1^{***} x_5 + 0.3^{***} x_2$
Stipule	0.20 (0.85)		0.27 (0.76)			0.22 (0.83)	$y = -1.0 + 0.3^{**} x_1 - 0.16^* x_5 + 0.01^* x_3$
Branch						0.76 (1.00)	$y = -34.6 + 2.6^{***} x_5$
Flower bud		0.12 (1.00)					$y = -1.8 + 0.006^{**} x_2$
Flower	0.40 (0.53)		0.48 (0.60)	0.44 (0.41)			$y = 25.8 + 2.0^{***} x_1 - 0.9^{***} x_4 + 0.02^* x_3$
Propagule		0.11 (0.97)				0.18 (0.97)	$y = -186 + 0.5^{**} x_2 + 2.8^* x_5$

Numerals in parenthesis are the tolerances of the coefficients of the multiple regression for a component.

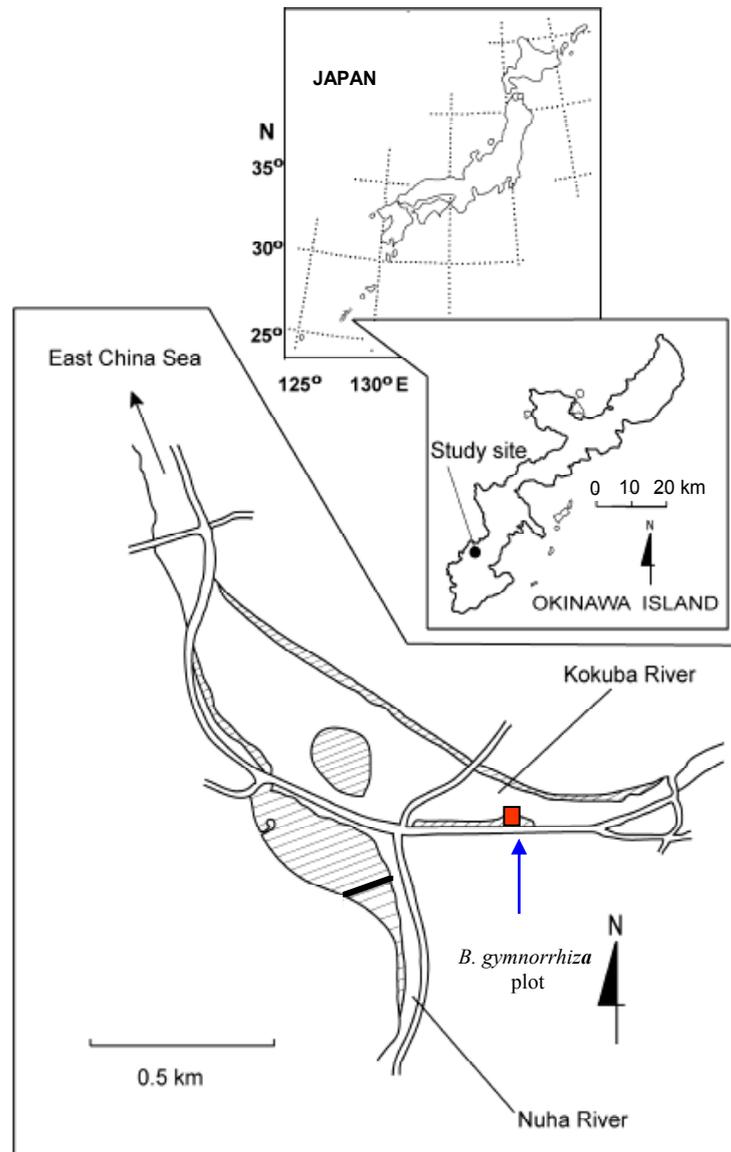
**Table 2-3.** Annual amounts of vegetative and reproductive litterfall components of *Bruguiera gymnorrhiza* during the study period.

Litterfall components	1 <sup>st</sup> year	2 <sup>nd</sup> year	3 <sup>rd</sup> year	4 <sup>th</sup> year	5 <sup>th</sup> year	Mean
Leaf	503 ± 5 (48)	386 ± 5 (50)	516 ± 5 (53)	539 ± 12 (44)	603 ± 20 (59)	509 ± 35 (50)
Stipule	62 ± 0.7 (6)	32 ± 0.6 (4)	65 ± 1 (7)	37 ± 0.5 (3)	55 ± 1 (6)	50 ± 7 (5)
Branch	9 ± 0.4 (1)	12 ± 0.4 (2)	90 ± 3 (9)	05 ± 6 (9)	126 ± 8 (12)	68 ± 24 (7)
Sum of vegetative organs	574 ± 6 (55)	431 ± 5 (56)	677 ± 7 (69)	681 ± 17 (55)	784 ± 28 (77)	629 ± 59 (62)
Flower bud primordium	0	4 ± 0.2 (1)	2 ± 0.1 (0.2)	0.5 ± 0.1 (0.1)	0	1 ± 0.7 (0.1)
Flower bud	4 ± 0.1 (0.4)	5 ± 0.2 (1)	7 ± 0.3 (0.7)	3 ± 0.1 (0.2)	1 ± 0.1 (0.1)	4 ± 0.9 (0.4)
Flower	156 ± 4 (15)	140 ± 2 (18)	139 ± 4 (14)	29 ± 0.8 (2)	101 ± 3 (10)	113 ± 22 (11.2)
Propagule	313 ± 9 (30)	192 ± 8 (25)	152 ± 4 (16)	519 ± 30 (42)	128 ± 5 (13)	260 ± 71 (26)
Sum of reproductive organs	473 ± 11 (45)	341 ± 8 (44)	294 ± 6 (31)	551 ± 30 (45)	231 ± 6 (23)	377 ± 58 (38)
Total	1046 ± 15	772 ± 13	971 ± 10	1232 ± 42	1015 ± 29	1007 ± 73

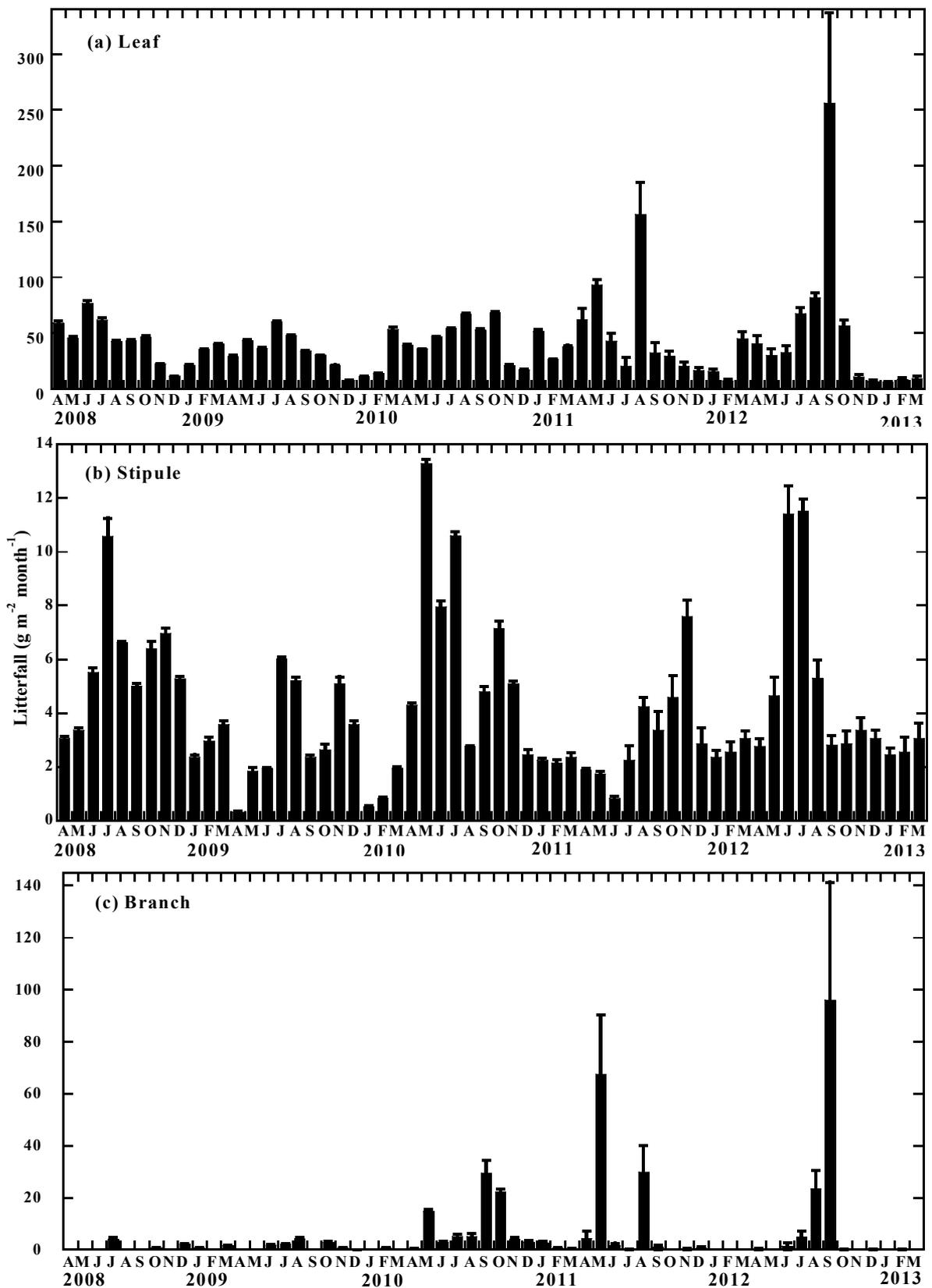
Values are mean ( $\text{g m}^{-2} \text{yr}^{-1}$ ) ± SE. Numerals in parenthesis represent percentages for the total amounts.

**Table 2-4.** Mean numbers of reproductive organs ( $\text{m}^{-2} \text{yr}^{-1} \pm \text{SE}$ ) of *Bruguiera gymnorrhiza* and their conversion rates ( $\% \pm \text{SE}$ ) during the study period.

Reproductive organs	1 <sup>st</sup> year	2 <sup>nd</sup> year	3 <sup>rd</sup> year	4 <sup>th</sup> year	5 <sup>th</sup> year	Mean
Flower	432.9 $\pm$ 43.1	505.2 $\pm$ 37.2	400.3 $\pm$ 39.4	116.1 $\pm$ 16.9	239.4 $\pm$ 39.2	338.8 $\pm$ 70.6
Propagule	48.9 $\pm$ 4.7	49.9 $\pm$ 10.2	41.6 $\pm$ 5.0	10.1 $\pm$ 1.1	28.5 $\pm$ 4.9	35.8 $\pm$ 7.5
Flower to propagule	10.3 $\pm$ 0.8	9.2 $\pm$ 2.0	9.6 $\pm$ 1.1	8.2 $\pm$ 0.6	11.7 $\pm$ 2.7	9.8 $\pm$ 0.6



**Fig. 2-1.** Location of the study area. The hatched zone indicates the mangrove area. Arrow indicates the plot area (*filled square*).



**Fig. 2-2.** Phenograms of the litterfall of the vegetative components of *B. gymnorhiza* in Manko Wetland. Vertical bars represent standard errors of the means,  $n = 5$ .

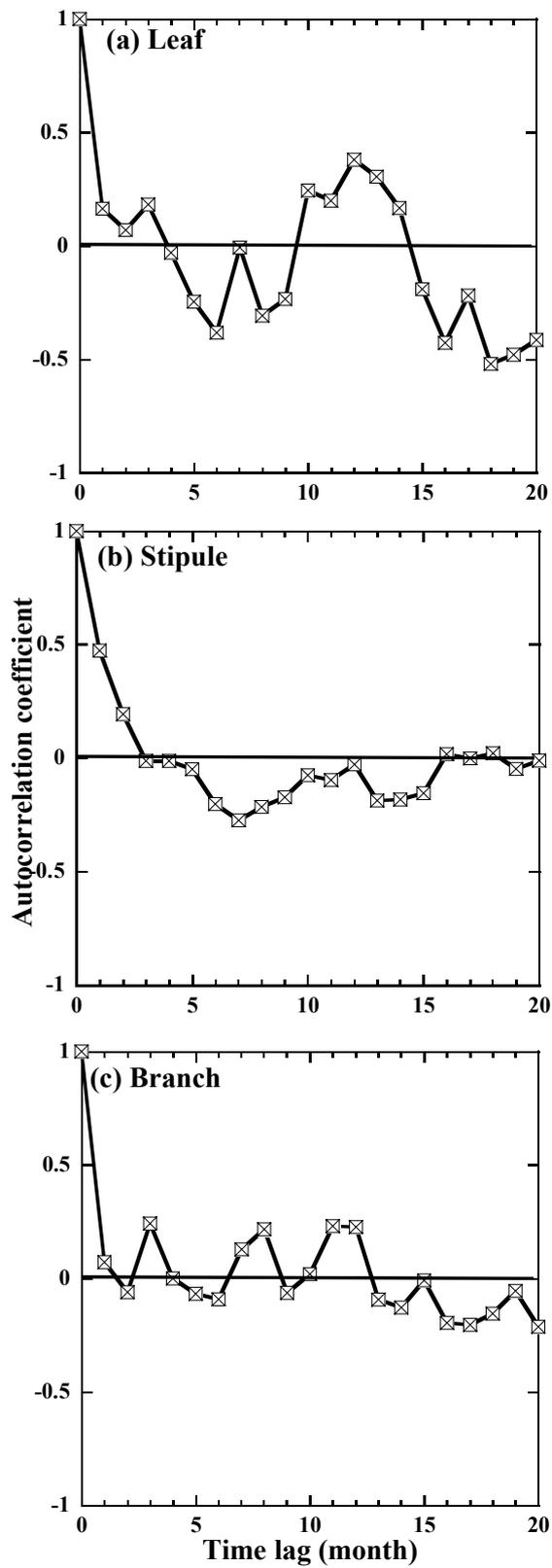
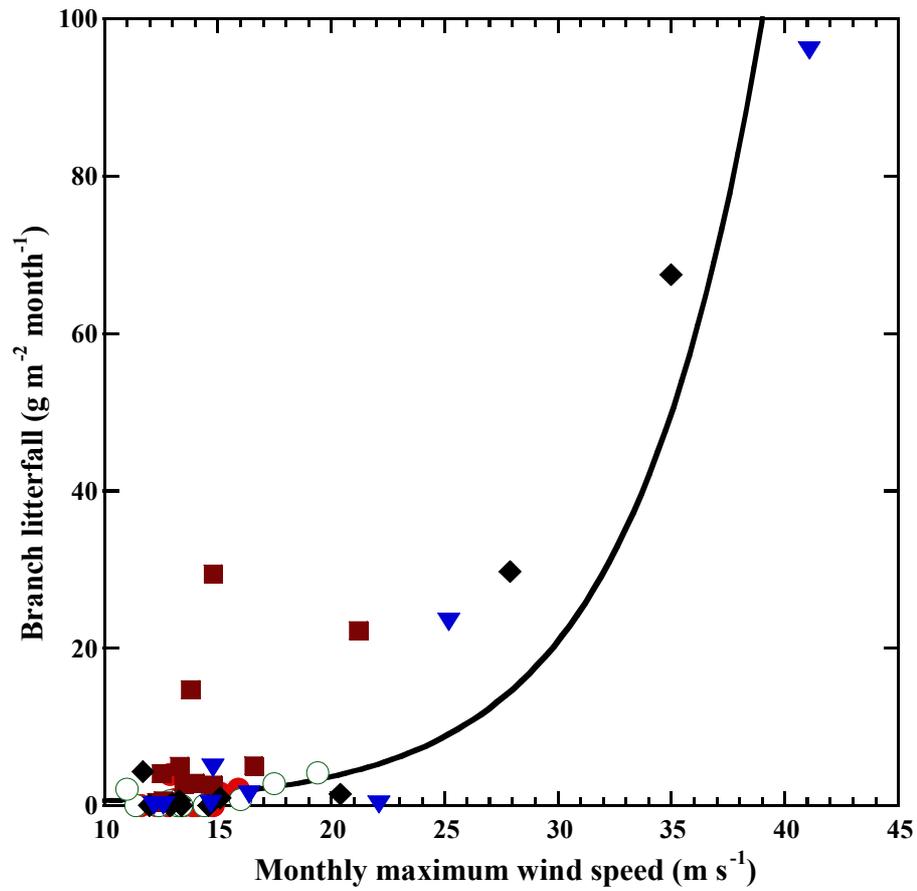
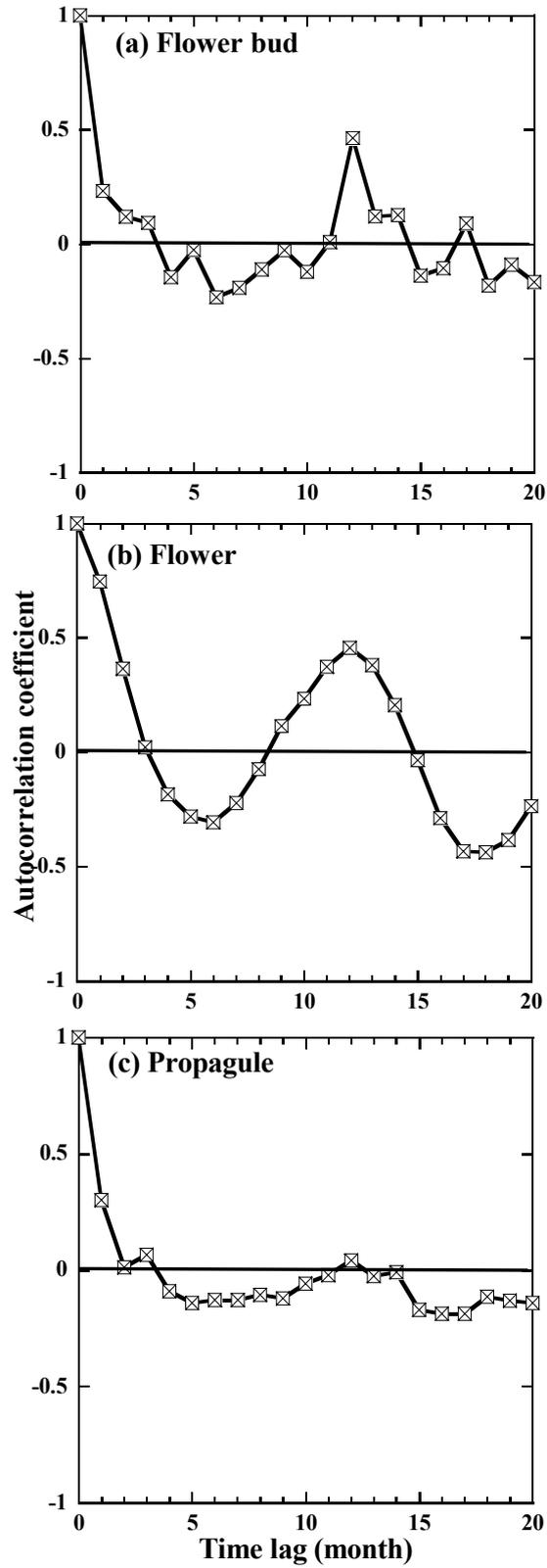


Fig. 2-3. Correlograms of *B. gymnorhiza* vegetative litterfall of in Manko Wetland.

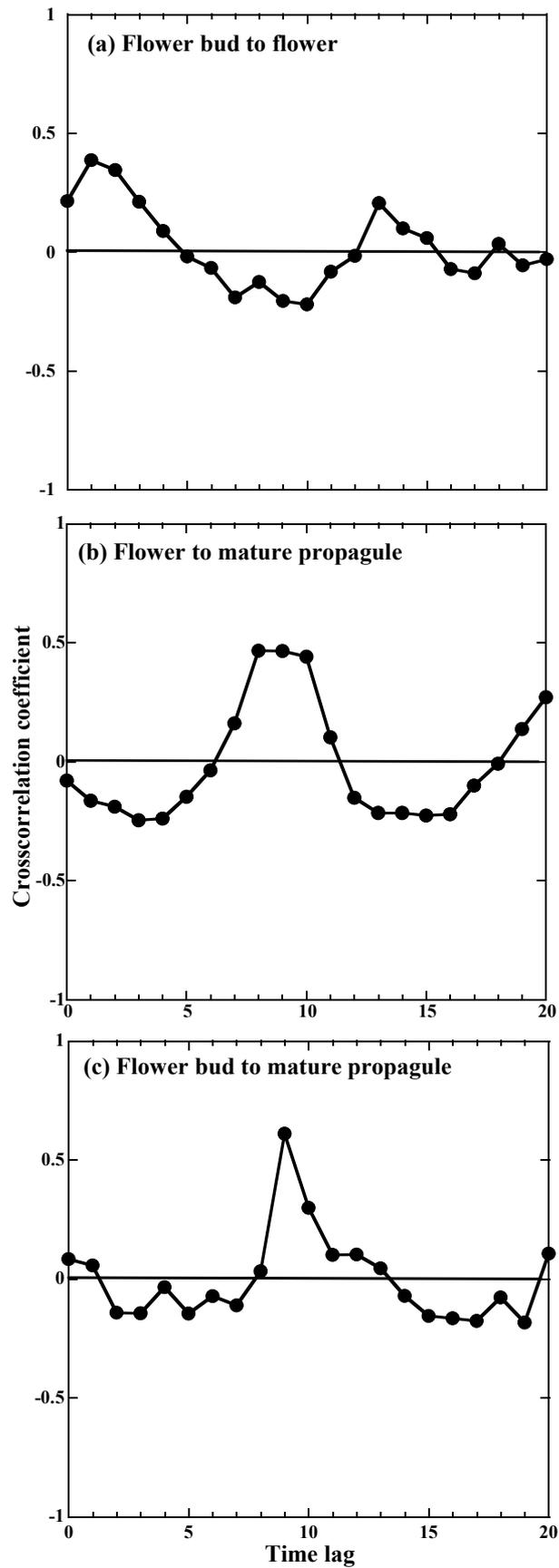


**Fig. 2-4.** Exponential relationship between monthly branch litterfall of *B. gymnorhiza* and monthly maximum wind speed ( $R^2 = 0.81$ ). ●: 1st year; ○: 2nd year; ■: 3rd year; ◆: 4th year; ▼: 5th year.





**Fig. 2-6.** Correlograms of *B. gymnorrhiza* reproductive litterfall in Manko Wetland.



**Fig. 2-7.** Crosscorrelation coefficients between pairs of the reproductive components of *B. gymnorrhiza* in Manko Wetland.

## CHAPTER III

### **Vegetative and Reproductive Phenology of the Mangrove *Kandelia obovata* (S., L.) Yong**

---

#### **3.1. Introduction**

Mangrove forests are among the world's most productive ecosystems and sustain a variety of marine and estuarine communities (Lugo and Snedaker 1975; Boto and Bunt 1982). However, mangroves are also one of the world's most threatened tropical and subtropical ecosystems and are being degraded in most countries mainly because of anthropogenic activities and unsustainable exploitation (Khan et al. 2007). Mangroves are the only tall tree forests situated between the land and sea (Kathiresan & Bingham 2001; Alongi 2002) and they are tightly bound to the coastal environments in which they occur. Once established, mangroves offer recreational potential, a sustainable supply of seafood for aquatic animals and useful products for community subsistence (Alongi 1996; Tyagi and Singh 1998). As a primary producer, mangrove also serves as food for herbivores and detritivores. Litterfall, consisting primarily of mangrove leaves, becomes available following leaf senescence and death.

Leaf litterfall studies in forest stands have been conducted for over a century. More recently, studies have focused on the ecological role of leaf litterfall in nutrient cycling and the possible interactions with biotic and abiotic variables (Zhou et al. 2007). Along with providing nutrients for the tree, leaf litterfall also provides energy and a living environment for soil fauna and microorganisms (Guo and Sims 1999). Litterfall is an indicator of phenological events of a species (Duke 1990; Clarke 1994). Phenological information is essential for understating ecosystem functioning (Janzen 1967) and to better manage mangrove ecosystems. Despite the importance of mangroves ecosystems, very few studies have considered the phenology of different mangrove species (Christensen and Wium-Andersen 1977; Wium-Andersen and Christensen 1978; Wium-Andersen 1981; Duke et al. 1984; Duke 1990; FAO 1994; Gwada et al. 2000; Tyagi 2003; Coupland et al. 2005; Mehlig 2006; Nagarajan et al. 2008). Most phenological studies have been confined to monitoring flowering and fruiting by direct observation, and very few studies have combined direct observations

and litterfall measurements to assess the phenology of this species (Duke et al. 1984). Phenological events in mangroves are influenced by local or regional environmental conditions, particularly day length, air temperature, rainfall, and water status (Saenger and Moverley 1985; Naido 1989; Duke 1990; Fernandes 1999).

*Kandelia obovata* (S., L.) Yong in regions of China and Japan has been reclassified as a new species that was previously recognized as *Kandelia candel* (L.) Druce (Sheue et al. 2003). According to Sheue et al. (2003), *K. obovata* is distributed from the Gulf of Tonkin northeastward to Kwangtung, Fukien, Taiwan, the Ryukyus, and southern Japan. Although this species grows to its northern limit, and mangrove forests grow under ambient climatic conditions, only a few studies have investigated the phenology of *K. obovata*. Leaf phenological traits only were reported by Gwada et al. (2000), and no previous studies examined the vegetative and reproductive phenology of *K. obovata*. Therefore, the aim of the present study was to determine the vegetative and reproductive phenology of a monospecific stand of *K. obovata* trees. The present study also aimed to identify the effect of climatic variables on *K. obovata* phenology as well as to determine the expansion period of each reproductive organ.

## **3.2. Materials and methods**

### **3.2.1. Study site**

The present study was conducted at the Manko wetland, located on Okinawa Island, Japan (26°11' N and 127°40' E), for over 5 years, starting in April 2006 and ending in March 2011. The study area (Fig. 3-1) was designated as a wetland of International importance under the Ramsar Convention and is in a subtropical region; the warmth index of the study area (i.e., cumulative temperature of mean monthly temperatures > 5°C) was  $219.96 \pm 1.31^\circ\text{C month}$ , which is within the 180–240°C month of a subtropical region defined by Kira (1991). Mangrove soil is muddy and the incoming water from the Kokuba River occasionally carries a heavy load of sediments. The study site had four pronounced seasons: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). Regular tidal inundation occurs at the study site, which also receives some fresh water supplied by runoff from an adjacent area (Khan et al. 2004). A monospecific stand of *K. obovata* dominates the

study site. Other mangrove species, such as *Rhizophora stylosa* Griff., *Bruguiera gymnorhiza* (L.) Lamk., and *Excoecaria agallocha* L., are present in patches. Tree density, mean tree height ( $H$ ), and mean stem diameter at  $H/10$  ( $D_{0.1H}$ ) were  $21456 \text{ ha}^{-1}$ ,  $4.27 \pm 0.87 \text{ m}$  (mean  $\pm$  standard error [SE]) m, and  $5.09 \pm 0.04$  (mean  $\pm$  SE) in 2010, respectively.

### **3.2.2. Climate data**

Meteorological data were collected from the Okinawa Meteorological Observatory, Naha, from April 2006 to March 2011 (i.e. over the time period in which the fieldwork was conducted). The temperature fluctuated approximately  $15^\circ\text{C}$  from the coldest month to the hottest month, and normal of the mean annual air temperature during the study period was  $23.3 \pm 0.2^\circ\text{C}$  (Fig. 3-2a). The mean annual sunshine hour was  $1709.7 \pm 73.8 \text{ h yr}^{-1}$  (mean  $\pm$  SE) (Fig. 3-2a). Mean annual day length was  $4363.3 \pm 2.3 \text{ h yr}^{-1}$ . Rainfall varied throughout the year, but during most months it exceeded  $100 \text{ mm month}^{-1}$  (Fig. 3-2b). The highest rainfall ranged from  $20 \text{ mm month}^{-1}$  in December 2008 to  $594 \text{ mm month}^{-1}$  in August 2009 during the study period, and the mean of annual rainfall was  $2226.5 \pm 267.3 \text{ mm yr}^{-1}$  (mean  $\pm$  SE). Most rainfall occurred during summer with less during winter. The mean monthly relative humidity was  $72.6 \pm 0.6 \%$  (mean  $\pm$  SE) (Fig. 3-2b). Monthly maximum wind speed varied from the lowest  $7.7 \text{ m s}^{-1}$  in March 2007 to the highest  $56.3 \text{ m s}^{-1}$  in July 2007.

### **3.2.3. Litterfall collection**

A 125-m long belt transect (5 m wide) was established perpendicular to the river current in the dense stand of *K. obovata*, and then divided into 25 plots (5 m  $\times$  5 m each). The total area of the belt transect was  $625 \text{ m}^2$ , indicated by the bold line in Figure 3-1. The gradient of the forest floor was almost flat. The phenology of this species was assessed using litterfall data. Litterfall data were collected using 50 net litter traps with a 1-mm mesh size and with a mouth area of  $0.2 \text{ m}^2$ . Two litter traps were placed in each plot, the traps were placed  $> 1 \text{ m}$  from the ground to avoid tidal water. The litter traps were emptied monthly, and the collected litterfall was kept in a cotton bag and carried to the laboratory where it was separated into leaves, stipules, branches, bud primordia, flower buds, flowers, fruits, and propagules. The separated litterfall components were dried at  $80^\circ\text{C}$  over 48 h and then weighed using a digital balance (EK-600H, A & D Company,

Tokyo, Japan). The numbers of reproductive components, such as flowers, fruits, and propagules, were counted to estimate the success of fruit and propagule sets. Following Duke (1990), we computed reproductive units and estimated the following: (i) fruit set was calculated as the percentage of fruit units (immature fruits + mature fruits + propagules)/ (flowers + immature fruits + mature fruits + propagules); and (ii) propagule set was calculated as the percentage of propagule units (propagules)/ (flowers + immature fruits + mature fruits + propagules).

### 3.2.4. Statistical analysis

Kendall's coefficient of concordance,  $W$ , was used to evaluate the degree of similarity in monthly change among years for each litterfall component. Litterfall data were ranked by monthly mass for every year, and  $W$  was calculated for monthly litterfall. When  $W = 1.0$ , the monthly changes in litterfall are concordant among years, while when  $W = 0.0$ , the monthly changes are completely different among years. The  $\chi^2$  test was used to determine the significance of the  $W$  value (Saito et al. 2003).

We performed a stepwise multiple regression analysis to determine the effects of five environmental factors — temperature, day length, rainfall, humidity, and maximum wind speed — on litterfall of leaves, stipules, branches, flower buds, flowers, and propagules, using MA-MACRO/MRA software (ver. 3.0, Practical Business Education Institute, Tokyo, Japan). The stepwise multiple regression was continued until the adjusted  $R^2$  value showed a decreasing trend. A criterion of  $F$  value  $> 2.0$  was set to determine the minimum significance of a variable to be included in the equation. Multiple regression analysis of environmental factors on mangrove litterfall is difficult because the environmental factors often co-vary. A criterion of tolerance  $> 0.1$  was selected to avoid multicollinearity among the variables (Shiga et al. 2004).

The autocorrelation coefficient  $r_{xx}(k)$  was calculated for each litterfall component to evaluate its yearly cycle:

$$r_{xx}(k) = \frac{\sum_{j=1}^{N-k} (X_j - \bar{X}_{1, N-k})(X_{j+k} - \bar{X}_{1+k, N})}{\sqrt{\sum_{j=1}^{N-k} (X_j - \bar{X}_{1, N-k})^2 \sum_{j=1}^{N-k} (X_{j+k} - \bar{X}_{1+k, N})^2}}, \text{ where } k (= 0, 1, 2, \dots) \text{ is the time}$$

lag in months;  $N (= 48)$  is the total number of months in the time series;  $X_j$  and  $X_{j+k}$  are litterfall components of the  $j^{\text{th}}$  month and  $(j+k)^{\text{th}}$  month, respectively; and  $\bar{X}_{1, N-k}$  and

$\bar{X}_{1+k, N}$  are the mean values of the components from the first to the  $(N-k)^{\text{th}}$  month and from the  $(1+k)^{\text{th}}$  to the  $N^{\text{th}}$  month, respectively.

The crosscorrelation coefficient  $r_{xy}(l)$  was calculated to identify the lag,  $l$ , in maturation time between reproductive organs using their time series data:

$$r_{xy}(l) = \frac{\sum_{j=1}^{N-l} (X_j - \bar{X}_{1, N-l})(Y_{j+l} - \bar{Y}_{1+l, N})}{\sqrt{\sum_{j=1}^{N-l} (X_j - \bar{X}_{1, N-l})^2 \sum_{j=1}^{N-l} (Y_{j+l} - \bar{Y}_{1+l, N})^2}}, \text{ where } l (= 0, 1, 2, \dots) \text{ is the time lag}$$

in months;  $N (= 48)$  is the total number of months in the time series;  $X_j$  and  $Y_{j+l}$  are the reproductive components, respectively, of the  $j^{\text{th}}$  month and  $(j+l)^{\text{th}}$  month;  $\bar{X}_{1, N-l}$  is the mean value of an element from the first to the  $(N-l)^{\text{th}}$  month; and  $\bar{Y}_{1+l, N}$  is the mean value of the other element from the  $(1+l)^{\text{th}}$  to the  $N^{\text{th}}$  month.

### 3.3. Results

#### 3.3.1. Vegetative phenology

New leaf production and leaf fall of *K. obovata* occurred continuously throughout the year, but showed a clear monthly trend. Leaf litterfall was closely linked with stipule litterfall. Figure 3-3a shows leaf litterfall, which followed a monthly pattern, that is, the highest peak in July and the lowest in January. Stipule litterfall, which is an indicator of leaf emergence, was highest during summer (April–August). Figure 3-3b shows that the highest peak of stipule litterfall was in July and the lowest was in January. Branch litterfall, including small twigs, bark, and large branches, did not show a clear monthly trend (Fig. 3-3c). Figure 3-4 depicts the exponential relationship between branch litterfall and monthly maximum wind speed. Branch litterfall increased exponentially with increasing monthly maximum wind speed. During typhoons, green leaves were damaged and fell into the ground individually or together with living broken branches. These green leaves contributed excessive leaf litterfall (Fig. 3-3a). Figure 3-3c presents the excessive branch litterfall data (e.g. July 2006, July 2007, and October 2010); this excessive litterfall was attributable to typhoon events with wind speed exceeding  $17.2 \text{ m s}^{-1}$ . The Japan Meteorological Agency defines a strong typhoon as having wind speeds of  $33\text{--}43 \text{ m s}^{-1}$  and a very strong typhoon as having wind speeds of  $44\text{--}53 \text{ m s}^{-1}$ . During the study period, 12 strong typhoons were observed and 105 typhoons approached

Okinawa. Figure 3-4 depicts the exponential relationship between branch litterfall and monthly maximum wind speed. Branch litterfall increased exponentially with increasing monthly maximum wind speed. Leaves were the dominant element of litterfall during the entire study period. The mean total litterfall amount was  $991.1 \pm 35.4 \text{ g m}^{-2} \text{ yr}^{-1}$  (mean  $\pm$  SE), of which leaves were the largest contributor, with an estimated amount of  $530.6 \pm 12.8 \text{ g m}^{-2} \text{ yr}^{-1}$  (Table 3-1). Table 3-1 presents the amounts of stipule and branch litterfalls, and their contributions to the total litterfall.

As shown in Fig. 3-5a, vegetative organ (including leaves, stipules, and branches) litterfall showed a clear monthly trend, with its highest peak in summer and lowest in winter. The  $W$  values suggested that monthly trends in the litterfalls of vegetative organs, except branch, did not change significantly among years (Table 3-2). Leaf litterfall was significantly related to monthly mean air temperature, monthly maximum wind speed, and monthly rainfall, whereas stipule litterfall was significantly related to monthly day length and monthly maximum wind speed. Branch litterfall was significantly correlated with monthly maximum wind speed and monthly mean air temperature (Table 3-3).

### **3.3.2. Reproductive phenology**

The reproductive cycle of *K. obovata* had a regular monthly periodicity (Fig. 3-6). Initiation of green bud primordia was observed in March and continued until April. It was very difficult to separate the flower bud primordia from the litterfall. In most cases, flower bud primordia were confused with inflorescence segments because *K. obovata* inflorescences are dichotomously branched two or three times (Sheue et al. 2003). Bud primordia eventually developed into green buds and then developed into mature buds. Flower bud litterfall started in March and continued until August, with a peak in April and May (Fig. 3-6a). Flower bud litterfall was not observed in the litter traps from September to February. Flowering started in May and continued until September with the most abundant flowering occurring in July and August, when most flowers fell into the traps, after this time the number of flowers in the traps was drastically reduced (Fig. 3-6b). If a flower was not fertilized, it was aborted and then fell from the trees within a few days. Pollinated flowers also fell. Figure 3-6b shows that the highest flower litterfall was in August and the lowest was in October. Flower litterfall was not observed

in the litter traps from November to April.

As shown in Figure 3-6c, fruiting started in August and continued until December. The highest fruit litterfall was observed in October and November. No fruit litterfall was observed in the litter traps from February to July. Hypocotyls developed from fruits and then turned into mature propagules. Propagules began to drop in March and continued until May (Fig. 3-6d). In March, mostly immature propagules were found in the litter traps, whereas mostly mature propagules were found in the litter traps during May. Figure 3-6d shows the clear monthly trend in propagule litterfall with a peak in April to May. Neither mature nor immature propagules were found in the litter traps from July to November. The average total reproductive organ litterfall was  $185.8 \pm 25.5 \text{ g m}^{-2} \text{ yr}^{-1}$  (mean  $\pm$  SE), which contributed 18.83 % to the total litterfall (Table 3-1). Table 3-1 shows the detailed amounts of flower bud primordium, flower bud, flower, fruit, and propagule litterfall, respectively, and their percentages of contribution to the total litterfall.

Figure 3-5b indicates that reproductive organs litterfall of *K. obovata* followed a very specific monthly periodicity. The calculated values of  $W$  suggested that these monthly trends in the litterfalls of reproductive organs did not change significantly among years (Table 3-2). As shown in Table 3-3, the flower bud litterfall of *K. obovata* was significantly correlated with monthly day length, monthly mean air temperature, and monthly mean air relative humidity, whereas flower litterfall was significantly correlated with only monthly mean air temperature rather than other climatic factors. Fruit and propagule litterfall related with monthly day length and monthly mean air temperature, respectively.

Similar to other mangrove species, *K. obovata* had a very small proportion of flowers that developed into propagules. The results show that only  $6.10 \pm 1.7 \%$  (mean  $\pm$  SE) of flowers developed into propagules, and  $23.1 \pm 5.3 \%$  (mean  $\pm$  SE) of the flowers developed into fruits, including both mature and immature fruits and propagules (Table 3-4).

As shown in Figure 3-7a, the development phase from flower buds to flowers took 2 months. The development phase from flower buds to fruits took 5 months (Fig. 3-7b). After fertilization was completed, flowers turned into fruits. The developmental phase from flower buds to mature propagules took 11 months (Fig. 3-7c). Development

from flowers to fruits took 3 months (Fig. 3-7d). As a species with viviparous germination, *K. obovata* followed the initiation of hypocotyl from fruit. Development from flowers to mature propagules and fruits to mature propagules took 9 months (Fig. 3-7e) and 6 months (Fig. 3-7f), respectively.

### 3.4. Discussion

#### 3.4.1. Vegetative phenology

Leaf litterfall (Fig. 3-3a) and stipule litterfall (Fig. 3-3b) of *K. obovata* followed the same seasonal pattern, that is, leaf fall and leaf production were lowest in winter and highest in summer. Another study in Ohura Bay, Okinawa Island, Japan recorded a similar pattern of leaf fall and leaf recruitment of *K. candel* (Hardiwinoto et al. 1989). The present study showed that peaks in leaf and stipule litterfall occurred in the same month, whereas Duke (1990) reported a time lag of 1 month between leaf emergence and leaf fall for *Avicennia marina* in Australia, Papua New Guinea, and New Zealand. In contrast to our results, leaf fall of *K. obovata* in Hong Kong, showed a bimodal pattern, with the highest peaks in spring (February–June) and in late summer (August–November) (Lee 1989). The leaf production period followed the same seasonal pattern as that found in other mangrove species. For example, *Rhizophora apiculata* BL. in southern Thailand and *A. marina* (Forssk.) Vierh., *Ceriops australis* (White) Ballment, Smith & Stoddart, *Rhizophora stylosa* Griff., and *Sonneratia alba* J. Simth. in northern Australia showed their highest peaks during the wet summer season, that is, in the monsoonal season with maximum temperature and rainfall (Christensen and Wium-Andersen 1977; Coupland et al. 2005; Coupland et al. 2006).

Litterfall seasonality is a common feature in most studies, but the cause for its seasonality is unclear (Gill and Tomlinson 1971; Lugo and Snedaker 1975; Wium-Anderson and Christensen 1978). The data presented in the present study demonstrate that leaf and stipule litterfall of *K. obovata* were significantly correlated with monthly mean air temperature, monthly maximum wind speed and monthly rain fall, and with monthly day length and monthly maximum wind speed, respectively. Our results are supported by the findings of Nakagoshi and Nehira (1986), who reported that cumulative temperature was directly proportional to the number of leaves and the rate of

leaf production in mangrove seedlings. A similar finding was observed in *K. obovata* (Gwada et al. 2000). In contrast to our results, most species in a tropical evergreen mountain rainforest show a good correlation with leaf shedding and precipitation (Bendix et al. 2006) and also display a bimodal peak in leaf production that is correlated with the rainy periods (Medway 1972). *Kandelia obovata* grows in intertidal areas and shows distinctly unimodal pattern, in contrast to tropical rain forests with a bimodal or multimodal pattern. High species diversity and appropriate humidity in tropical rain forests could cause multi-mode peaks of litterfall. The diversity and water condition in tropical rain forests differ substantially from mangrove ecosystems.

The present study showed that the leaves of *K. obovata* were dominant (53.3 %) in the total litterfall (Table 3-1). Our results coincide with the findings of Wafar et al. (1997), who reported that the percentage contribution of leaf litterfall to total litterfall in the mangrove species *Rhizophora apiculata* Blume., *Rhizophora mucronata* Lamk., *Sonneratia alba* J. E. Smith, and *Avicennia officinalis* L. on the central west coast of India were 61.2, 61, 57.7, and 43 % respectively. The contribution of leaf litterfall to the total litterfall in *K. obovata* was lower than that recorded in other mangrove species such as *A. marina* in Kenya, where leaf litterfall constituted 514.6 g m<sup>-2</sup> (83 %) of the total litterfall (Ochieng and Erfemeijer 2002). Another study on *A. marina* var. *australasica* in New Zealand found that leaf litterfall contributed 140–200 g m<sup>-2</sup> (73 %) to the total litterfall (May 1999). The contribution (7.79 %) of the stipule litterfall of the present *K. obovata* was similar to those of *R. apiculata* (7 %) and *R. mucronata* (6.3 %) in India (Wafar et al. 1997).

Branch litterfall showed a less clear monthly pattern than leaf and stipule litterfall (Fig. 3-3). In a typhoon month, branch litterfall was excessive compared with the litterfall in other months because all dead branches including broken living branches fell to the ground. This phenomenon shows the strong effect of the typhoon. The present observation supports the findings of Hardiwinoto et al. (1989) who reported that typhoons had strong effects on branch litterfall in Ohura Bay, Okinawa Island, Japan.

#### **3.4.2. Reproductive phenology**

We found that flower bud initiation in *K. obovata* started during spring (Fig. 5a), whereas flowering occurred during summer (Fig. 5b). During spring and summer,

temperature, sunshine hour, rainfall, and humidity were at their maximum (Fig. 2). Our results showed that flower bud and flower litterfall of *K. obovata* were significantly correlated with monthly day length, monthly mean air temperature, and monthly mean air relative humidity and with monthly mean air temperature, respectively, in agreement with Duke's (1990) finding that climatic factors such as day length and temperature had a strong influence on *A. marina* flowering in Australia, Papua New Guinea, and New Zealand. Similar findings have been reported by Wium-Andersen and Christensen (1978), who observed flower buds and flowers of *C. tagal* in southern Thailand in April to June, consistent with the wet season. The peak period of flower bud (Fig. 3-6a) and flower production (Fig. 3-6b) of *K. obovata* coincided with the peak period of leaf emergence (stipule litterfall) (Fig. 3-3b), suggesting that growth of reproductive organs affects apex vigor (Gill and Tomlinson 1971).

Flowering and fruiting of *R. apiculata*, *R. mucronata*, *S. alba*, and *A. officinalis* were found to be confined to specific periods during a year, and the contributions of these species to flower and fruit litterfall to total litterfall were 21.8, 23.2, 17.3, and 18.1 %, respectively (Wafar et al. 1997). Our results showed that the contribution of the reproductive components of *K. obovata* to the total litterfall was very similar to other mangrove species reported by Wafar et al. (1997). According to May (1999), the flower and fruit litterfall of *A. marina* var. *australasica* contributed 11 % to the total litterfall.

This is the first study to report the maturation periods of reproductive organs of *K. obovata* in its northern limit of geographical distribution. The developmental phase of flower bud initiation to mature propagules took 11 months (Fig. 3-7). Gill and Tomlinson (1971) reported that the development time to mature propagules for *Rhizophora mangle* L. in Florida was 8–13 months. The developmental phase of bud initiation to mature propagules was 6–8 months in *Bruguiera cylindrica* (L.) BL. and 16–21 months in *Ceriops tagal* (Perr.) C.B. Rob. in southern Thailand (Wium-Andersen and Christensen 1978). According to Christensen and Wium-Andersen (1977), *R. apiculata* in southern Thailand took nearly 3 years to develop from flower bud primordia to mature propagules. In comparison with already reported data of species belonging to the family Rhizophoraceae, it appears that *K. obovata* growing at the northern limit of its geographical distribution has a relatively short maturation period.

The present study found that a small portion of flowers developed into

propagules (6.1 %). Although *K. obovata* produces a large number of flowers, the flowers are small in size, self-compatible, and pollinated by small insects, which is similar to *K. candel* (Tomlinson 1994). A similar observation was made by Gill and Tomlinson (1971) who reported that 0–7.2 % of *R. mangle* flowers were fertilized. Although 23.1 % of the fertilized flowers developed into fruits, not all of the fruits grew, which may have been because of the energy required during development as well as tree size. This rate was higher than the range of 2.4– 5.3 % for *R. stylosa*, *R. mangle*, and *B. gymnorhiza* reported by Tyagi (2003) and for *R. stylosa* and *C. australis* reported by Coupland et al. (2006). It has been suggested that *K. obovata* has the least specialized pollination among Rhizophoraceae species as several types of small insects visit its flowers (Tomlinson 1994). Entomophilous pollination could be connected with the relatively high fruit set of *K. obovata*.

### 3.5. Conclusion

The vegetative and reproductive phenology data of *K. obovata* was repeated each year over five years, although there was no significant variation among the years for the vegetative and reproductive components. *Kandelia obovata* showed unimodal leaf and stipule litterfall peaks in subtropical regions. The periodicity of flowering and fruiting are restricted to the season and it coincides with the monthly day length, monthly mean air temperature, and monthly mean air relative humidity. *Kandelia obovata* growing at the northern limit of its biogeographical distribution has a relatively short maturation period of the reproductive organs.

### References

- Alongi DM (1996) The dynamics of benthic nutrient pools and fluxes in tropical mangrove forests. *J Mar Res* 54:123–148
- Alongi DM (2002) Present status and future of the world's mangrove forests. *Environ Conserv* 9:331–349
- Bendix J, Homeier J, Cueva Ortiz E, Emck P, Breckle WS, Richter M, Beck E (2006) Seasonality of weather and tree phenology in a tropical evergreen mountain rain forest. *Int J Biomet* 50:370–384
- Boto KG, Bunt JS (1982) Carbon export from mangroves. In: Clough BF (ed) *Mangrove*

- Ecosystems in Australia. ANU Pres, Canberra, Australia, pp 239–257
- Christensen B, Wium-Andersen S (1977) Seasonal growth of mangrove trees in southern Thailand. I. Phenology of *Rhizophora apiculata* BL. *Aquat Bot* 3:281–286
- Clarke PJ (1994) Baseline studies of temperate mangrove growth and reproduction; demographic and litterfall measures of leafing and flowering. *Aust J Bot* 42:37–48
- Coupland GT, Paling EI, McGuinness KA (2005) Vegetative and reproductive phenologies of four mangrove species from northern Australia. *Aust J Bot* 53:109–117
- Coupland GT, Paling EI, McGuinness KA (2006) Floral abortion and pollination in four species of tropical mangroves from northern Australia. *Aquat Bot* 84:151–157
- Duke NC (1990) Phenological trends with latitude in the mangrove tree *Avicennia marina*. *J Ecol* 78:113–133
- Duke NC, Bunt JS, Williams WT (1984) Observations on the floral and vegetative phenologies of north-eastern Australian mangroves. *Aust J Bot* 32:87–99
- FAO (1994) *Mangrove Forest Management Guidelines*. FAO Forestry Paper No. 117, Food and Agricultural Organization of the United Nations, Rome
- Fernandes MEB (1999) Phenological patterns of *Rhizophora* L., *Avicennia* L. and *Laguncularia* Gaertn. f. in Amazonian mangrove swamps. *Hydrobiologia* 413:53–62
- Gill AM, Tomlinson PB (1971) Studies on the growth of red mangrove (*Rhizophora magle* L.). 3. Phenology of the shoot. *Biotropica* 3:109–124
- Guo LB, Sims REH (1999) Litter decomposition and nutrient release via litter decomposition in New Zealand eucalypt short rotation forests. *Agric Ecosyst Environ* 75:133–140
- Gwada P, Makoto T, Uezu Y (2000) Leaf phenological traits in the mangrove *Kandelia candel* (L.) Druce. *Aquat Bot* 68:1–14
- Hardiwinoto S, Nakasuga T, Takabatake S (1989) Litter production and decomposition of a mangrove forest at Ohura Bay, Okinawa. *Res Bull Coll Exp For, Hokkaido Univ* 46:577–594
- Janzen DH (1967) Synchronization of sexual reproduction of trees within the dry season

- in Central America. *Evolution* 21:620–673
- Kathiresan K, Bingham BL (2001) Biology of mangroves and mangrove ecosystems. *Adv Mar Biol* 40:81–251
- Khan MNI, Suwa R, Hagihara A, Ogawa K (2004) Interception of photosynthetic photon flux density in a mangrove stand of *Kandelia candel* (L.) Druce. *J Forest Res* 9:205–210
- Khan MNI, Suwa R, Hagihara A (2007) Carbon and nitrogen pools in a mangrove stand of *Kandelia obovata* (S., L.) Yong: vertical distribution in the soil–vegetation system. *Wetl Ecol Manage* 15:141–153
- Kira T (1991) Forest ecosystems of East and Southeast Asia in a global perspective. *Ecol Res* 6:185–200
- Lee SY (1989) Litter production and turnover of the mangrove *Kandelia candel* (L.) Druce in a Hong Kong tidal shrimp pond. *Estuar Coast Shelf Sci* 29:75–87
- Lugo AE, Snedaker SC (1975) Properties of a mangrove forest in southern Florida. In: Walsh GE, Snedaker SC, Teas HJ (eds) *Proceedings of the International Symposium on Biology and Management of Mangroves*. University of Florida, Gainesville, pp170–212
- May JD (1999) Spatial variation in litter production by the mangrove *Avicennia marina* var. *australasica* in Rangaunu Harbour, Northland, New Zealand. *NZ J Mar Freshw Res* 33:163–172
- Medway L (1972) Phenology of a tropical rain forest in Malaya. *Biol J Linn Soc* 4:117–146
- Mehlig U (2006) Phenology of the red mangrove, *Rhizophora mangle* L. in the Caete Estuary, Para, equatorial Brazil. *Aquat Bot* 84:158–164
- Nagarajan B, Pandiarajan C, Krishnamoorthy M, Sophia P (2008) Reproductive fitness and success in mangroves: Implication on conservation. In: Sengupta M, Dalwani R (eds) *Proceedings of Taal 2007: the 12<sup>th</sup> World Lake Conference*, pp 29–33
- Naido G (1989) Seasonal plant water relations in a South African mangrove swamp. *Aquat Bot* 33:233–242
- Nakagoshi K, Nehira K (1986) Growth and mortality of mangrove seedlings transplanted to Hiroshima. *Hikobia* 9:439–449

- Ochieng CA, Erftemeijer PLA (2002) Phenology, litterfall and nutrient resorption in *Avicennia marina* (Forssk.) Vierh in Gazi Bay, Kenya. *Trees* 16:167–171
- Saenger P, Moverley J (1985) Vegetative phenology of mangroves along the Queensland coastline. In: *Proceedings of the Ecological Society of Australia* 13, pp 257–265
- Saito K, Okuno T, Asai A, Haga T, Kawai M, Kudo H, Miyamoto K, Masamara M, Osawa Y, Kawamura M, Goto H (2003) Lectures on modern statistics. Practical Business Education Institute, Tokyo (in Japanese)
- Sheue CR, Liu HY, Yong JWH (2003) *Kandelia obovata* (Rhizophoraceae), a new mangrove species from Eastern Asia. *Taxon* 52:287–294
- Shiga T, Okuhara M, Nozawa M (2004) Lectures on multiple regression analysis using Excel. Practical Business Education Institute, Tokyo (in Japanese)
- Tomlinson PB (1994) *The Botany of Mangroves*. Cambridge University Press, New York, USA
- Tyagi AP (2003) Location and interseasonal variation in flowering, propagule setting and propagule size in mangroves species of the family Rhizophoraceae. *Wetl Ecol Manage* 11:167–174
- Tyagi AP, Singh VV (1998) Pollen fertility and intraspecific compatibility in mangroves of Fiji. *Sex Plant Reprod* 11:60–63
- Wafar S, Untawale AG, Wafar M (1997) Litterfall and energy flux in a mangrove ecosystem. *Estuar Coast Shelf Sci* 44:111–124
- Wium-Andersen S (1981) Seasonal growth of mangrove trees in southern Thailand. III. Phenology of *Rhizophora mucronata* Lamk. and *Scyphiphora hydrophyllaceae* Gaertn. *Aquat Bot* 10:371–376
- Wium-Andersen S, Christensen B (1978) Seasonal growth of mangrove trees in southern Thailand. II. Phenology of *Bruguiera cylindrica*, *Ceriops tagal*, *Lumnitzera littorea* and *Avicennia marina*. *Aquat Bot* 5:383–390
- Zhou G, Guan L, Wei X, Zhang D, Zhang Q, Yan J, Wen D, Liu J, Liu S, Huang Z, Kong G, Mo J, Yu Q (2007) Litterfall production along successional and altitudinal gradients of subtropical monsoon evergreen broadleaved forests in Guangdong, China. *Plant Ecol* 188:77–89

**Table 3-1.** Annual amounts of vegetative and reproductive litterfall components of *Kandelia obovata* during the study period.

Litterfall components	1 <sup>st</sup> year	2 <sup>nd</sup> year	3 <sup>rd</sup> year	4 <sup>th</sup> year	5 <sup>th</sup> year	Mean
Leaf	594.58 ± 14.05 (56.8)	600.75 ± 13.73 (49.7)	545.30 ± 16.82 (60.0)	482.28 ± 10.05 (52.6)	429.96 ± 9.09 (49.2)	530.58 ± 12.75 (53.3)
Stipule	92.77 ± 2.66 (8.87)	96.95 ± 2.08 (8.02)	82.73 ± 3.18 (9.10)	52.39 ± 2.06 (5.72)	59.50 ± 2.14 (6.80)	76.87 ± 2.42 (7.79)
Branch	204.82 ± 14.79 (19.6)	357.08 ± 19.26 (29.5)	88.89 ± 10.65 (9.78)	159.72 ± 9.87 (17.4)	178.69 ± 8.61 (20.4)	197.84 ± 12.64 (20.1)
Sum of vegetative organs	892.17 ± 31.51 (85.3)	1054.79 ± 35.07 (87.3)	716.91 ± 30.65 (78.9)	694.39 ± 21.97 (75.8)	668.15 ± 19.83 (76.4)	805.28 ± 27.81 (81.2)
Bud primordium	15.58 ± 1.07 (1.49)	26.17 ± 1.57 (2.17)	21.78 ± 0.74 (2.40)	32.31 ± 0.72 (3.52)	19.06 ± 0.41 (2.18)	22.98 ± 0.90 (2.33)
Flower bud	14.58 ± 0.61 (1.39)	10.57 ± 0.58 (0.87)	5.93 ± 0.27 (0.65)	8.88 ± 0.54 (0.97)	12.47 ± 0.47 (1.42)	10.48 ± 0.49 (1.06)
Flower	8.72 ± 1.12 (0.83)	20.11 ± 2.07 (1.66)	25.40 ± 2.72 (2.79)	44.26 ± 2.09 (4.83)	40.57 ± 1.88 (4.64)	27.81 ± 1.98 (2.82)
Fruit	0.85 ± 0.21 (0.08)	3.56 ± 0.41 (0.29)	3.43 ± 0.36 (0.38)	6.49 ± 0.40 (0.71)	4.27 ± 0.70 (0.49)	3.72 ± 0.41 (0.38)
Propagule	114.35 ± 27.35 (10.9)	93.45 ± 14.09 (7.73)	135.77 ± 22.20 (14.9)	130.24 ± 22.98 (14.2)	130.35 ± 22.13 (14.9)	120.83 ± 21.75 (12.2)
Sum of reproductive organs	154.07 ± 30.36 (14.7)	153.86 ± 18.72 (12.7)	192.32 ± 26.29 (21.2)	222.17 ± 26.72 (24.2)	206.72 ± 25.59 (23.6)	185.83 ± 25.54 (18.8)
Total	1046.24 ± 42.54	1208.64 ± 32.50	909.24 ± 26.47	916.56 ± 48.70	874.87 ± 26.53	991.11 ± 35.35

Values are mean ( $\text{g m}^{-2} \text{ yr}^{-1}$ ) ± SE. Numerals in parenthesis represent the percentage for the total amounts.

**Table 3-2.** Kendall's consistency coefficient,  $W$ , showing agreement in the monthly changes in litterfall components of *Kandelia obovata* among five years of this study.

Litterfall component	$W$	$\chi^2$ ( $p$ -value)
Leaf	0.7589	41.74 (< 0.001)
Stipule	0.7192	39.55 (< 0.001)
Branch	0.3270	17.99 (0.0813)
Flower bud primordium	0.6120	33.66 (< 0.001)
Flower bud	0.4775	26.26 (< 0.01)
Flower	0.8043	44.24 (< 0.001)
Fruit	0.6867	37.77 (< 0.001)
Propagule	0.6504	35.77 (< 0.001)
Total litterfall	0.8151	44.83 (< 0.001)

Degrees of freedom of the  $\chi^2$  distribution are 11.

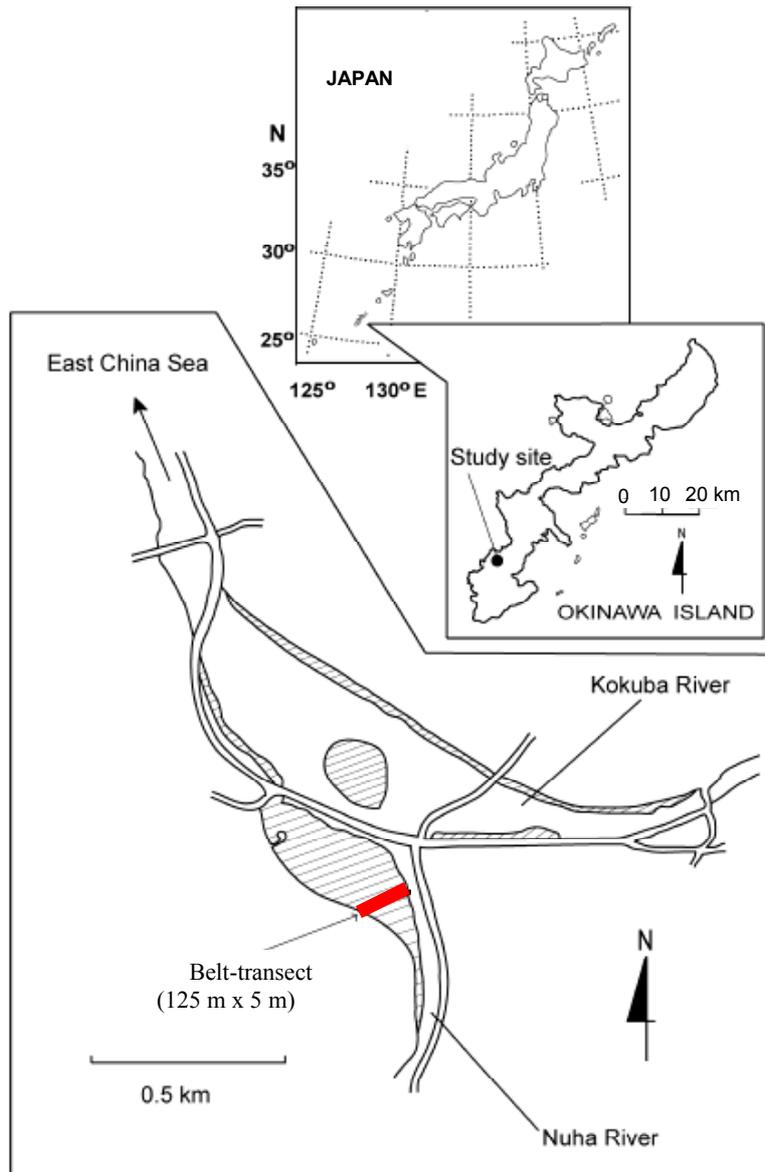
**Table 3-3.** Adjusted  $R^2$  values from stepwise method of multiple regression analysis of vegetative and reproductive litterfall components of *Kandelia obovata* in relation to environmental factors. Significant probabilities of the coefficient value are indicated by \* ( $p \leq 0.05$ ), \*\* ( $p \leq 0.01$ ), or \*\*\* ( $p \leq 0.001$ ).

Component	Monthly mean temperature °C ( $x_1$ )	Monthly day length h month <sup>-1</sup> ( $x_2$ )	Monthly rainfall mm month <sup>-1</sup> ( $x_3$ )	Monthly mean relative humidity % ( $x_4$ )	Monthly maximum wind speed m s <sup>-1</sup> ( $x_5$ )	Equation
Leaf	0.31 (0.88)		0.57 (0.86)		0.48 (0.93)	$y = -67.0 + 4.0^{***} x_1 + 2.1^{***} x_5 - 0.1^{***} x_3$
Stipule		0.37 (0.99)			0.41 (0.99)	$y = -15.0 + 0.05^{***} x_2 + 0.1^* x_5$
Branch	0.56 (0.96)				0.53 (0.96)	$y = -90.5 + 3.9^{***} x_5 + 1.8^* x_1$
Flower bud	0.45 (0.44)	0.31 (0.89)		0.55 (0.42)		$y = -12.9 + 0.03^{***} x_2 - 0.23^{***} x_1 + 0.1^{***} x_4$
Flower	0.28 (1.00)					$y = -13.4 + 0.68^{***} x_1$
Fruit	0.20 (0.50)	0.03 (0.50)				$y = 2.8 - 0.01^{***} x_2 + 0.1^{***} x_1$
Propagule	0.44 (0.50)	0.11 (0.50)				$y = -84.1 + 0.48^{***} x_2 - 3.5^{***} x_1$

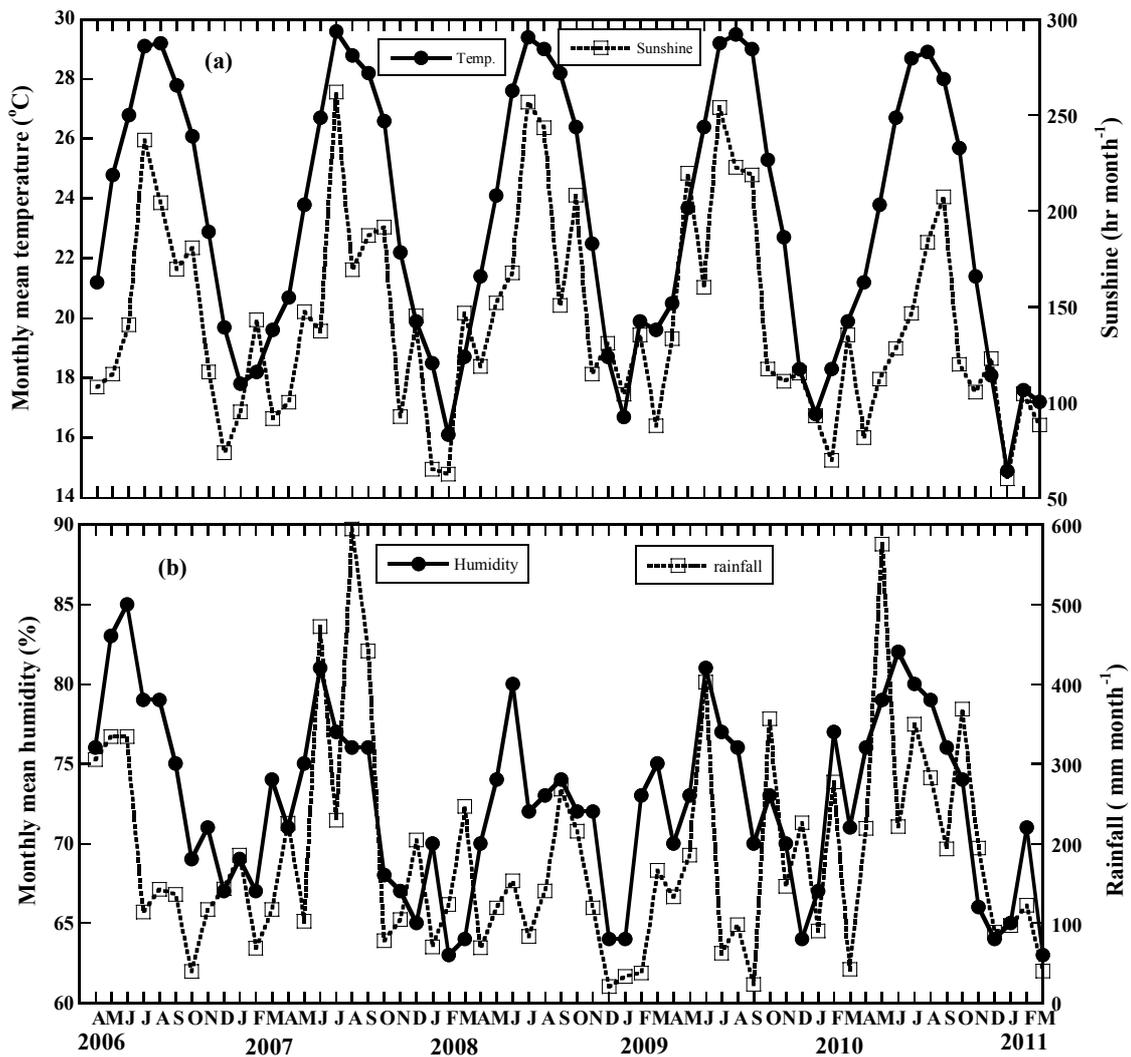
Numerals in parenthesis are the tolerances of the coefficients of the multiple regression for a component.

**Table 3-4.** Mean numbers of reproductive organs ( $\text{m}^{-2} \text{yr}^{-1} \pm \text{SE}$ ) of *Kandelia obovata* and their conversion rates ( $\% \pm \text{SE}$ ) during the study period.

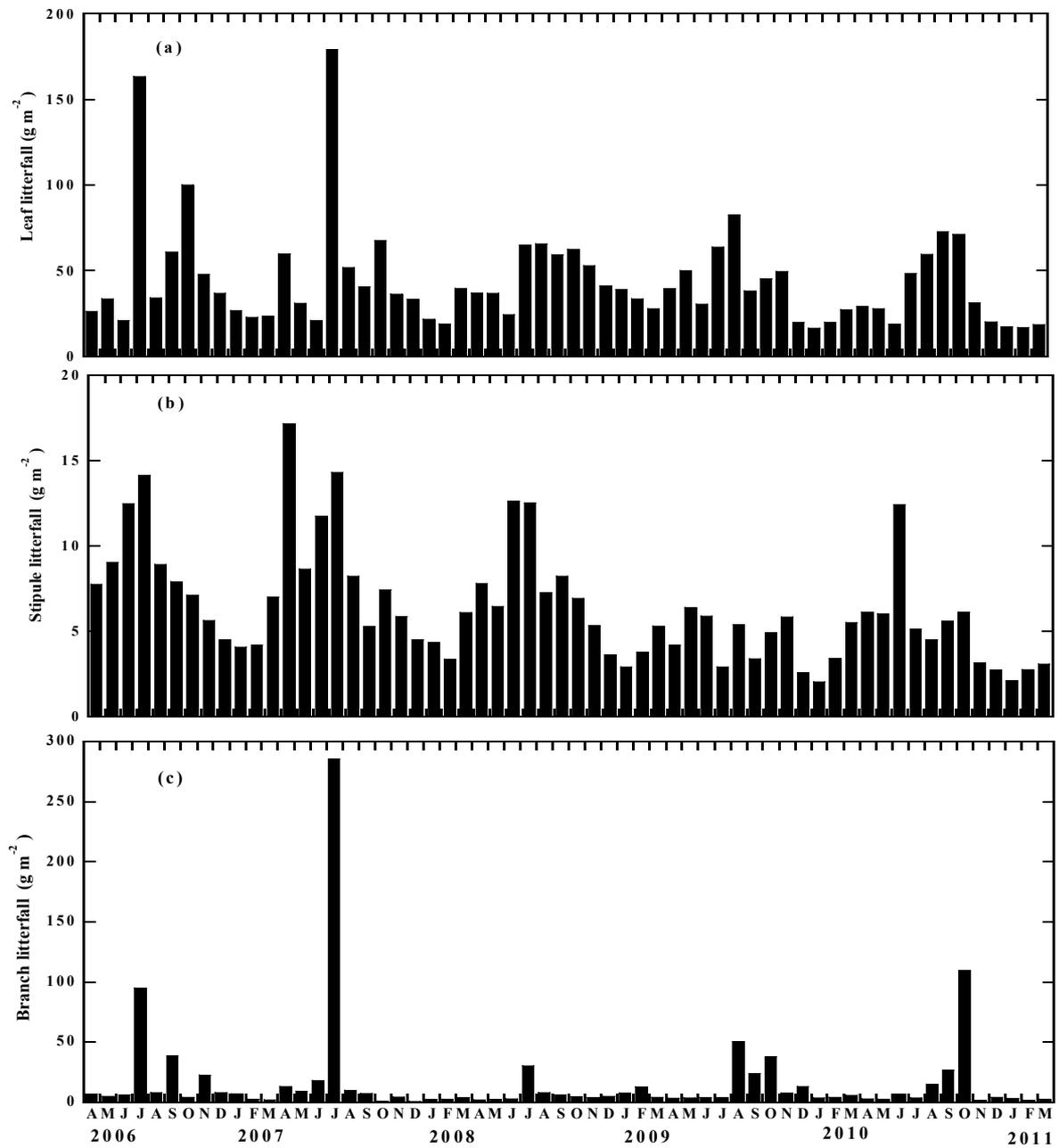
Reproductive organs	1 <sup>st</sup> year	2 <sup>nd</sup> year	3 <sup>rd</sup> year	4 <sup>th</sup> year	5 <sup>th</sup> year	Mean
Flower	121.8 $\pm$ 7.0	319.9 $\pm$ 16.1	430.5 $\pm$ 20.6	793.1 $\pm$ 44.8	669.1 $\pm$ 35.7	466.9 $\pm$ 120.3
Fruit	65.8 $\pm$ 3.0	68.4 $\pm$ 2.8	84.3 $\pm$ 3.5	92.2 $\pm$ 2.9	95.0 $\pm$ 3.6	81.2 $\pm$ 6.0
Propagule	27.6 $\pm$ 1.2	16.4 $\pm$ 0.9	27.1 $\pm$ 1.5	33.0 $\pm$ 1.6	40.2 $\pm$ 2.2	28.9 $\pm$ 3.9
Flower to fruit	43.4 $\pm$ 2.3	21.0 $\pm$ 1.1	20.6 $\pm$ 1.3	13.6 $\pm$ 0.8	16.8 $\pm$ 0.9	23.1 $\pm$ 5.3
Fruit to propagule	29.6 $\pm$ 1.1	19.3 $\pm$ 1.2	24.3 $\pm$ 1.2	26.4 $\pm$ 1.3	29.7 $\pm$ 1.2	25.9 $\pm$ 1.9
Flower to propagule	12.8 $\pm$ 0.8	4.1 $\pm$ 0.9	5.0 $\pm$ 0.8	3.6 $\pm$ 0.9	5.0 $\pm$ 0.7	6.1 $\pm$ 1.7



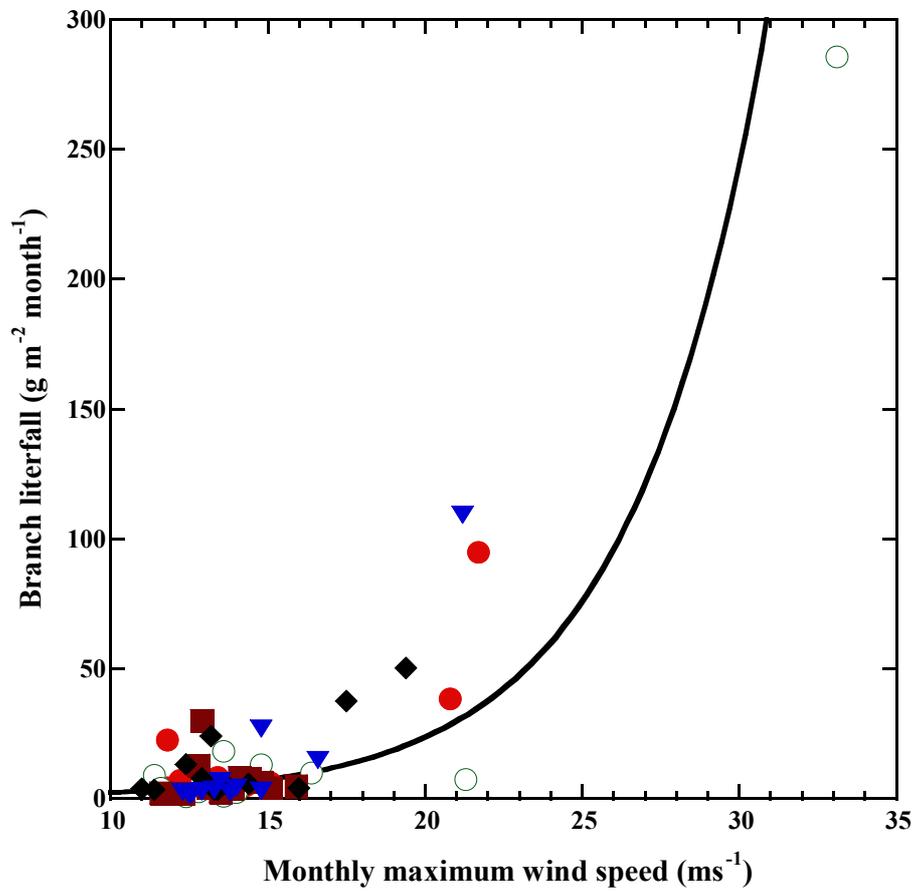
**Fig. 3-1.** Location of the study area. The hatched zone indicates the mangrove area. Arrow indicates the plot area (*bold line*).



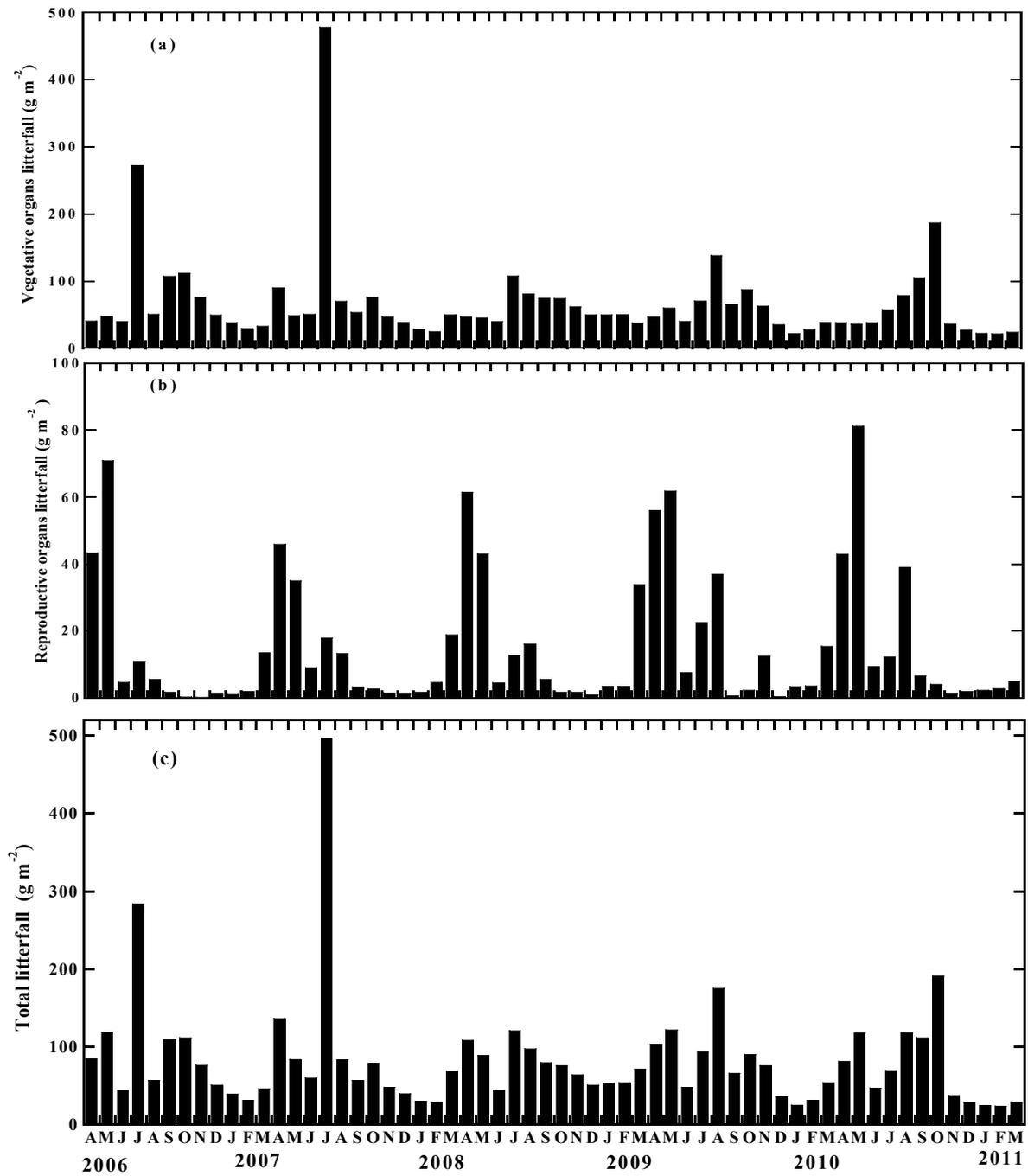
**Fig. 3-2.** Climatic diagram of the four climatic factors examined (temperature, sunshine, humidity, and rainfall). Data were obtained from the Okinawa Meteorological Observatory, Naha, Okinawa.



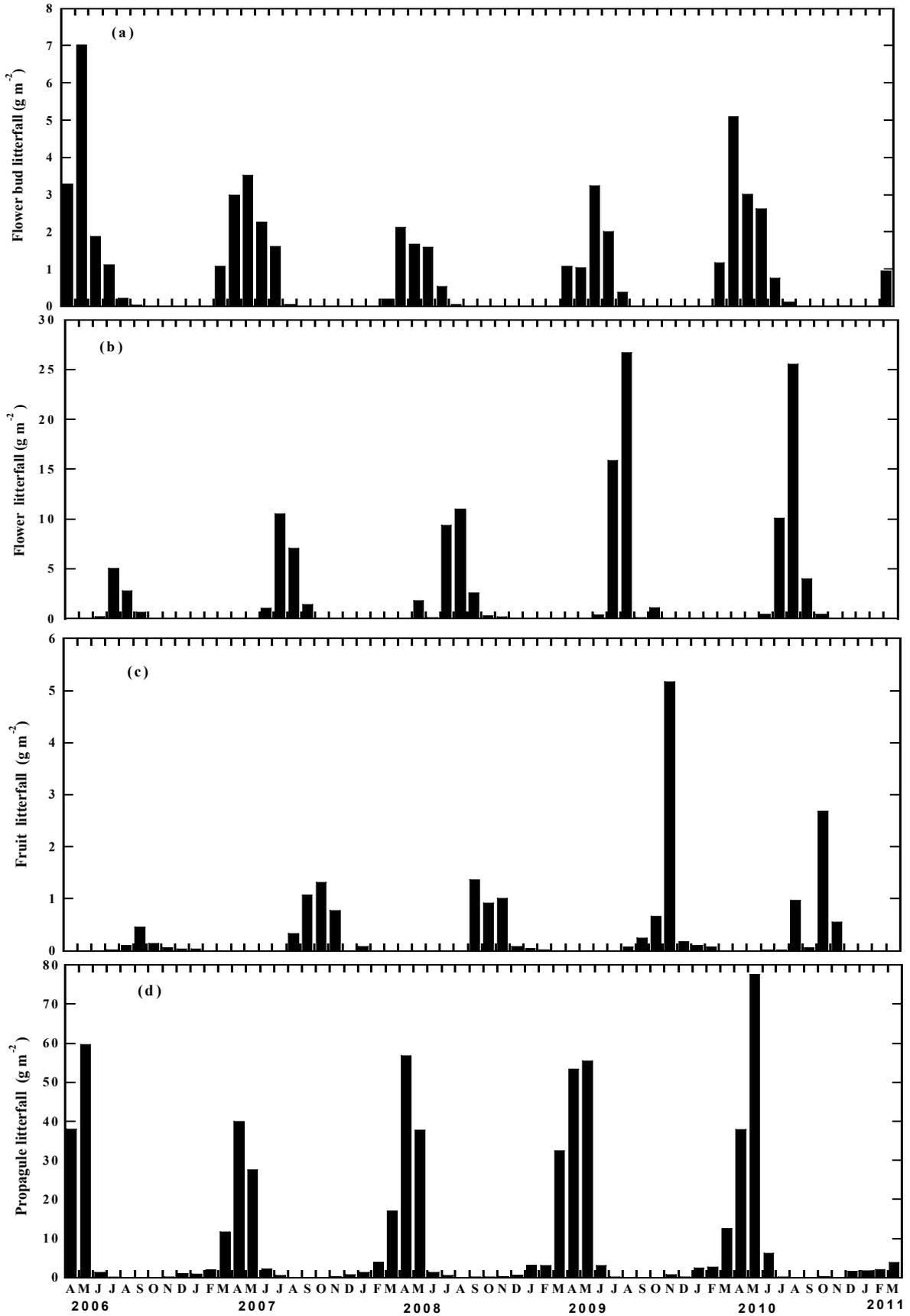
**Fig. 3-3.** Phenograms of the litterfall of the vegetative components of *K. obovata* in Manko Wetland.



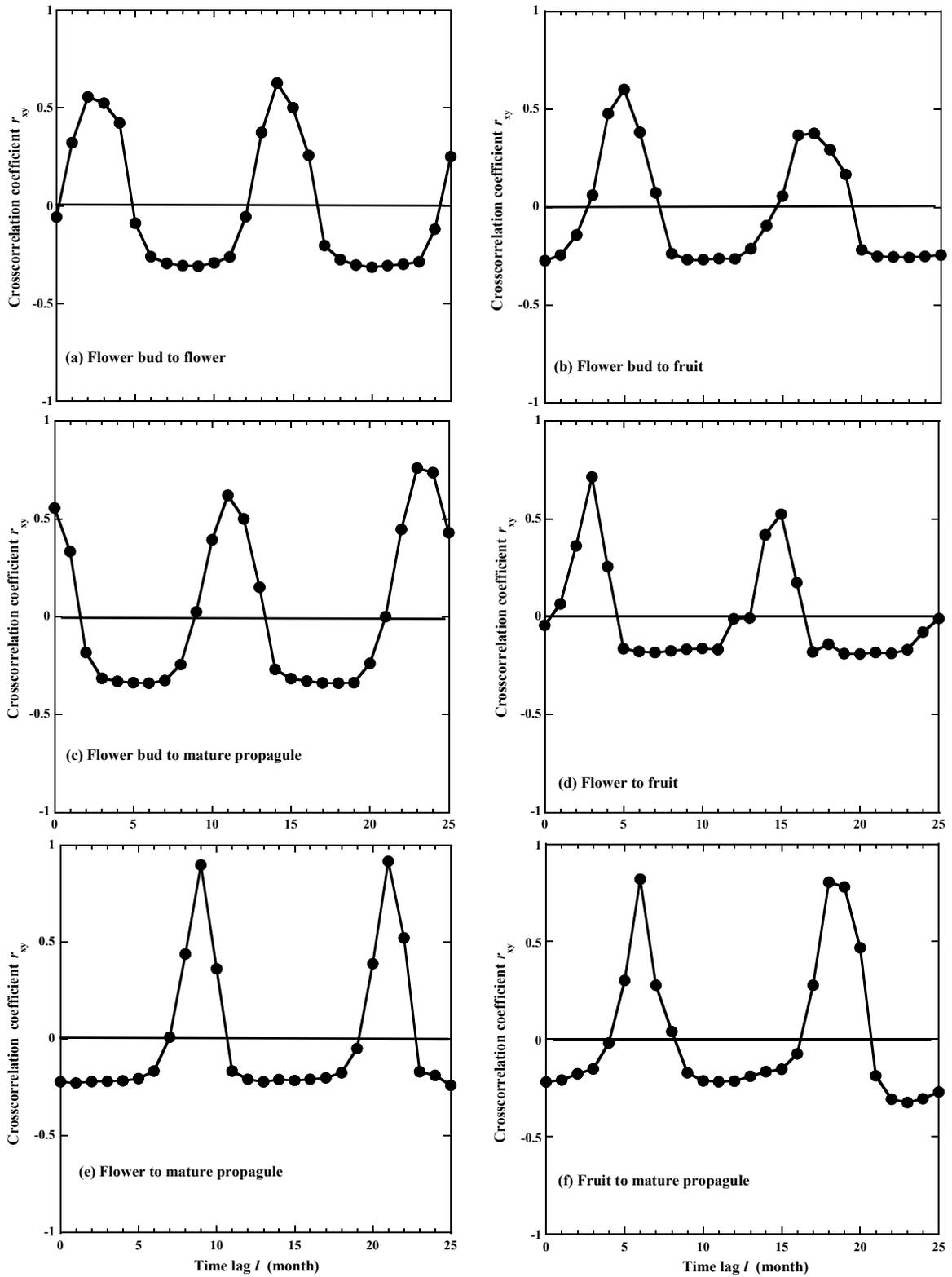
**Fig. 3-4.** Exponential relationship between monthly branch litterfall of *K. obovata* and monthly maximum wind speed ( $R^2 = 0.83$ ). ●: 1st year; ○: 2nd year; ■: 3rd year; ◆: 4th year; ▼: 5th year.



**Fig. 3-5.** Phenograms of the litterfall of the vegetative and reproductive components and the total litterfall of *K. obovata* in Manko Wetland.



**Fig. 3-6.** Phenograms of the litterfall of the reproductive components of *K. obovata* in Manko Wetland.



**Fig. 3-7.** Crosscorrelation coefficient between pairs of the reproductive components of *K. obovata* in Manko Wetland.

## CHAPTER IV

### **Phenological Traits of the Mangrove *Rhizophora stylosa* Griff.**

---

#### **4.1. Introduction**

Mangroves are important contributors of nutrients to coastal ecosystems. Their litterfall is a valuable indicator of their productivity and the input of materials and energy into sub-tidal systems (Mackey and Smail 1995). Litterfall also indicates phenological events in mangrove species (Leach and Burgin 1985; Duke 1990; Clark 1994), when the time-lag between the formation and shedding of plant organs is known (Mehlig 2006). Mangrove phenology is important for understanding both the contribution of mangroves to near-shore productivity and plant-animal interactions within the community itself (Coupland et al. 2005). Phenological events in mangrove communities have been suggested to be influenced by local or regional environmental conditions, particularly day length, air temperature, rainfall, and water status (Saenger and Moverley 1985; Naido 1989; Duke 1990; Fernandes 1999). Many studies have documented mangrove litterfall to assess mangrove productivity; however, fewer studies have documented mangrove phenology, particularly reproductive phenology.

*Rhizophora stylosa* Griff. is widespread in the Indo-Pacific region, extending in the western Pacific from New South Wales to Fiji and the Marshall Islands and north to Okinawa Island (Vannucci 2002; Duke 2006; Wilson and Saintilan 2012). The Kesashi River in Higashi Village, Okinawa Island, Japan, is the northern limit of the biogeographical distribution for *R. stylosa* and is 66 km north of the study area. The present study was conducted at Manko Wetland, Okinawa Island, which is inhabited by *R. stylosa* and other species of the family Rhizophoraceae. Because Okinawa has a distinctly seasonal climate, its mangroves must cope with substantial seasonal changes in environmental factors. Only one previous study examined the phenology of *R. stylosa* growing at the northern limit of its biogeographical distribution (Sharma et al. 2011), although a few studies have investigated growth (Wilson and Saintilan 2012), phenology (Duke et al. 1984; Coupland et al. 2005, 2006; Juliana et al. 2011), and litterfall production (Woodroffe 1984; Leach and Burgin 1985) of *R. stylosa*. In light of

this, we aimed to investigate the vegetative and reproductive phenology of *R. stylosa* growing in a subtropical region, to determine the development period of each reproductive organ, and to identify how climatic factors affect *R. stylosa* phenology.

## **4.2. Materials and methods**

### **4.2.1. Study site**

The study was conducted at Manko Wetland, Okinawa Island, Japan (26°11'N, 127°40'E) (Fig. 4-1), over four years from April 2008 to March 2013. This wetland is an important area for migratory birds and has been registered on the Ramsar List of Wetlands of International Importance (a Ramsar site) since 1999. The study area is a brackish tidal flat covering an extensive area at low tide; the tidal range is 3–212 mm. The mangroves grow in a mud flat area composed mainly of clay particles (RIS 1999). The area is subtropical, as determined by a warmth index of  $219.8 \pm 15.4$  (SE) °C month from 2000–2009 (Okinawa Meteorological Observatory, Naha, Japan), within the warmth index range of 180–240°C month for subtropical regions (Kira 1991).

### **4.2.2. Forest structure**

Four mangrove species grow at the study site. Three belong to the family Rhizophoraceae: *Rhizophora stylosa* Griff, *Kandelia obovata* Sheue, Liu & Yong, and *Bruguiera gymnorhiza* (L.) Lamk. The fourth species, *Excoecaria agallocha* L., is from the family Euphorbiaceae. We established five plots (4 m x 4 m each) in a *R. stylosa* stand to represent the full tidal range at which the species occurred. The number of plots was based on the availability of pure stands. All trees in the study plots were numbered, and height (*H*) and stem diameter at breast height (DBH) were measured in April 2010 and 2012. The tree density, mean *H*, and mean DBH of *R. stylosa* were  $2.2 \pm 0.1$  m<sup>-2</sup>,  $4.3 \pm 0.1$  m, and  $4.0 \pm 0.2$  cm, respectively, as of 2012.

### **4.2.3. Climate data**

Meteorological data were obtained from the Okinawa Meteorological Observatory, Naha, Japan, from April 2008 to March 2013 (i.e., the time period over which the field work was conducted). The Observatory is 2.8 km from the study area. During the study period, the temperature fluctuated approximately 15°C from the coldest month to the

warmest, and mean annual air temperature was  $23.2 \pm 0.2^\circ\text{C}$ . Mean annual day length was  $4362.7 \pm 2.5 \text{ h yr}^{-1}$ . Rainfall varied throughout the year but exceeded 100 mm month<sup>-1</sup> in most months. The monthly rainfall ranged from 20 mm month<sup>-1</sup> in December 2008 to 674 mm month<sup>-1</sup> in August 2012 (the minimum and maximum for the study period, respectively), and mean annual rainfall was  $2224.5 \pm 247.0 \text{ mm yr}^{-1}$ . The mean monthly relative humidity was  $73.5 \pm 0.8 \%$ . Monthly maximum wind speed ranged from  $10.6 \text{ m s}^{-1}$  in February 2012 to  $35 \text{ m s}^{-1}$  in May 2011.

#### **4.2.4. Litterfall collection**

Litterfall was collected using 1-mm mesh litter traps with a collection area of  $0.2 \text{ m}^2$ . Two litter traps were placed in each plot  $> 1 \text{ m}$  above the ground to avoid tidal water. Litter traps were emptied monthly, and collected litterfall was kept in a cotton bag and carried to the laboratory where it was separated into leaves, stipules, branches, flower bud primordia, flower buds, flowers, fruits, and propagules. Individual components of the litterfall were dried at  $80^\circ\text{C}$  for 48 h, desiccated at room temperature, and then weighed using a digital balance (EK-600H, A & D Co., Ltd., Tokyo, Japan). Reproductive organs (i.e., flowers, fruits, and propagules) were counted to estimate successful fruits and propagules. Following Duke (1990), the conversion rates from flower to fruit, fruit to propagule, and flower to propagule were calculated as (immature fruits + mature fruits + propagules) / (flowers + immature fruits + mature fruits + propagules), as (propagules) / (immature fruits + mature fruits + propagules), and as (propagules) / (flowers + immature fruits + mature fruits + propagules), respectively.

#### **4.2.5. Statistical analysis**

Kendall's coefficient of concordance,  $W$ , was used to evaluate the degree of similarity in monthly change among years for each litterfall component. Litterfall data were ranked by monthly mass for every year, and  $W$  was calculated for monthly litterfall. If  $W = 1.0$ , the monthly changes in litterfall would be concordant among years, whereas if  $W = 0.0$ , the monthly changes would be completely different among years. A  $\chi^2$  test with degrees of freedom of  $n - 1$  was used to determine the significance of the  $W$  value (Saito et al. 2003).

We performed a stepwise multiple regression analysis to determine the effects

of five environmental factors — temperature, day length, rainfall, humidity, and maximum wind speed — on the litterfall of leaves, stipules, branches, flower buds, flowers, fruits, and propagules, using MA-MACRO/MRA software (ver. 3.0, Practical Business Education Institute, Tokyo, Japan). The stepwise multiple regression was continued until the adjusted  $R^2$  value showed a decreasing trend. A criterion of  $F$  value  $> 2.0$  was set to determine the minimum significance of a variable to be included in the equation. Multiple regression analysis of environmental factors on mangrove litterfalls is difficult because the environmental factors often co-vary. A criterion of tolerance  $> 0.1$  was selected to avoid multicollinearity among the variables (Shiga et al. 2004).

The autocorrelation coefficient  $r_{xx}(k)$  was calculated for each litterfall component to evaluate its yearly cycle:

$$r_{xx}(k) = \frac{\sum_{j=1}^{N-k} (X_j - \bar{X}_{1, N-k})(X_{j+k} - \bar{X}_{1+k, N})}{\sqrt{\sum_{j=1}^{N-k} (X_j - \bar{X}_{1, N-k})^2 \sum_{j=1}^{N-k} (X_{j+k} - \bar{X}_{1+k, N})^2}}, \text{ where } k (= 0, 1, 2, \dots) \text{ is the time}$$

lag in months;  $N (= 48)$  is the total number of months in the time series;  $X_j$  and  $X_{j+k}$  are the litterfall component mass of the  $j^{\text{th}}$  month and  $(j+k)^{\text{th}}$  month, respectively; and  $\bar{X}_{1, N-k}$  and  $\bar{X}_{1+k, N}$  are the mean values of the component mass from the first to the  $(N-k)^{\text{th}}$  month and from the  $(1+k)^{\text{th}}$  to the  $N^{\text{th}}$  month, respectively.

The cross-correlation coefficient  $r_{xy}(l)$  was calculated to identify the lag,  $l$ , in maturation time between reproductive organs using their time series data:

$$r_{xy}(l) = \frac{\sum_{j=1}^{N-l} (X_j - \bar{X}_{1, N-l})(Y_{j+l} - \bar{Y}_{1+l, N})}{\sqrt{\sum_{j=1}^{N-l} (X_j - \bar{X}_{1, N-l})^2 \sum_{j=1}^{N-l} (Y_{j+l} - \bar{Y}_{1+l, N})^2}}, \text{ where } l (= 0, 1, 2, \dots) \text{ is the time lag}$$

in months;  $N (= 48)$  is the total number of months in the time series;  $X_j$  and  $Y_{j+l}$  are the reproductive organ mass for the  $j^{\text{th}}$  month and  $(j+l)^{\text{th}}$  month, respectively;  $\bar{X}_{1, N-l}$  is the mean value of a reproductive organ mass from the first to the  $(N-l)^{\text{th}}$  month; and  $\bar{Y}_{1+l, N}$  is the mean value of the other reproductive organ mass from the  $(1+l)^{\text{th}}$  to the  $N^{\text{th}}$  month.

## 4.3. Results

### 4.3.1. Vegetative phenology

Figure 4-2 shows the monthly patterns of vegetative (leaf, stipule, branch) organ

litterfall in the *R. stylosa* stand. Leaf litterfall (Fig. 4-2a) and stipule litterfall (Fig. 4-2b) occurred continuously throughout the year, and each showed a clear monthly trend. Leaf litterfall was highest in summer (June–August) and lowest in winter (December–February). In contrast to other years, excessive leaf litterfall occurred in May and August 2011, and September 2012 because of a typhoon. Thereafter, the rates in that year decreased distinctly in June and July (summer). Stipule litterfall, which is an indicator of new leaf production, was also highest in summer months (June–August) and lowest in winter months (December–February). Kendall’s coefficient of concordance,  $W$ , revealed that the monthly leaf and stipule litterfall were strongly and significantly concordant among study years (Table 4-1). As illustrated in Fig. 4-3, the autocorrelation coefficient revealed that the leaf (Fig. 4-3a) and stipule (Fig. 4-3b) litterfall showed a one-year cycle. Branch litterfall, including small twigs, bark, and large branches, showed no clear monthly pattern (Fig. 4-2c, Table 4-1) or annual cycle (Fig. 4-3c). Figure 4-4 depicts the exponential relationship between branch litterfall and monthly maximum wind speed. Branch litterfall increased exponentially with increasing monthly maximum wind speed.

Table 4-2 presents the results from the stepwise multiple regression analyses for variation in vegetative and reproductive (flower bud, flower, fruit, propagule) organ litterfall with variation in environmental factors. Leaf litterfall was significantly influenced by monthly maximum wind speed and monthly day length, whereas stipule litterfall was significantly correlated with monthly mean air temperature and monthly mean air relative humidity. Branch litterfall was correlated with monthly maximum wind speed.

Table 4-3 summarizes the amount of vegetative and reproductive organ litterfall components and their contributions to the total litterfall. Mean total litterfall was  $1225.0 \pm 120.5 \text{ g m}^{-2} \text{ yr}^{-1}$ , of which leaves were the largest contributor (56.5%), with an estimated amount of  $692.7 \pm 48.0 \text{ g m}^{-2} \text{ yr}^{-1}$ .

#### **4.3.2. Reproductive phenology**

Reproductive components of *R. stylosa* were present in litter traps with regular periodicity across years. Flower bud primordia were very difficult to separate from other litterfall. In most cases, primordia were confused with segments of inflorescences.

Therefore, we were unable to detect any monthly pattern in the litterfall of primordia for *R. stylosa* (Table 4-1). Litterfall of flower buds, including both immature and mature buds, was highest in summer (June–August) and lowest in winter (December–February) (Fig. 4-5a). In contrast to other years, excessive flower bud litterfall occurred in May 2011 because of a typhoon. Kendall’s *W* values revealed that the monthly trend in flower bud litterfall was significantly concordant among years (Table 4-1). Most of the flower litterfall was observed from April to October, with the highest abundance in July (Fig. 4-5b). Unfertilized flowers aborted and fell quickly from trees, and some pollinated flowers also fell. Kendall’s *W* values revealed that the monthly trend in flower litterfall showed strong and significant concordance among years (Table 4-1). Fruit litterfall of *R. stylosa* was highest in July and lowest in January, except in May 2011 (Fig. 4-5c). Propagules began to drop in July and continued dropping until September, but the abundance of mature propagules was highest in August and September (Fig 4-5d). Kendall’s *W* values also revealed that the fruit and propagule litterfall had significant monthly trends (Table 4-1). The autocorrelation coefficient revealed that flower bud (Fig. 4-6a), flower (Fig. 4-6b), fruit (Fig 4-6c), and propagule (Fig. 4-6d) litterfall each had a cycle of approximately one year in length.

Flower bud litterfall was significantly influenced by monthly mean relative humidity, monthly maximum wind speed, monthly mean air temperature, and monthly day length, whereas flower litterfall was significantly associated with monthly day length (Table 4-2). Fruit and propagule litterfall was significantly related to monthly mean air temperature. The mean total reproductive organ litterfall was  $263.6 \pm 40.3 \text{ g m}^{-2} \text{ yr}^{-1}$ , which contributed 21.5 % to the total litterfall (Table 4-3).

As shown in Fig. 4-7a, the development of flower buds to flowers took approximately 2–3 months. After fertilization was complete, flowers turned into fruits. The development phase from flower buds to fruits took approximately 4–5 months (Fig. 4-7b). The development phase from flower buds to mature propagules took around 11–12 months (Fig. 4-7c). Development from flowers to fruits took 2 months (Fig. 4-7d). As a species with viviparous germination, *R. stylosa* followed the initiation of hypocotyls from fruit. Development from flowers to mature propagules and fruits to mature propagules took around 9–10 months (Fig. 4-7e) and 8 months (Fig. 4-7f), respectively.

Table 4-4 represents the mean number of reproductive organs and their mean survivorship. Mean survivorship from flowers to fruits was  $34.7 \pm 8.8$  %, whereas mean survivorship from fruits to propagules was  $8.2 \pm 2.0$  %. The mean conversion percentage of flowers to propagules was  $2.2 \pm 0.4$  % for *R. stylosa*.

#### 4.4. Discussion

Both leaf and stipule litterfall of *R. stylosa* at the northern limit of its biogeographical distribution were highest in summer. This is consistent with *R. stylosa* on Motupore Island, Papua New Guinea (Leach and Burgin 1985), and at its southern latitudinal limit in eastern Australia (Wilson and Saintilan 2012). Our results agree with the summarization by Duke (2006), who reported that peak leaf litterfall in *R. stylosa* in the Northern Hemisphere occurred from April–August and peak stipule litterfall occurred from May–August. In contrast to the present study, Duke et al. (1984) reported that *R. stylosa* litterfall on Hinchinbrook Island, northeastern Australia, showed a bimodal pattern. Results similar to ours were observed in southern Thailand in the congeneric species *R. mucronata* Lamk., which showed unimodal patterns with maximum leafing and shedding rates during the tropical monsoon season, characterized by high air temperatures and heavy rainfalls (Wium-Andersen 1981). Unimodal leaf and stipule litterfall peaks have been observed in the same genus in subtropical areas (Gill and Tomlinson 1971), whereas in tropical areas, unimodal and bimodal patterns have been observed in species of the same genus (Wium-Andersen 1981; Christensen and Wium-Andersen 1977). The tropical climate may cause multimode peaks of leaf and stipule litterfall in mangroves.

New leaf production and leaf litterfall in *R. stylosa* were related to increases in mean air temperature and relative humidity, and with monthly maximum wind speed and monthly day length, respectively. This is in agreement with Gill and Tomlinson's (1971) findings that leaf production by *R. mangle* L. in Florida, USA, was most common in summer when solar radiation and temperature levels were highest. Similar findings were also reported by Leach and Burgin (1985), who found that leaf litterfall from *R. stylosa* on Motupore Island was significantly correlated with mean maximum air temperature. Temperature, day length, and relative humidity may be the important external controlling factors for *R. stylosa* leaf initiation and leaf abscission in

subtropical regions.

Mangroves at Manko Wetland face frequent typhoons, which disrupt the seasonality of branch litterfall and could be the main reason for the higher monthly litterfall, especially of branches, that we observed. Excessive branch litterfall in some months (e.g., May and August 2011) is attributed to typhoons with wind speeds exceeding  $17.2 \text{ m s}^{-1}$ . Six strong typhoons (Kompasu, Chaba, Songda, Muifa, Bolaven, Jelawat) occurred on 1 September and 27 October 2010, 28 May and 5 August 2011, and on 26 August and 29 September 2012, respectively. During the typhoons, green leaves were damaged and fell to the ground individually or attached to living broken branches. These green leaves contributed to excessive leaf litterfall in May and August 2011, and August and September 2012 (Fig. 4-2a).

The mean total litterfall of *R. stylosa* ( $12.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ; Table 4-3) was higher than the  $7.77 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  recorded on Vaitupu, Tuvalu, South Pacific (Woodroffe 1984). Litterfall was lower than the  $14.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  reported for this species on Motupore Island (Leach and Burgin 1985) and was also higher than the  $11.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  measured for *R. apiculata* Blume and *R. mucronata* Lamk in the central west coast of India (Wafar et al. 1997). Our data suggest that litterfall production by *R. stylosa* at the northern limit of its biogeographical distribution may be comparable to that found in other mangrove species in tropical regions. Similar to other studies (Wafar et al. 1997; Ochieng and Erftemeijer 2002), the leaves of *R. stylosa* were the major contributors to total litterfall production.

All the reproductive components of *R. stylosa* showed distinct monthly peaks. Flower and propagule litterfall in our study followed the same monthly pattern as in other mangrove species. For example, flowers and propagules of *R. mucronata* (Shunula and Whittick 1999) in tropical regions had one reproductive peak in summer. The portion of reproductive organ litterfall to the total litterfall of *R. stylosa* (21.5 %) at Manko Wetland was more than 2 % higher than reported for the same species (Woodroffe 1984) and was almost identical with those of *R. apiculata* (21.8 %) and *R. mucronata* (23.2 %) on the central west coast of India (Wafar et al. 1997).

At Manko Wetland, reproductive organs were associated with long monthly day length (flowers) and monthly mean air temperature (fruits and propagules), in agreement with Borchert's (2012) findings that expansion of dormant flower buds may

be triggered by increasing exposure to sunlight or the first heavy rains of the wet season. In contrast to our results, the flower bud and flower litterfall of *R. stylosa* on Motupore Island was significantly positively correlated with rainfall (Leach and Burgin 1985). At Manko Wetland, rainfall exceeds 100 mm in most months, and thus rainfall would not be a triggering factor for reproductive organ production. It may be concluded that air temperature, day length, and relative humidity or rainfall are the environmental clues that control the seasonality of reproductive organ litterfall in *R. stylosa*.

This is the first study to report the maturation periods of reproductive organs of *R. stylosa* at the northern limit of its biogeographical distribution. We estimated that the *R. stylosa* needed 11–12 months to complete its reproductive cycle, which agrees with the 10–11 months reported by Juliana et al. (2011) for *R. stylosa* in Peninsular Malaysia and the 8–13 months reported by Gill and Tomlinson (1971) for *R. mangle* in Florida, USA. At Manko Wetland, flowers took 9–10 months to form mature propagules, in agreement with 11 months and 11–12 months respectively recorded for this species in northern (Coupland et al. 2005) and northeastern (Duke et al. 1984) Australia. The present reproductive cycle was shorter than that reported for *R. apiculata* in Malaysia (14–16 months) by Akmar and Juliana (2012) but almost identical to Farihah's (2011) findings (11–12 months). In comparison with previously reported data, *R. stylosa* growing at the northern limit of its biogeographical distribution appears to have a similar maturation period to the same or congeneric species inhabiting tropical and subtropical regions.

The mean conversion rate of flowers to mature propagules for *R. stylosa* (2.2 %) at Manko Wetland, Okinawa Island, was higher than those reported for the same species at Darwin Harbour, Australia (0.5 %; Coupland et al. 2006), in Fiji (0.8–2.1 %; Tyagi 2003), on Motupore Island (0.6 %; Leach and Burgin 1985), and on Hinchinbrook Island (1.5 %; Duke et al. 1984). Coupland et al. (2006) reported that lower rate of fertilization might be due to limiting maternal resources and the lack of flower adaptation to either animal or wind pollination. Another possibility is that because of the availability of effective pollinators in the study area, the present rate of successful fertilization and subsequent propagule production were higher.

#### **4.5. Conclusion**

In summary, the vegetative and reproductive litterfalls of *R. stylosa* were measured monthly over four years; there was no significant monthly variation among the years in either. The periodicity of leaf initiation and leaf abscission in subtropical regions showed unimodal patterns and were governed mainly by air temperature and day length. The annual litterfall production of *R. stylosa* and its contribution to the Manko Wetland ecosystem was relatively high. The period of reproductive organ development agreed with previous reports for this species or for congeneric species in tropical and subtropical regions.

## References

- Akmar NZ, Juliana WAW (2012) Reproductive phenology of two *Rhizophora* species in Sungai Pulai Forest Reserve, Johor, Malaysia. *Malays Appl Biol* 41:11–21
- Borchert R (2012). The phenology of tropical trees. KU Undergraduate Biology Program, University of Kansas Web. [http://www.biology.ku.edu/tropical\\_tree\\_phenology/](http://www.biology.ku.edu/tropical_tree_phenology/). Accessed 05 October 2012
- Christensen B, Wium-Andersen S (1977) Seasonal growth of mangrove trees in southern Thailand. I. The phenology of *Rhizophora apiculata* BL. *Aquat Bot* 3:281–286
- Clarke PJ (1994) Baseline studies of temperate mangrove growth and reproduction; demographic and litterfall measures of leafing and flowering. *Aust J Bot* 42:37–48
- Coupland GT, Paling EI, McGuinness KA (2006) Floral abortion and pollination in four species of tropical mangroves from northern Australia. *Aquat Bot* 84:151–157
- Coupland GT, Paling EI, McGuinness KA (2005) Vegetative and reproductive phenologies of four mangrove species from northern Australia. *Aust J Bot* 53:109–117
- Duke NC (2006) *Rhizophora apiculata*, *R. mucronata*, *R. stylosa*, *R. x annamalai*, *R. x lamarckii* (Indo-West Pacific stilt mangrove), ver. 2.1. In: Elevitch CR (ed) Species profiles for Pacific Island Agroforestry. Permanent Agriculture Resources (PAR), HŌlualoa, Hawaii. <http://www.traditionaltree.org>
- Duke NC (1990) Phenological trends with latitude in the mangrove tree *Avicennia marina*. *J Ecol* 78:113–133
- Duke NC, Bunt JS, Williams WT (1984) Observations on the floral and vegetative

- phenologies of north-eastern Australian mangroves. *Aust J Bot* 32:87–99
- Fariyah AB (2011) Fenologi pembiakan *Rhizophora* di Tanjung Tuan dan Pantai Morib. Master of Science (MSc) Thesis. Universiti Kebangsaan Malaysia, Bangi (after Akmar NZ and Juliana 2012)
- Fernandes MEB (1999) Phenological patterns of *Rhizophora* L., *Avicennia* L. and *Laguncularia* Gaertn. f. in Amazonian mangrove swamps. *Hydrobiologia* 413:53–62
- Gill AM, Tomlinson PB (1971) Studies on the growth of red mangrove (*Rhizophora mangle* L.). 3. Phenology of the shoot. *Biotropica* 3:109–124
- Juliana WAW, Fariyah AB, Akmar ZN, Razali SM, Nuhanim MN (2011) Phenology of *Rhizophora* species at three Peninsular Malaysia mangrove forests. Proceedings of the 10<sup>th</sup> International Annual symposium (UMTAS 2011), Universiti Malaysia Terengganu, pp12–17
- Kira T (1991) Forest ecosystems of east and southeast Asia in a global perspective. *Ecol Res* 6:185–200
- Leach GJ, Burgin S (1985) Litter production and seasonality of mangroves in Papua New Guinea. *Aquat Bot* 23:215–224
- Mackey AP, Smail G (1995) Spatial and temporal variation in litter fall of *Avicennia marina* (Forssk.) Vierh. in the Brisbane River, Queensland, Australia. *Aquat Bot* 52:133–142
- Mehlig U (2006) Phenology of the red mangrove, *Rhizophora mangle* L., in the Caeté Estuary, Pará, equatorial Brazil. *Aquat Bot* 84:158–164
- Naido G (1989) Seasonal plant water relations in a South African mangrove swamp. *Aquat Bot* 33:87–100
- Ochieng CA, Erftemeijer PLA (2002) Phenology, litterfall and nutrient resorption in *Avicennia marina* (Forssk.) Vierh in Gazi Bay, Kenya. *Trees* 16:167–171
- RIS (1999) Information sheet on Ramsar Wetlands (RIS). In: A directory of wetlands of international importance. Ramsar Sites Database. [http://www.org/RSIS/-COP9 Directory/.../2Jp011.html](http://www.org/RSIS/-COP9Directory/.../2Jp011.html). Accessed 18 June 2012
- Saenger P, Moverley J (1985) Vegetative phenology of mangroves along the Queensland coastline. Proceedings of the 13<sup>th</sup> Annual meeting of Ecological Society of Australia, pp257–265
- Saito K, Okuno T, Asai A, Haga T, Kawai M, Kudo H, Miyamoto K, Masamara M,

- Osawa Y, Kawamura M, Goto H (2003) Lectures on modern statistics. Practical Business Education Institute, Tokyo (in Japanese)
- Sharma S, Kamruzzaman M, Hoque ATMR, Analuddin K, Hagihara A (2011) Vegetative and reproductive phenology, and litterfall production of *Rhizophora stylosa* in Okinawa Island, Japan. *Int J Env* 1:21–26
- Shiga T, Okuhara M, Nozawa M (2004) Lectures on multiple regression analysis using Excel. Practical Business Education Institute, Tokyo (in Japanese)
- Shunula JP, Whittick A (1999) Aspects of litter production in mangroves from Unguja Island, Zanzibar, Tanzania. *Estuar Coast Shelf Sci* 49:51–54
- Tyagi AP (2003) Location and interseasonal variation in flowering, propagule setting and propagule size in mangroves species of the family Rhizophoraceae. *Wetl Ecol Manag* 11:167–174
- Vannucci M (2002) Indo-West Pacific mangroves. In: Lacerda LD (ed) *Mangrove Ecosystems: Function and Management*. Springer, Berlin, pp 123–215
- Wafar S, Untawale AG, Wafar M (1997) Litter fall and energy flux in a mangrove ecosystem. *Estuar Coast Shelf Sci* 44:111–124
- Wilson NC, Saintilan N (2012) Growth of the mangrove species *Rhizophora stylosa* Griff. at its southern latitudinal limit in eastern Australia. *Aquat Bot* 101:8–17
- Wium-Andersen S (1981) Seasonal growth of mangrove trees in Southern Thailand. III. Phenology of *Rhizophora mucronata* Lamk. and *Scyphiphora hydrophyllacea* Gaertn. *Aquat Bot* 10:371–376
- Woodroffe CD (1984) Litter fall beneath *Rhizophora stylosa* Griff., Vaitupu, Tuvalu, South Pacific. *Aquat Bot* 18:249–255

**Table 4-1.** Kendall's coefficient of concordance,  $W$ , showing agreement in the monthly changes in litterfall components of *Rhizophora stylosa* among five years of this study.

Litterfall component	$W$	$\chi^2$ ( $p$ -value)
Leaf	0.83	45.6 (< 0.001)
Stipule	0.83	45.6 (< 0.001)
Branch	0.27	15.1 (0.1779)
Sum of vegetative organs	0.83	45.6 (< 0.001)
Flower bud primordium	0.14	7.9 (0.7215)
Flower bud	0.50	27.3 (< 0.01)
Flower	0.90	49.6 (< 0.001)
Fruit	0.60	26.5 (< 0.01)
Propagule	0.50	27.7 (< 0.01)
Sum of reproductive organs	0.90	40.1 (< 0.001)
Total litterfall	0.89	38.7 (< 0.001)

**Table 4-2.** Adjusted  $R^2$  values from the stepwise multiple regression analysis of vegetative and reproductive litterfall components from *Rhizophora stylosa* in relation to environmental factors. Significant probabilities are indicated by \* ( $p \leq 0.05$ ), \*\* ( $p \leq 0.01$ ), or \*\*\* ( $p \leq 0.001$ ).

Component	Monthly mean temperature °C ( $x_1$ )	Monthly day length h month <sup>-1</sup> ( $x_2$ )	Monthly rainfall mm month <sup>-1</sup> ( $x_3$ )	Monthly mean relative humidity % ( $x_4$ )	Monthly maximum wind speed m s <sup>-1</sup> ( $x_5$ )	Equation
Leaf		0.76 (0.97)			0.57 (0.97)	$y = -346.5 + 8.2^{***} x_5 + 0.8^{***} x_2$
Stipule	0.44 (0.53)			0.49 (0.53)		$y = -30.3 + 0.6^{**} x_1 + 0.3^{**} x_4$
Branch					0.65 (1.00)	$y = -91.7 + 6.8^{***} x_5$
Flower bud	0.31 (0.40)	0.36 (0.40)		0.27 (0.42)	0.30 (0.87)	$y = -23.5 + 0.2^{***} x_4 + 0.2^{**} x_5 - 0.3^{**} x_1 + 0.03^* x_2$
Flower		0.39 (1.00)				$y = -39.9 + 0.1^{***} x_2$
Fruit	0.19 (1.00)					$y = -7.9 + 0.5^{***} x_1$
Propagule	0.20 (1.00)					$y = -66.4 + 3.4^{***} x_1$

Numerals in parentheses are tolerances of the coefficients of the multiple regression for a component.

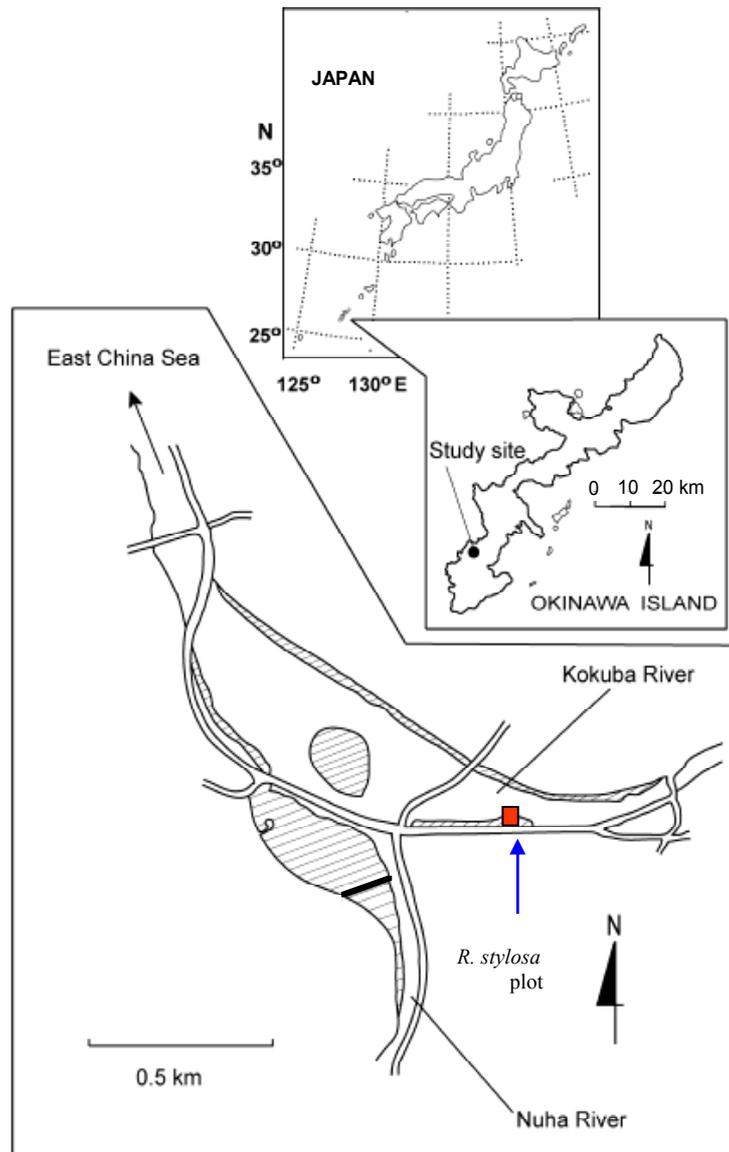
**Table 4-3.** Annual amounts of vegetative and reproductive litterfall components of *Rhizophora stylosa* during the study period.

Litterfall components	1 <sup>st</sup> year	2 <sup>nd</sup> year	3 <sup>rd</sup> year	4 <sup>th</sup> year	5 <sup>th</sup> year	Mean
Leaf	610.0 ± 9.5 (63.1)	666.6 ± 13.5 (56.3)	577.2 ± 10.2 (56.4)	810.2 ± 26.0 (61.8)	799.5 ± 26.5 (48.7)	692.7 ± 48.0 (56.5)
Stipule	104.3 ± 1.8 (10.8)	94.4 ± 1.6 (8.0)	126.8 ± 2.1 (12.4)	118.6 ± 1.7 (9.1)	112.9 ± 1.5 (6.9)	111.4 ± 5.6 (9.1)
Branch	70.7 ± 4.3 (7.3)	66.3 ± 2.5 (5.6)	83.9 ± 2.1 (8.2)	198.5 ± 10.5 (15.2)	366.9 ± 26.7 (22.4)	157.3 ± 57.8 (12.8)
Sum of vegetative organs	785.1 ± 13.4 (81.0)	827.4 ± 15.0 (70.0)	787.9 ± 12.1 (77.0)	1127.2 ± 36.8 (86.0)	1279.3 ± 52.3 (78.0)	961.4 ± 101.9 (78.5)
Flower bud primordium	36.1 ± 1.0 (3.7)	13.2 ± 0.8 (1.1)	4.1 ± 0.2 (0.4)	9.7 ± 0.5 (0.7)	0	12.6 ± 6.3 (1.0)
Flower bud	13.5 ± 0.4 (1.4)	11.8 ± 0.3 (1.0)	22.2 ± 0.5 (2.2)	42.5 ± 1.7 (3.3)	19.7 ± 0.5 (1.2)	22.0 ± 5.5 (1.8)
Flower	26.6 ± 0.9 (2.6)	47.8 ± 1.5 (4.0)	44.7 ± 1.4 (4.4)	36.0 ± 1.3 (2.7)	118.0 ± 3.5 (7.2)	54.6 ± 16.3 (4.5)
Fruit	39.7 ± 0.8 (4.1)	60.3 ± 2.2 (5.1)	35.6 ± 1.1 (3.5)	26.8 ± 1.1 (2.1)	18.0 ± 0.6 (1.1)	36.1 ± 7.1 (2.9)
Propagule	65.2 ± 3.5 (6.6)	223.2 ± 14.0 (18.9)	128.6 ± 6.8 (12.6)	68.1 ± 3.4 (5.2)	206.6 ± 12.6 (12.5)	138.3 ± 33.3 (11.3)
Sum of reproductive organs	181.1 ± 5.1 (19.0)	356.5 ± 14.4 (30.0)	235.2 ± 9.2 (23.0)	183.1 ± 4.9 (14.0)	362.3 ± 14.8 (22.0)	263.6 ± 40.3 (21.5)
Total	966.2 ± 17.3	1183.8 ± 24.8	1023.1 ± 20.6	1310.3 ± 40.6	1641.6 ± 57.1	1225.0 ± 120.5

Values are mean ( $\text{g m}^{-2} \text{yr}^{-1}$ ) ± SE. Numerals in parentheses represent percentages to total litterfall.

**Table 4-4.** Mean numbers of reproductive organs ( $\text{m}^{-2} \text{yr}^{-1} \pm \text{SE}$ ) of *Rhizophora stylosa* and their conversion rates ( $\% \pm \text{SE}$ ) during the study period.

Reproductive organs	1 <sup>st</sup> year	2 <sup>nd</sup> year	3 <sup>rd</sup> year	4 <sup>th</sup> year	5 <sup>th</sup> year	Mean
Flower	443.1 $\pm$ 46.6	331.0 $\pm$ 39.4	442.1 $\pm$ 56.1	345.3 $\pm$ 63.8	921.3 $\pm$ 102.0	496.6 $\pm$ 108.7
Fruit	389.1 $\pm$ 59.7	372.8 $\pm$ 48.6	325.4 $\pm$ 51.7	87.6 $\pm$ 15.5	54.5 $\pm$ 6.2	245.9 $\pm$ 72.3
Propagule	12.5 $\pm$ 2.8	22.4 $\pm$ 1.1	20.2 $\pm$ 1.4	10.2 $\pm$ 2.8	8.8 $\pm$ 2.0	14.8 $\pm$ 2.7
Flower to fruit	46.9 $\pm$ 2.7	54.3 $\pm$ 3.0	43.5 $\pm$ 2.3	22.3 $\pm$ 0.7	6.7 $\pm$ 1.0	34.7 $\pm$ 8.8
Fruit to propagule	3.0 $\pm$ 0.4	6.0 $\pm$ 0.8	6.4 $\pm$ 1.1	11.4 $\pm$ 3.1	14.3 $\pm$ 3.4	8.2 $\pm$ 2.0
Flower to propagule	1.4 $\pm$ 0.2	3.2 $\pm$ 0.4	2.7 $\pm$ 0.4	2.5 $\pm$ 0.7	0.9 $\pm$ 0.3	2.2 $\pm$ 0.4



**Fig. 4-1.** Location of the study area. The hatched zone indicates the mangrove area. Arrow indicates the plot area (*filled square*).



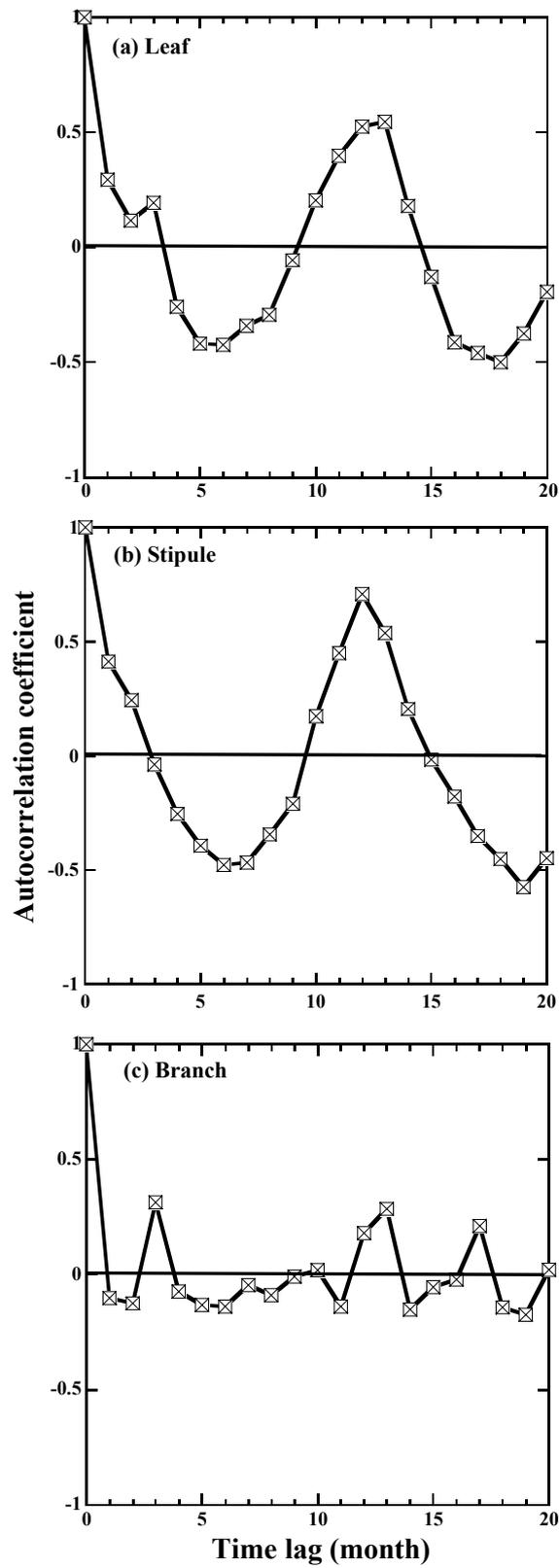
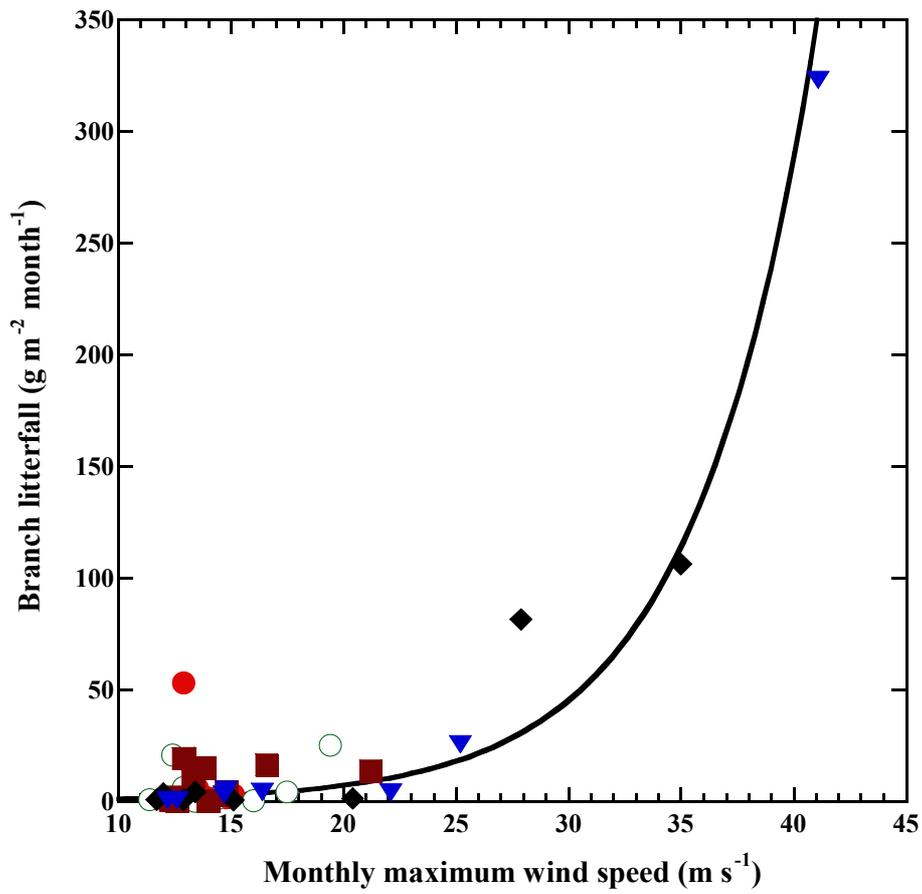
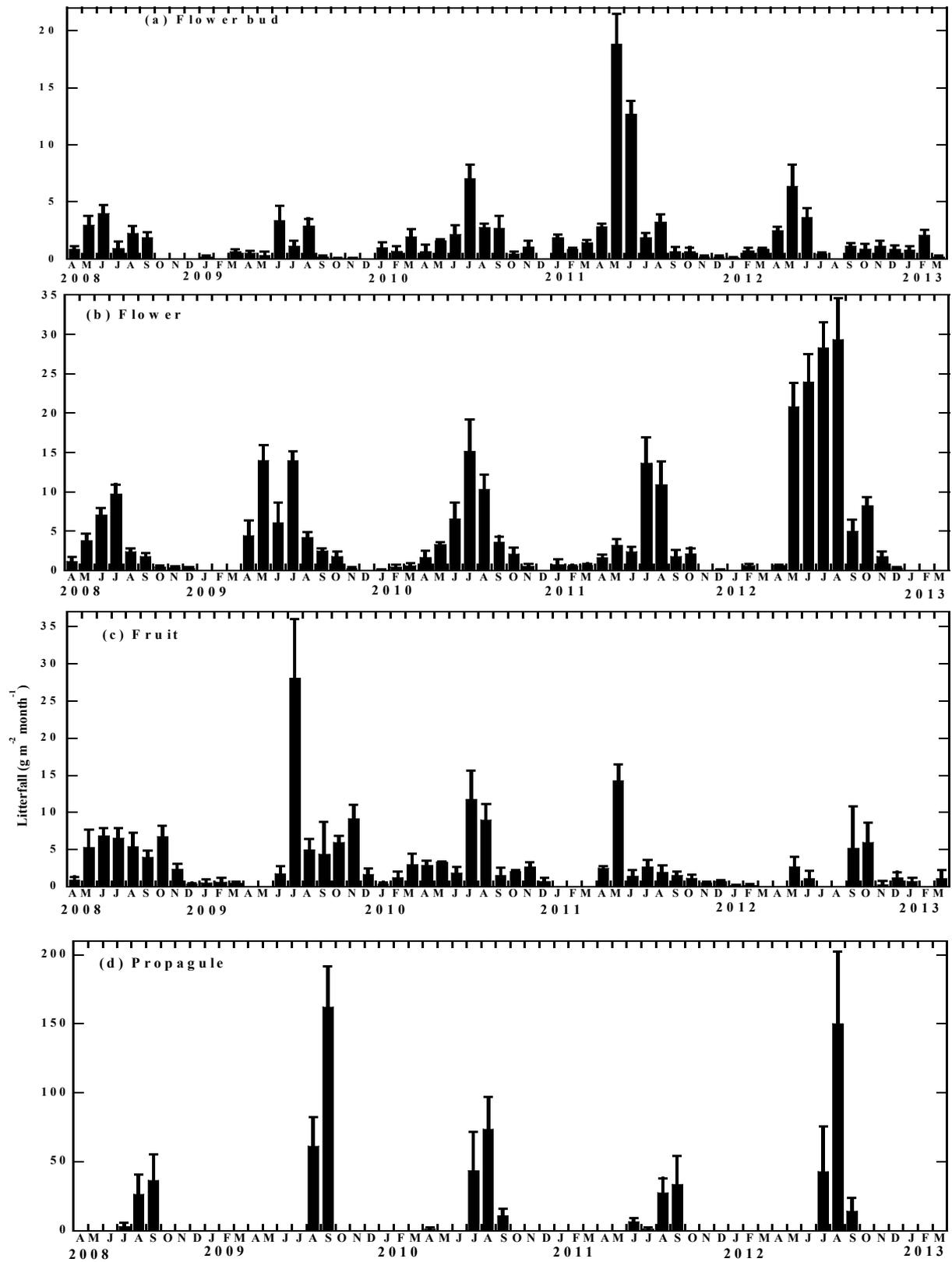


Fig. 4-3. Correlograms of vegetative litterfall.



**Fig. 4-4.** Exponential relationship between monthly branch litterfall and monthly maximum wind speed ( $R^2 = 0.95$ ). ●: 1st year; ○: 2nd year; ■: 3rd year; ◆: 4th year; ▼: 5th year.



**Fig. 4-5.** Phenograms of reproductive litterfall. Vertical bars represent standard errors of the means,  $n = 5$ .

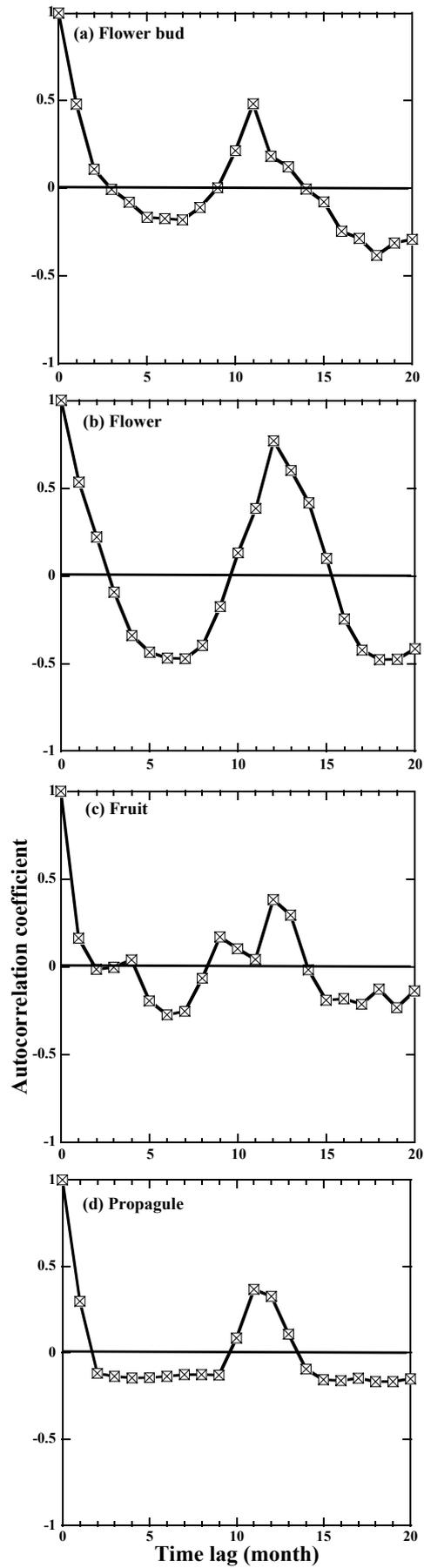
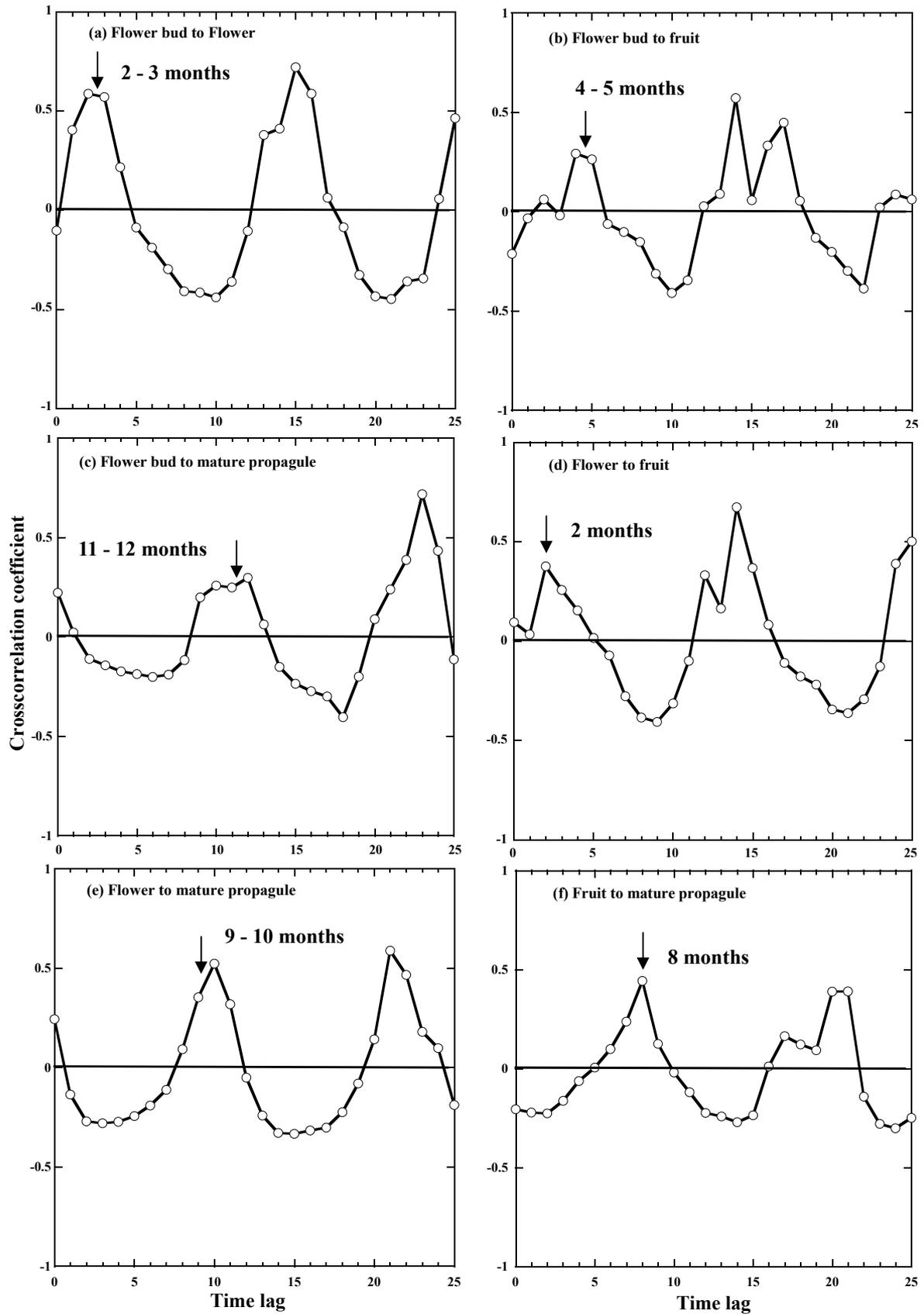


Fig. 4-6. Correlograms of reproductive litterfall.



**Fig. 4-7.** Crosscorrelation coefficients between pairs of reproductive components of *R. stylosa* in Manko Wetland, Okinawa Island, Japan. Arrows indicate maturation periods.

## CHAPTER V

### Litterfall of Three Subtropical Mangrove Species in the Family Rhizophoraceae

---

#### 5.1. Introduction

Mangrove forests are among the world's most productive ecosystems, as well as unique wetland ecosystems in inter-tidal coastal regions of the tropics and subtropics (Lugo and Snedaker 1975; Nagarajan et al. 2008). Litterfall is one of the important components of primary productivity, especially in view of its contribution to estuarine ecosystems (Woodroffe et al. 1988; Bunt 1995; Tam et al. 1998; Metcalfe et al. 2011). Mangrove litterfall consists primarily of leaves, which become available to consumers and decomposers. Litterfall is also an indicator of phenological events such as leaf recruitment, leaf fall, flowering, and fruiting (Leach and Burgin 1985; Duke 1990; Clarke 1994), if the possible time lag between formation and shedding of plant organs is known (Mehlig 2006). There are numerous studies on litterfall production in mangroves, especially in tropical regions of Australia (Bunt 1982; Mackey and Smail 1995), Thailand (Christensen 1978; Angsupanich and Aksornkoae 1994), and Malaysia (Ashton et al. 1999), but data on species commonly found in subtropical regions are comparatively scarce (Gwada et al. 2000; Khan et al. 2009; Sharma et al. 2012).

This study was conducted on Okinawa Island, Japan, an area that is very important for migratory birds, aquatic animals, and crustaceans (RIS 1999). The study area is occupied primarily by *Rhizophora stylosa* Griff., *Kandelia obovata* (S., L.) Yong, and *Bruguiera gymnorhiza* (L.) Lamk., all in the family Rhizophoraceae, the most important family of true mangroves, which consists of 22 mangrove species and numerous hybrids found in tropical and subtropical areas of the world. However, very few studies have documented litter production (Hardiwinoto et al. 1989; Mokolensang and Tokuyama 1998) or leaf phenology and litterfall production (Gwada et al. 2000; Khan et al. 2009; Analuddin et al. 2009; Sharma et al. 2011, 2012) of these three species in the subtropics. Therefore, the objectives of the present study were to investigate phenological changes and compare litterfall production among *R. stylosa*, *K. obovata*, and *B. gymnorhiza*. This study also aimed to determine the rate of successful conversion

from flowers to propagules.

## 5.2. Materials and methods

### 5.2.1. Study site

The study was conducted in Manko Wetland, Okinawa Island, Japan (26°11'N, 127°40'E), over 3 years from April 2008 to March 2011 (Fig. 5-1). The study site is located at the junction of the Noha and the Kokuba Rivers. This area receives regular tidal inundation and some fresh water supply through run-off from adjacent areas (Khan et al. 2004). In 1999, the study area was recognized as an important wetland under the Ramsar Convention. The study area is a brackish tidal flat, covering an extensive area at low tide, and the average tidal range varies from 3 mm to 212 mm. The mud flat area is mainly composed of clay particles (RIS 1999). The area belongs to the subtropical zone, as determined by the warmth index ( $\pm$  SE) (i.e., the cumulative value of mean monthly temperatures  $> 5^{\circ}\text{C}$ ), which was  $219.8 \pm 15.4^{\circ}\text{C}$  month (2000 to 2009; Okinawa Meteorological Agency, Naha), within the defined range of 180 to  $240^{\circ}\text{C}$  month for subtropical regions (Kira 1991). Annual mean rainfall ( $\pm$  SE) was  $2070.2 \pm 231.3$  mm year<sup>-1</sup>.

### 5.2.2. Forest structure

Four mangrove species are found at the study site, three of which belong to the family Rhizophoraceae, *Rhizophora stylosa*, *Kandelia obovata*, and *Bruguiera gymnorhiza*. The fourth species, *Excoecaria agallocha* L., is in the family Euphorbiaceae and just a very few trees were found in a small patch of the study area. *Kandelia obovata* in China and Japan has recently been reclassified, and was previously recognized as *Kandelia candel* (L.) Druce (Sheue et al. 2003). This is the dominant species at the study site and occupies the majority of the area. In some places it grows together with *R. stylosa* and *B. gymnorhiza*.

We established 25 plots (5 m  $\times$  5 m each) in *K. obovata* stands and five plots each (4 m  $\times$  4 m each) in *R. stylosa* and *B. gymnorhiza* stands. The plots of each species covered the full tidal range in which each species occurred. The numbers and sizes of the plots differed between the species because of the availability of pure stands of the

species. Seedlings were not found growing under closed canopies. All trees in the study plots were numbered and height ( $H$ ), stem diameter at  $H/10$  ( $D_{0.1H}$ ), and diameter at breast height (DBH) were measured. The mean densities of *K. obovata*, *R. stylosa*, and *B. gymnorhiza* were 2.2, 2.3, and 1.8  $\text{m}^{-2}$ , respectively, and the mean heights ( $\pm$  SE) were  $4.3 \pm 0.9$ ,  $3.9 \pm 0.7$ , and  $3.0 \pm 0.1$  m as of April 2010. The mean  $D_{0.1H}$  of *K. obovata* and *B. gymnorhiza* ( $\pm$  SE) was  $5.1 \pm 0.1$  and  $3.8 \pm 0.2$  cm, respectively, and the mean DBH ( $\pm$  SE) of *R. stylosa* was  $4.3 \pm 0.1$  cm.

### 5.2.3. Litterfall collection

Litterfall was collected using 1-mm mesh litter traps with a mouth area of  $0.2 \text{ m}^2$ . Two litter traps were placed at 1 m above the ground in each plot to avoid tidal water. Litterfall was collected monthly in a cotton bag and separated in the laboratory into leaves, stipules, branches, flower bud primordia, flower buds, flowers, fruits, and propagules. These separated components of the litter were dried at  $80^\circ\text{C}$  for 48 h, desiccated at room temperature, and then weighed using a digital balance (EK-600H, A & D, Tokyo, Japan). Reproductive parts (i.e., flowers, fruits, and propagules) were counted to estimate successful fruits and propagules. Following Duke (1990), the conversion rates from flower to fruit, fruit to propagule and flower to propagule were calculated as (immature fruits + mature fruits + propagules) / (flowers + immature fruits + mature fruits + propagules), as (propagules) / (immature fruits + mature fruits + propagules) and as (propagules) / (flowers + immature fruits + mature fruits + propagules), respectively.

### 5.2.4. Statistical analysis

Kendall's coefficient of concordance  $W$  was used to evaluate a degree of the similarity in the monthly change among years for each litterfall component. When  $W = 1.0$ , the monthly changes of the litterfall are concordant among years, while when  $W = 0.0$ , the monthly changes are completely different among years.  $\chi^2$  ( $= (n-1) \cdot k \cdot W$ ) test with  $n - 1$  degrees of freedom was used to determine the significance of the  $W$  value. The autocorrelation coefficient was calculated for each litterfall component to evaluate its yearly cycle. The simple regression method was used to understand the effect of reproductive organ litterfall on the vegetative organ litterfall. The annual mass of

stipules and reproductive components of litterfalls was calculated by summing the monthly data of each plot. A one-way ANOVA was run to test significance differences in the numbers of flowers, fruits, and propagules, and in the annual masses of litterfall components among the species. The number of replicates was 15 for *R. stylosa*, 75 for *K. obovata*, and 15 for *B. gymnorhiza*. Bonferroni's multiple comparison was used for post-hoc-tests using SPSS software (ver. 11.5, SPSS Inc., New York, USA).

### 5.3. Results

All three species showed a similar pattern in the seasonality of leaf litterfall (Fig. 5-2a). Leaf litterfall of *R. stylosa* was greatest in July and lowest in December. *Kandelia obovata* also exhibited a unimodal leaf litterfall pattern, with a peak in August and lowest amounts of litterfall in January. In *B. gymnorhiza*, leaf litterfall was highest in summer (June–August) and lowest in winter (December–February). Stipule litterfall, an indicator of leaf emergence, was also highest in summer and lowest in winter for all three species (Fig. 5-2b). Kendall's coefficient of concordance,  $W$ , revealed that the monthly trends in leaf and stipule litterfalls for the three species showed strong and significant concordance among the study years (Table 5-1). However, branch litterfall did not show any clear monthly trend in any of the three species. There was very high branch litterfall in August and October 2009 and October 2010 due to typhoons (wind speed  $>17.2 \text{ m s}^{-1}$ ) (Fig. 5-2c). Three strong typhoons (Morakot, Muifa, and Chaba) occurred on 6 August and 7 October 2009 and 27 October 2010, respectively. Litterfall of branches during the typhoons constituted a large portion of the annual branch litterfall. Branches that fell during the typhoons in 2009 and 2010 accounted for 44.1 % and 16.4 % of total annual branch fall for *R. stylosa*, 54.9 % and 61.1 % for *K. obovata*, and 57.1 % and 24.6 % for *B. gymnorhiza*, respectively.

Flower bud primordia were very difficult to separate from other litterfall. In most cases, primordia were confused with segments of inflorescences. Therefore, we were unable to detect any seasonal pattern in litterfall of primordia for any of the species (Table 5-1).

Litterfall of flower buds from *R. stylosa* was highest in summer (June–August) and lowest in winter (December–February; Fig. 5-2d). In December, no flower buds were observed in the litterfall. Flower bud litterfall of *K. obovata* started in March and

continued to August, and was not observed from September to February. That of *B. gymnorhiza* fluctuated throughout the year, but was highest from spring through summer and lowest in winter. We found mature flower buds in litterfall from April to August. Kendall's *W* values revealed that litterfall of flower buds of *R. stylosa* showed strong and significant concordance among years, whereas that of *K. obovata* and *B. gymnorhiza* had less clear monthly trends (Table 5-1).

Litterfall of *R. stylosa* flowers was observed from April through October, with the highest abundance in July (Fig. 5-2e). Unfertilized flowers were aborted and fell from trees within a few days, and some pollinated flowers also fell. No *R. stylosa* flowers were found in litterfall between November and February. Flower litterfall from *K. obovata* was observed from May through September, with a peak in August, after which their abundance was dramatically reduced. No *K. obovata* flowers were observed in litterfall from November to April. Flowers from *B. gymnorhiza* were found in most months of the year, with a maximum in September and a minimum in January. Kendall's *W* values revealed that monthly trends of flower litterfall for all three species showed strong and significant concordance among years (Table 5-1).

Figure 5-2f shows the monthly patterns of fruit litterfall of *R. stylosa* and *K. obovata*. Fruit litterfall of *R. stylosa* was highest in July and lowest in January, while that of *K. obovata* was primarily observed between August and December, and no fruits were found from February to July. *Bruguiera gymnorhiza* has no apparent fruit stage because propagule development immediately follows fertilization with a single hypocotyl emerging from an attached mature calyx. Kendall's *W* values revealed that monthly trends of fruit litterfall for *R. stylosa* and *K. obovata* showed strong and significant concordance among years (Table 5-1).

Over the course of time, hypocotyls developed from flowers or fruits and matured into propagules. Mature propagules of *R. stylosa* dropped from July to September, with a peak in September (Fig. 5-2g). *Kandelia obovata* propagules dropped primarily between March and May. Most propagules found in February and March were immature, while propagules found in April and May were mostly mature. *Bruguiera gymnorhiza* propagules were found throughout the year, but abundance was highest in summer and lowest in winter. Kendall's coefficient of concordance *W* values revealed that monthly trends in propagule litterfall showed strong and significant concordance

among years for *K. obovata*, but seasonal patterns were unclear for *R. stylosa* and *B. gymnorhiza* (Table 5-1). Total litterfall for all three species showed a unimodal pattern, with a peak in summer and lowest levels in winter (Fig. 5-2h). Kendall's *W* values showed that seasonal trends in total litterfall of all the three species showed strong and significant concordance among years (Table 5-1).

As shown in Table 5-2, the mean numbers of flowers produced did not differ significantly between *R. stylosa* and *B. gymnorhiza*, but there was a significant difference in the number of flowers between these two species and *K. obovata*. Fruit production differed significantly only between *R. stylosa* and *K. obovata*, and propagule number differed significantly between *R. stylosa* and the other two species. Table 5-3 represents the mean conversion percentage of flowers to propagules ( $\pm$  SE) was  $2.3 \pm 0.4$  % for *R. stylosa*,  $5.9 \pm 0.3$  % for *K. obovata*, and  $10.3 \pm 0.5$  % for *B. gymnorhiza*.

Young, tender, green, and yellow leaves contributed the most to total litterfall. Mean leaf litterfall ( $\pm$  SE) of *R. stylosa*, *K. obovata*, and *B. gymnorhiza* was  $618.0 \pm 21.7$ ,  $485.8 \pm 9.0$ , and  $468.4 \pm 20.3$  g m<sup>-2</sup> year<sup>-1</sup>, respectively, which represent 58.4, 54.0, and 50.4% of the total litterfall for each species, respectively (Table 5-4). Mean propagule litterfall ( $\pm$  SE) of *R. stylosa*, *K. obovata*, and *B. gymnorhiza* was  $139.0 \pm 24.6$ ,  $132.1 \pm 12.8$ , and  $219.0 \pm 29.5$  g m<sup>-2</sup> year<sup>-1</sup>, respectively, which contributed 13.1, 14.7, and 23.6 % to the total litterfall, respectively. Mean total litterfall ( $\pm$  SE) was  $1057.7 \pm 52.6$  g m<sup>-2</sup> year<sup>-1</sup> for *R. stylosa*,  $900.2 \pm 15.7$  g m<sup>-2</sup> year<sup>-1</sup> for *K. obovata*, and  $929.8 \pm 46.8$  g m<sup>-2</sup> year<sup>-1</sup> for *B. gymnorhiza*. There was no significant difference in total litterfall between *K. obovata* and *B. gymnorhiza*, but that of both of these species differed significantly from total litterfall for *R. stylosa*.

The autocorrelation coefficient revealed that leaf litterfall (Fig. 5-3a) of the three species demonstrated an annual cycle. Figure 5-3b illustrates that stipule litterfall of *R. stylosa* and *K. obovata* showed a one-year cycle. Litterfall of branches (Fig. 5-3c) and flower bud primordia (Fig. 5-3d) of all three species did not show any clear annual cycle. Litterfall of flower buds, fruits, and propagules had clear annual cycles for *R. stylosa* and *K. obovata*, but not for *B. gymnorhiza* (Fig. 5-3e). Flower litterfall of all three species showed a clear annual cycle (Fig. 5-3f).

Figure 5-4 shows the correlation between litterfall of stipules and litterfall of reproductive organ. *Rhizophora stylosa* (Fig. 5-4a) and *K. obovata* (Fig. 5-4b) showed a

reduction in new leaf production with increasing production of reproductive organ. In contrast to the results of these two species, litterfall of stipules of *B. gymnorhiza* increased with increasing litterfall of reproductive organ (Fig. 5-4c).

#### **5.4. Discussion**

This study showed that maximum leaf and stipule litterfall of all three investigated species occurred in summer and minimum litterfall of leaves and stipules was in winter. Other studies on Okinawa Island have recorded similar patterns of leaf and stipule litterfalls for *K. obovata* (Hardiwinoto et al. 1989; Gwada et al. 2000) and *B. gymnorhiza* (Hardiwinoto et al. 1989). Similar findings were observed by Duke (2006), with peak leaf litterfall of *R. stylosa* in the northern hemisphere occurring between April–August, and peak stipule litterfall between May–August. In contrast to the present study, Lee (1989) reported that *K. obovata* in Hong Kong had a bimodal pattern of leaf and stipule litterfall, with peaks in spring (February–June) and late summer (August–November). Unimodal leaf and stipule litterfalls peaks were also observed in Rhizophoraceae species in subtropical areas (Gill and Tomlinson 1971; Steinke 1988), whereas in tropical areas unimodal, bimodal, and trimodal patterns were observed in the species of the same family (Wium-Andersen and Christensen 1978; Wium-Andersen 1981; Leach and Burgin 1985). The tropical climate could cause multimode peaks of leaf and stipule litterfalls in mangroves in this region.

While there was no clear seasonal pattern in branch litterfall, it was normally low, but was very high in months with typhoons due to strong winds. Similar observations were recorded on Okinawa Island by Sharma et al. (2012) for *K. obovata* in Manko wetland and Hardiwinoto et al. (1989) for *K. obovata* and *B. gymnorhiza* in Ohura Bay. Mackey and Smail (1995) also reported that branch litterfall of *Avicennia marina* (Forssk.) Vierh. was correlated with storms on the Brisbane River, Queensland, Australia. The frequent typhoons in Okinawa could be the main reason for the higher total branch litterfall rate of *K. obovata*, when compared to *R. stylosa* and *B. gymnorhiza* due to *K. obovata*'s incompact stem structure, which may weaken in strong wind (Chen et al. 2009).

Litterfall of flowers of all three species peaked in summer. The timing of litterfall of mature propagules of *R. stylosa* was similar to that reported by Coupland et

al. (2005) in northern Australia. Litterfall of propagules was highest between April and May for *K. obovata* and in July for *B. gymnorhiza*, which was consistent with the findings of Hardiwinoto et al. (1989) in Ohura Bay, Okinawa Island, Japan. Many mangrove species growing in tropical regions have one reproductive peak a year (Shunula and Whittick 1999; Ochieng and Erfemeijer 2002; Coupland et al. 2005) and their flowering and fruiting occur in summer months, similarly to as in the present study (Clark 1994; May 1999).

The mean conversion rate of flowers to propagules for *R. stylosa* (2.3 %) was lower than the 3 % reported in Darwin Harbour, Australia (Coupland et al. 2006) and the 3.8% observed in northeastern Australia (Duke et al. 1984). Hogarth (1999) reported the conversion rate of flowers to propagules was 7 % for *Rhizophora mangle* L. and 13% for *R. apiculata* BL. *Rhizophora stylosa* has the largest propagules among the three species in this study and this could have resulted in the low rate of the conversion from flowers to propagules. Duke et al. (1984) noted that the low conversion of flowers to comparatively large fruits is a feature common in tropical areas. The mean conversion rates of flowers to propagules for *K. obovata* (5.9 %) and *B. gymnorhiza* (10.3 %) was higher than the rate reported for *B. gymnorhiza* (3.2–4.9 %) in Fiji (Tyagi 2003), but lower than that of *B. gymnorhiza* (16.8 %) in northeastern Australia (Duke et al. 1984). According to Primack et al. (1981), the high rates of the conversion rates of flowers to propagules in *K. obovata* and *B. gymnorhiza* indicate self-compatibility, as in *Sonneratia alba* J. Simth. The conversion rates of flowers to propagules in the present study varied from species to species, which may be due to variation in pollinators, nutrients, substrates, or internal conditions of the plants.

The mean total litterfall of *R. stylosa* observed in the present study (1057.7 g m<sup>-2</sup> year<sup>-1</sup>) was higher than that in the South Pacific (777 g m<sup>-2</sup> year<sup>-1</sup>; Woodroffe and Moss 1984), and lower than that in Papua New Guinea (1430 g m<sup>-2</sup> year<sup>-1</sup>; Leach and Burgin 1985). Litterfall of *K. obovata* (900.2 g m<sup>-2</sup> year<sup>-1</sup>) was within the range reported in other studies (872–1107 g m<sup>-2</sup> year<sup>-1</sup>; Hardiwinoto et al. 1989; Lee 1989; Khan et al. 2009). The mean total litterfall of *B. gymnorhiza* (929.8 g m<sup>-2</sup> year<sup>-1</sup>) was higher than that recorded in Ohura Bay, Okinawa Island (773 g m<sup>-2</sup> year<sup>-1</sup>; Hardiwinoto et al. 1989). Compared to previous results, the results of the present study may indicate that productivity of these mangrove species is relatively high in the Manko Wetland.

Leaves constituted over 50 % of the total litterfall for all three species, which is similar to the 61.2 % and 61.0 % reported for *Rhizophora apiculata* and *R. mucronata* Lamk, respectively (Wafar et al. 1997). The contributions of reproductive organ litterfall to total litterfall observed in the present study (24.4 % for *R. stylosa*, 23.0 % for *K. obovata*, and 40.0 % for *B. gymnorhiza*) were higher than those observed for other mangrove species such as *R. apiculata* (21.8 %) and *R. mucronata* (23.2 %) (Wafar et al. 1997).

*Rhizophora stylosa* and *K. obovata* exhibited a decreasing tendency in new leaf production, when the productions of reproductive organ were in maximum. This may be because the production of flowers and propagules imposes a heavy burden on leaf recruitment. Wium-Andersen and Christensen (1978) observed the same pattern in *B. cylindrica* and *Ceriops tagal* in southern Thailand. Duke et al. (1984) suggested that coordination between vegetative and reproductive organ production may indicate resource partitioning within plants. Potential partitioning of resources within mangroves was observed by Coupland et al. (2005) for *S. alba*, which showed a clear depression in leaf production at the time of peak flowering and fruiting. Duke (1990) also reported that leaf production was suspended in favor of propagule development in *A. marina* and subsequently leaf emergence accompanied propagule litterfall.

In *B. gymnorhiza*, flowering occurred throughout the year and propagules were produced for more than half of the year. Flower buds and flowers of *B. gymnorhiza* are reddish or yellow in color (Allen and Duke 2006) and contain red or yellow carotenoids, which contributes less to photosynthetic output of the plants (Frank and Cogdell 1996). It is therefore assumed that *B. gymnorhiza* requires more leaves for photosynthesis during reproductive organ production. High production of newly flushed leaves helps trees produce more energy, which is used to produce more reproductive organs. The correlation was based only on litterfall of stipules and reproductive organs without consideration of trunk and root growth. The peak periods of litterfall of flower buds and flowers for all three species coincided with peak litterfall of stipules, which suggests that growth of reproductive organs negatively affects the vigor of the apex (Gill and Tomlinson 1971).

## 5.5. Conclusion

In summary, our result showed that the very clear seasonal pattern of vegetative as well as reproductive phenology of the three species and did not show any significant variation among the years for the vegetative and reproductive components of the species. The periodicity of flowering and fruiting of all the species were restricted to the season. All the species produced a large number of flowers but only a few of them were come into mature propagule.

## References

- Allen JA, Duke NC (2006) *Bruguiera gymnorhiza* (large-leafed mangrove), ver. 2.1. In: Elevitch CR (ed) Species Profiles for Pacific Island Agroforestry. Permanent Agriculture Resources (PAR), Hōlualoa, Hawaii. <http://www.traditionaltree.org>
- Analuddin K, Sharma S, Suwa R, Hagihara A (2009) Crown foliage dynamics of mangrove *Kandelia obovata* in Manko Wetland, Okinawa Island, Japan. J Oceanogr 65:121–127
- Angsupanich S, Aksornkoae S (1994) Mangrove litter production in Phang-nga Bay, southern Thailand. Tropics 4:35–40
- Ashton EC, Hogarth PJ, Ormond R (1999) Breakdown of mangrove leaf litter in a managed mangrove forest in Peninsular Malaysia. Hydrobiologia 413:77–88
- Bunt JS (1982) Studies of mangrove litterfall in tropical Australia. In: Clough BF(ed) Mangrove Ecosystems in Australia: Structure, Function and Management. Australian National Univ press, Canberra 193–210
- Bunt JS (1995) Continental scale patterns in mangrove litterfall. Hydrobiologia 295:135–140
- Chen L, Zan Q, Li M, Shen J, Liao W (2009) Litter dynamics and forest structure of the introduced *Sonneratia caseolaris* mangrove forest in Shenzhen, China. Estuar Coast Shelf Sci 85:241–246
- Christensen B (1978) Biomass and primary production of *Rhizophora apiculata* Bl. in a mangrove in southern Thailand. Aquat Bot 4:43–52
- Clarke PJ (1994) Baseline studies of temperate mangrove growth and reproduction; demographic and litterfall measures of leafing and flowering. Aust J Bot 42:37–48
- Coupland GT, Paling EI, McGuinness KA (2005) Vegetative and reproductive phenologies of four mangrove species from northern Australia. Aust J Bot

53:109–117

- Coupland GT, Paling EI, McGuinness KA (2006) Floral abortion and pollination in four species of tropical mangroves from northern Australia. *Aquat Bot* 84:151–157
- Duke NC (1990) Phenological trends with latitude in the mangrove tree *Avicennia marina*. *J Ecol* 78:113–133
- Duke NC (2006) *Rhizophora apiculata*, *R. mucronata*, *R. stylosa*, *R. × annamalai*, *R. × lamarckii* (Indo-West Pacific stilt mangroves), ver. 2.1. In: Elevitch CR (ed) Species Profiles for Pacific Island Agroforestry. Permanent Agriculture Resources (PAR), Hōlualoa, Hawaii. <http://www.traditionaltree.org>
- Duke NC, Bunt JS, Williams WT (1984) Observations on the floral and vegetative phenologies of north-eastern Australian mangroves. *Aust J Bot* 32:87–99
- Frank HA, Cogdell RJ (1996) Carotenoids in photosynthesis. *Photochem Photobiol* 63: 257–264
- Gill AM, Tomlinson PB (1971) Studies on the growth of red mangrove (*Rhizophora mangle* L.). 3. Phenology of the shoot. *Biotropica* 3:109–124
- Gwada P, Makoto T, Uezu Y (2000) Leaf phenological traits in the mangrove *Kandelia candel* (L.) Druce. *Aquat Bot* 68: 1–14
- Hardiwinoto S, Nakasuga T, Igarashi T (1989) Litter production and decomposition of a mangrove forest at Ohura Bay, Okinawa. *Res Bull Coll Exp For, Hokkaido Univ* 46:577–594
- Hogarth PJ (1999) *The biology of mangroves*, Oxford Univ Press, Oxford
- Khan MNI, Suwa R, Hagihara A (2009) Biomass and aboveground net primary production in a subtropical mangrove stand of *Kandelia obovata* (S., L.) Yong at Manko Wetland, Okinawa, Japan. *Wetlands Ecol Manage* 17:585–599
- Khan MNI, Suwa R, Hagihara A, Ogawa K (2004) Interception of photosynthetic photon flux density in a mangrove stand of *Kandelia candel* (L.) Druce. *J For Res* 9:205–210
- Kira T (1991) Forest ecosystems of east and southeast Asia in a global perspective. *Ecol Res* 6:185–200
- Leach GJ, Burgin S (1985) Litter production and seasonality of mangroves in Papua New Guinea. *Aquat Bot* 23:215–224
- Lee SY (1989) Litter production and turnover of the mangrove *Kandelia candel* (L.)

- Druce in a Hong Kong tidal shrimp pond. *Estuar Coast Shelf Sci* 29:75–87
- Lugo AE, Snedaker SC (1975) Properties of a mangrove forest in southern Florida. In: Walsh G, Snedaker S, Teas H (eds) *Proceedings of the International Symposium on Biology and Management of Mangroves*. University of Florida, Gainesville, pp 170–212
- Mackey AP, Smail G (1995) Spatial and temporal variation in litter fall of *Avicennia marina* (Forssk.) Vierh. in the Brisbane River, Queensland, Australia. *Aquat Bot* 52:133–142
- May JD (1999) Spatial variation in litter production by the mangrove *Avicennia marina* var. *australsica* in Rangaunu Harbour, Northland, New Zealand. *N Z J Mar Freshwat Res* 33:163–172
- Mehlig U (2006) Phenology of the red mangrove, *Rhizophora mangle* L., in the Caeté Estuary, Pará, equatorial Brazil. *Aquat Bot* 84:158–164
- Metcalf KN, Franklin DC, McGuinness KA (2011) Mangrove litterfall: Extrapolation from traps to a large tropical macrotidal harbour. *Estuar Coast Shelf Sci* 95:245–252
- Mokolensang JF, Tokuyama A (1998) Litter production of mangrove forest at the Gesashi River. *Bull Coll Sci, Univ of Ryukyus* 65:73–79
- Nagarajan B, Pandiarajan C, Krishnamoorthy M, Sophia P (2008) Reproductive fitness and success in mangroves: Implication on conservation. In: Sengupta M, Dalwani R (eds) *Proceedings of Taal 2007: The 12<sup>th</sup> World Lake Conference*, pp 29–33
- Ocheing CA, Erftemeijer PLA (2002) Phenology, litterfall and nutrient resorption in *Avicennia marina* (Forssk.) Vierh in Gazi Bay, Kenya. *Trees* 16:167–171
- Primack RB, Duke NC, Tomlinson PB (1981) Floral morphology in relation to pollination ecology in five Queensland coastal plants. *Austrobaileya* 4:346–355
- RIS (1999) Information sheet on Ramsar Wetlands (RIS). In: *A Directory of Wetlands of International Importance*. Ramsar Sites Database <<http://www.org/RSIS/-COP9/Directory/.../2Jp011.html>>
- Sharma S, Kamruzzaman M, Hoque ATMR, Analuddin K, Hagihara A (2011) Vegetative and reproductive phenology, and litterfall production of *Rhizophora stylosa* in Okinawa Island, Japan. *Int J Environ* 1:20–26
- Sharma S, Hoque ATMR, Analuddin K, Hagihara A (2012) Litterfall dynamics in an

- overcrowded mangrove *Kandelia obovata* (S.,L.) Yong stand over five years. *Estuar Coast Shelf Sci* 98:31–41
- Sheeue CR, Liu HY, Yong JWH (2003) *Kandelia obovata* (Rhizophoraceae), a new mangrove species from Eastern Asia. *Taxon* 52:287–294
- Shunula JP, Whittick A (1999) Aspects of litter production in mangroves from Unguja Island, Zanzibar, Tanzania. *Estuar Coast Shelf Sci* 49:51–54
- Steinke TD (1988) Vegetative and floral phenology of three mangrove in Mgeni Estuary. *S Afr J Bot* 54:97-102
- Tam NFY, Won YS, Lan CY, Wang LN (1998) Litter production and decomposition in a subtropical mangrove swamp receiving wastewater. *J Exp Mar Biol Ecol* 226:1–18
- Tyagi AP (2003) Location and interseasonal variation in flowering, propagule setting and propagule size in mangroves species of the family Rhizophoraceae. *Wetlands Ecol Manage* 11:167–174
- Wafar S, Untawale AG, Wafar M (1997) Litter fall and energy flux in a mangrove ecosystem. *Estuar Coast Shelf Sci* 44:111–124
- Wium-Andersen S, Christensen B (1978) Seasonal growth of mangrove trees in southern Thailand. II. Phenology of *Bruguiera cylindrica*, *Ceriops tagal*, *Lumnitzera littorea* and *Avicennia marina*. *Aquat Bot* 5:383–390
- Wium-Andersen S (1981) Seasonal growth of mangrove trees in southern Thailand. III. Phenology of *Rhizophora mucronata* Lamk. and *Scyphiphora hydrophyllaceae* Gaertn. *Aquat Bot* 10:371–376
- Woodroffe CD, Bardseley KN, Ward PJ, Hanley JR (1988) Production of mangrove litter in a macrotidal embayment, Darwin Harbour, NT, Australia. *Estuar Coast Shelf Sci* 26:581–598
- Woodroffe CD, Moss TJ (1984) Litter fall beneath *Rhizophora stylosa* Griff., Vaitupu, Tuvalu, South Pacific. *Aquat Bot* 18:249–255

**Table 5-1.** Kendall's coefficient of concordance  $W$  showing the degree of similarity in the monthly changes for the litterfall components of *Rhizophora stylosa*, *Kandelia obovata*, and *Bruguiera gymnorhiza* among the years during the study period.

Litterfall component	<i>R. stylosa</i>	<i>K. obovata</i>	<i>B. gymnorhiza</i>
Leaf	0.925 <sup>**</sup>	0.790 <sup>**</sup>	0.699 <sup>*</sup>
Stipule	0.877 <sup>**</sup>	0.703 <sup>*</sup>	0.739 <sup>*</sup>
Branch	0.261	0.579	0.371
Flower bud primordium	0.204	0.544	0.242
Flower bud	0.763 <sup>**</sup>	0.347	0.362
Flower	0.892 <sup>**</sup>	0.855 <sup>**</sup>	0.866 <sup>**</sup>
Fruit	0.641 <sup>*</sup>	0.653 <sup>*</sup>	-
Propagule	0.491	0.925 <sup>**</sup>	0.488
Total	0.932 <sup>**</sup>	0.834 <sup>**</sup>	0.801 <sup>**</sup>

<sup>\*\*</sup>significance level <1%, <sup>\*</sup>significance level <5%.

**Table 5-2.** Mean number of flowers, fruits, and propagules ( $\text{m}^{-2} \text{year}^{-1}$ ) of the three species during the study period.

Reproductive organ	<i>R. stylosa</i>	<i>K. obovata</i>	<i>B. gymnorhiza</i>
Flower	405.4 $\pm$ 29.2 <sup>a</sup>	630.9 $\pm$ 27.3 <sup>b</sup>	446.1 $\pm$ 24.4 <sup>a</sup>
Fruit	362.4 $\pm$ 29.5 <sup>a</sup>	90.5 $\pm$ 1.81 <sup>b</sup>	-
Propagule	18.4 $\pm$ 1.53 <sup>a</sup>	45.3 $\pm$ 2.88 <sup>b</sup>	50.9 $\pm$ 4.19 <sup>b</sup>

Within an organ, with the same letter were not significantly different at a 5% level of significance using Bonferroni's multiple comparison.

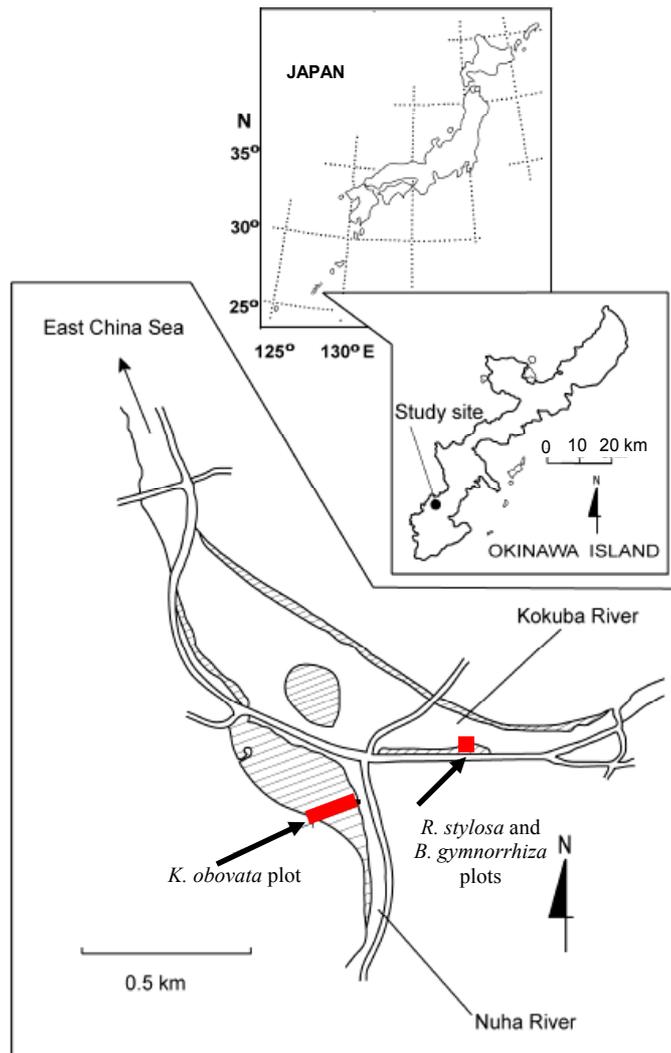
**Table 5-3.** Mean conversion rates (%  $\pm$  SE) of fertilized flowers into fruits and propagules of the three species during the study period.

Reproductive organs	<i>R. stylosa</i>	<i>B. gymnorhiza</i>	<i>K. obovata</i>
Flower to fruit	48.4 $\pm$ 3.4	-	17.7 $\pm$ 0.1
Fruit to propagule	4.8 $\pm$ 2.4	-	33.3 $\pm$ 2.2
Flower to propagule	2.3 $\pm$ 0.4	10.3 $\pm$ 0.5	5.9 $\pm$ 0.3

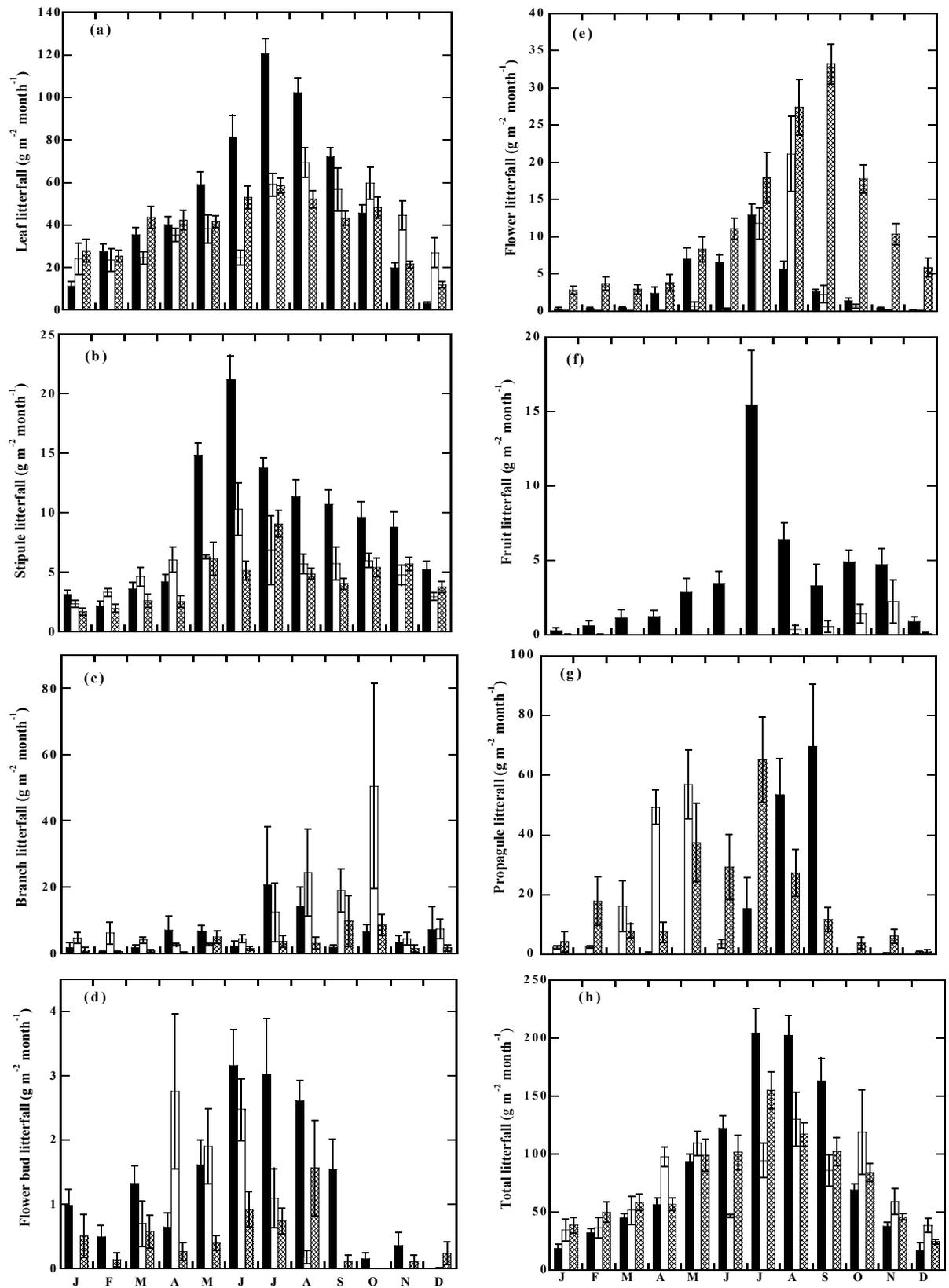
**Table 5-4.** Mean annual mass ( $\text{g m}^{-2} \text{ year}^{-1} \pm \text{SE}$ ) of litterfall components of the three species during the study period.

Litterfall component	<i>R. stylosa</i>	<i>K. obovata</i>	<i>B. gymnorhiza</i>
Leaf	618.0 $\pm$ 21.7 (58.3) <sup>a</sup>	485.8 $\pm$ 9.0 (54.0) <sup>b</sup>	468.4 $\pm$ 20.3 (50.4) <sup>b</sup>
Stipule	108.5 $\pm$ 6.2 (10.3) <sup>a</sup>	64.9 $\pm$ 2.1 ( 7.2) <sup>b</sup>	52.9 $\pm$ 4.5 ( 5.6) <sup>b</sup>
Branch	73.7 $\pm$ 21.2 ( 7.0) <sup>a</sup>	142.4 $\pm$ 7.1 (15.8) <sup>b</sup>	37.1 $\pm$ 13.7 ( 4.0) <sup>a</sup>
Sum of vegetative organs	800.1 $\pm$ 36.6 (75.6) <sup>a</sup>	693.2 $\pm$ 9.9 (77.0) <sup>b</sup>	558.5 $\pm$ 32.1(60.0) <sup>c</sup>
Flower bud primordium	17.8 $\pm$ 4.2 ( 1.7) <sup>a</sup>	24.4 $\pm$ 0.8 ( 2.7) <sup>b</sup>	1.8 $\pm$ 0.5 ( 0.2) <sup>c</sup>
Flower bud	15.9 $\pm$ 1.9 ( 1.5) <sup>a</sup>	9.1 $\pm$ 0.4 ( 1.0) <sup>b</sup>	5.5 $\pm$ 1.0 ( 0.6) <sup>c</sup>
Flower	39.7 $\pm$ 3.9 ( 3.8) <sup>a</sup>	36.7 $\pm$ 1.6 ( 4.1) <sup>a</sup>	144.8 $\pm$ 6.7 (15.6) <sup>b</sup>
Fruit	45.2 $\pm$ 6.0 ( 4.3) <sup>a</sup>	4.7 $\pm$ 0.3 ( 0.5) <sup>b</sup>	-
Propagule	139.0 $\pm$ 24.6 (13.1) <sup>a</sup>	132.1 $\pm$ 12.8 (14.7) <sup>a</sup>	219.0 $\pm$ 29.5 (23.6) <sup>b</sup>
Sum of reproductive organs	257.6 $\pm$ 28.5 (24.4) <sup>a</sup>	207.1 $\pm$ 13.8 (23.0) <sup>a</sup>	371.2 $\pm$ 32.4 (40.0) <sup>b</sup>
Total	1057.7 $\pm$ 52.6 <sup>a</sup>	900.2 $\pm$ 15.7 <sup>b</sup>	929.8 $\pm$ 46.8 <sup>b</sup>

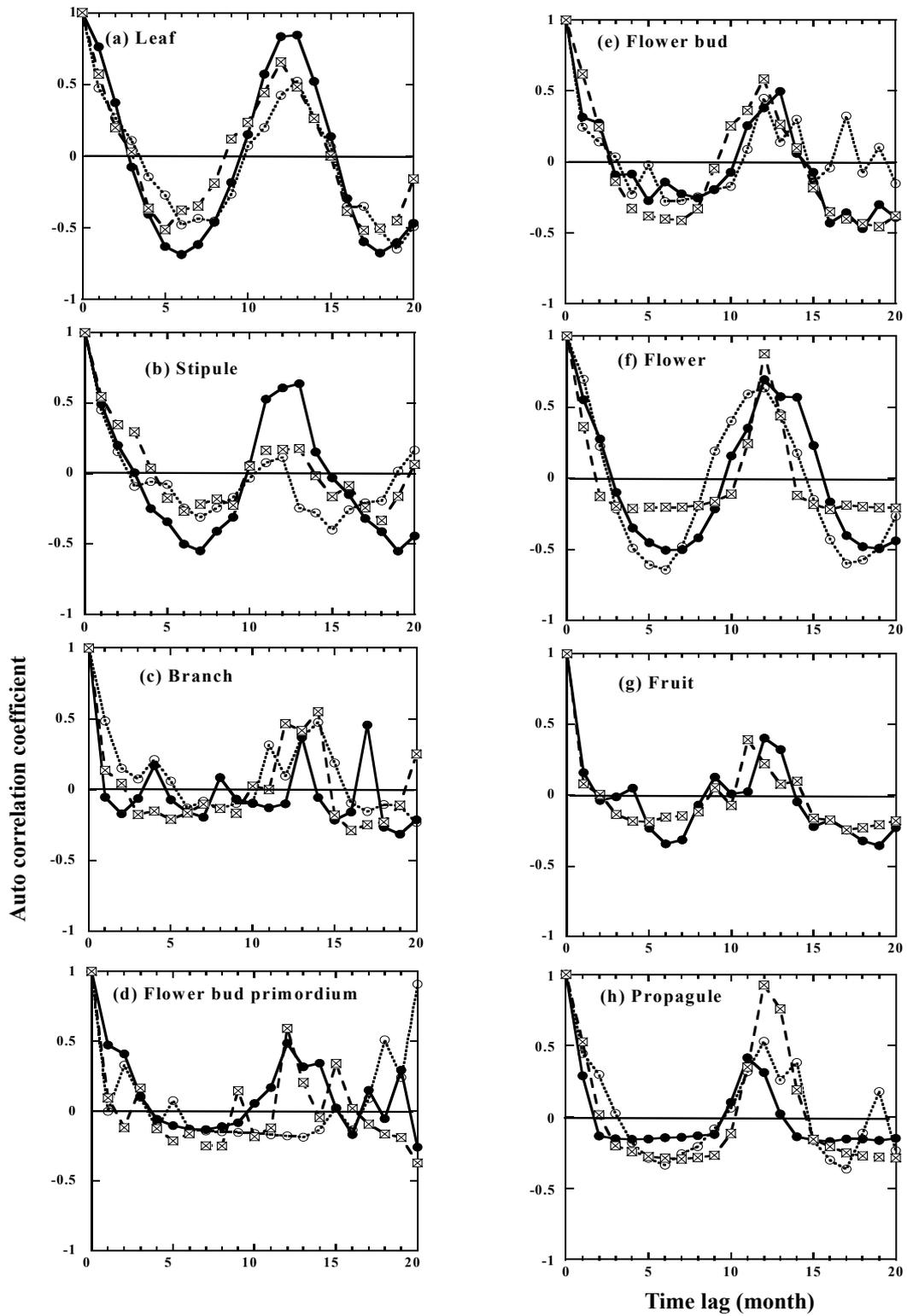
Values with the same letter were not statistically different among species at a 5% level of significance using Bonferroni's multiple comparison. Numbers in parentheses represent the percentage of total litterfall.



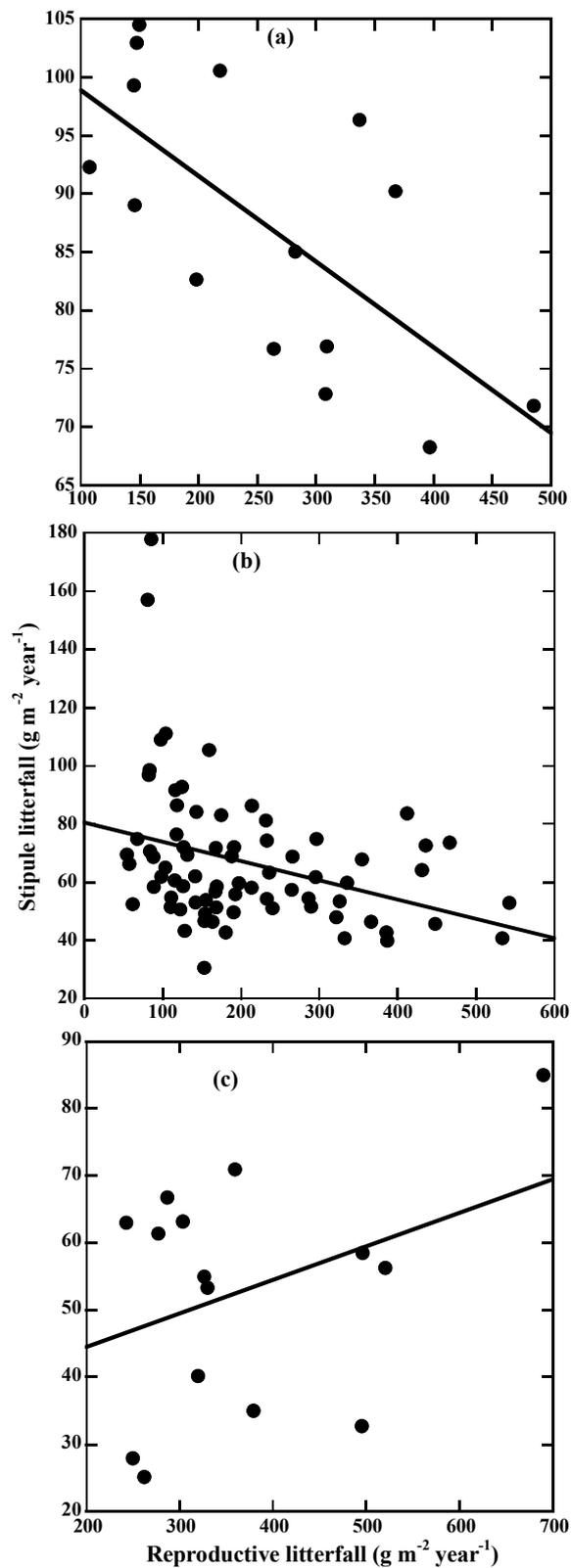
**Fig. 5-1.** Location of the study area. The hatched zone indicates the mangrove area. Arrows indicate the plot area.



**Fig. 5-1.** Monthly patterns of litterfall of vegetative and reproductive components, and total litterfall, of *R. stylosa* (filled columns), *K. obovata* (open columns), and *B. gymnorhiza* (hatched columns). Vertical bars represent the standard error of the mean.



**Fig. 5-3.** Correlograms of monthly vegetative and reproductive litterfall components of *R. stylosa* (filled circles), *K. obovata* (hatched square), and *B. gymnorhiza* (open circles).



**Fig. 5-4.** Relationships between stipule litterfall and reproductive litterfall for *R. stylosa* ( $r = -0.675$ ,  $p = 0.005$ ) (a), *K. obovata* ( $r = -0.332$ ,  $p = 0.003$ ) (b), and *B. gymnorhiza* ( $r = 0.367$ ,  $p = 0.178$ ) (c).

## CHAPTER VI

### Temporal Variation in Litterfall Production of *Bruguiera gymnorrhiza* Stands along the Okukubi River

---

#### 6.1. Introduction

Mangroves are principal contributors of nutrients to coastal ecosystems. Litterfall is an important component of primary productivity, especially in light of its contribution to estuarine ecosystems (Metcalf et al. 2011). Mangrove litterfall consists primarily of leaves, which become available to consumers and decomposers. In addition to leaf litterfall, reproductive organs of mangrove plants are often a valuable food source for a wide variety of animals, including insects and crabs (Robertson et al. 1992). Litterfall collection is a standard non-destructive technique for assessing the productivity, phenology, and turnover of biomass in a forest (Newbould 1967). Litterfall studies in forest stands have been conducted for more than a century. More recently, studies have focused on leaf litterfall dynamics and the ecological role of litterfall in nutrient cycling, as well as possible interactions with biotic and abiotic factors (Zhou et al. 2007; Imgraben and Dittmann 2008; Sánchez-Andrés et al. 2010).

Litterfall is also an indicator of phenological events for mangrove species (Leach and Burgin 1985; Duke 1990; Clarke 1994). Seasonal variation in mangrove litter production is influenced by local or regional environmental factors (Wium-Andersen 1981; Duke et al. 1984; Wafar et al. 1997; Chen et al. 2009). In addition, mangrove ecosystems are highly influenced by tidal conditions and salinity levels (Coupland et al. 2005). There are numerous studies on litterfall production and decomposition in mangroves, especially in tropical regions of Australia (Queensland), Thailand, and Malaysia. However, data on species commonly found in subtropical regions are comparatively scarce (Hardiwinoto et al. 1989; Mokolensang and Tokuyama 1998; Mfilinge et al. 2005; Sharma et al. 2012; Kamruzzaman et al. 2012, 2013).

*Bruguiera gymnorrhiza* (L.) Lamk. is widely distributed from the southeastern coast of Africa through Asia to subtropical Australia and the southwestern Pacific (Allen and Duke 2006). The present study was conducted along the Okukubi River on Okinawa Island, Japan, which is occupied by *B. gymnorrhiza* of the family

Rhizophoraceae. Only a few studies have investigated litterfall production of *B. gymnorrhiza* (L.) Lamk. stands (Hardiwinoto et al. 1989; Mokolensang and Tokuyama 1998; Kamruzzaman et al. 2012) growing at the northern limit of its biogeographical distribution (Spadling et al. 2000). Therefore, we investigated monthly change in litterfall production of *B. gymnorrhiza* in relation to environmental factors, determined the developmental period of each reproductive organ, examined the relationship between leaf litterfall per tree and tree density, and evaluated the relationship between leaf and reproductive organ production.

## 6.2. Materials and methods

### 6.2.1. Study site

The study was conducted in a monospecific *Bruguiera gymnorrhiza* (L.) Lamk. forest along the Okukubi River (26°27' N, 127°56' E) (Fig.6-1), on Okinawa Island, Japan, over 3 years from February 2010 to January 2013. We established a non-continuous (215 m × 5 m) belt-transect and divided it into 43 plots (5 m × 5 m each) in the *B. gymnorrhiza* forest. Tree height ( $H$ ) and stem diameter at  $H/10$  ( $D_{0.1H}$ ) were measured in August 2010, 2011, and 2012. The means of tree density ( $\rho$ ),  $H$ , and  $D_{0.1H}$  were  $0.70 \pm 0.09 \text{ m}^{-2}$ ,  $6.8 \pm 0.3 \text{ m}$ , and  $9.3 \pm 0.5$  (SE) cm, respectively, as of 2012.

### 6.2.2. Climate data

Meteorological data were obtained from Nago Meteorological Station, Nago, Okinawa, Japan, from February 2010 to January 2013 (i.e., over the time period during which the field work was conducted). The observatory station is approximately 15.4 km away from the study area. During the study period, the monthly mean temperature fluctuated approximately 15°C from the coldest month to the hottest month, and mean annual air temperature was  $22.7 \pm 0.2^\circ\text{C}$  (SE). The mean annual day length was  $4363.0 \pm 1.4 \text{ h yr}^{-1}$ . Rainfall varied throughout the year but exceeded 100 mm month<sup>-1</sup> in most months. The monthly rainfall during the study period ranged from 35 mm in March 2011 to 703 mm in August 2012 with an annual mean of  $2482.2 \pm 145.7 \text{ mm yr}^{-1}$ . The mean monthly relative humidity was  $75.1 \pm 0.1\%$ . Monthly maximum wind speed varied from the lowest value of  $9.4 \text{ m s}^{-1}$  in April 2011 to the highest of  $36.2 \text{ m s}^{-1}$  in May 2011.

### 6.2.3. Litterfall collection

Litterfall was collected using 1-mm mesh litter traps with a mouth area of 0.2 m<sup>2</sup>. Two litter traps were placed in each plot; the traps were placed > 1 m above the ground to avoid tidal water. The litter traps were emptied monthly; the collected litterfall was kept in a cotton bag and carried to the laboratory where it was separated into leaves, stipules, branches, flower buds, flowers, and propagules. Individual litterfall components were dried at 80°C for 48 h, desiccated at room temperature, and then weighed using a digital balance (EK-600H, A & D Co., Ltd., Tokyo, Japan). Reproductive organs (i.e., flowers and propagules) were counted to estimate successful propagules. Following Tyagi (2003), propagule litterfall was separated into immature and mature propagules. Following Duke (1990), the conversion rates from flower to propagule, flower to immature propagule, and flower to mature propagule were calculated as (immature propagules + mature propagules)/(flowers + immature propagules + mature propagules), immature propagules/(flowers + immature propagules + mature propagules), and mature propagules/(flowers + immature propagules + mature propagules), respectively.

### 6.2.4. Leaf longevity

Leaf mass of the standing trees,  $w_L$ , (kg) was estimated using the allometric equation for *B. gymnorrhiza* (Deshar et al. 2012) as follows:

$$w_L = 0.01349(D_{0.1H}^2 \cdot H)^{0.7779} \quad (6-1)$$

where  $H$  is the tree height (m) and  $D_{0.1H}$  is the stem diameter at  $H/10$  (cm).

In a stand undergoing self-thinning leaf biomass stabilizes when annual leaf production is balanced by annual leaf litterfall (Waring and Running 1998; Deshar et al. 2012; Sharma et al. 2012). Leaf biomass of the stand was estimated by applying Eq. (6-1) to the census data of each plot in 2010, 2011 and 2012. The ratio of leaf biomass,  $B$ , (kg m<sup>-2</sup>) to annual leaf litterfall,  $F$ , (kg m<sup>-2</sup> yr<sup>-1</sup>) provides an estimate of mean leaf longevity,  $L$ , (yr) for trees in the stand:

$$L = \frac{B}{F} \quad (6-2)$$

### 6.2.5. Statistical analysis

Kendall's coefficient of concordance,  $W$ , was used to evaluate the degree of similarity in monthly change among years for each litterfall component. Monthly production of each litterfall component was ranked by weight within each year.  $W$  was calculated for

monthly litterfall as: 
$$W = \frac{12 \sum_{i=1}^n \left\{ R_i - (n+1) \frac{m}{2} \right\}^2}{\left( n^3 - n \right) m^2}$$
, where  $R_i$  is the sum of rank  $i$

of monthly litterfall in each year,  $n$  ( $= 12$ ) is the number of months in a year, and  $m$  ( $= 3$ ) is the number of years. If  $W = 1.0$ , the monthly changes in litterfall are concordant among years, whereas if  $W = 0.0$ , the monthly changes are completely different among years. A  $\chi^2$  test was used to determine the significance of the  $W$  value (Hasegawa 1997).

The autocorrelation coefficient,  $r_{xx}(k)$ , was calculated for each litterfall component to evaluate its yearly cycle:

$$r_{xx}(k) = \frac{\sum_{j=1}^{N-k} (X_j - \bar{X}_{1, N-k})(X_{j+k} - \bar{X}_{1+k, N})}{\sqrt{\sum_{j=1}^{N-k} (X_j - \bar{X}_{1, N-k})^2 \sum_{j=1}^{N-k} (X_{j+k} - \bar{X}_{1+k, N})^2}},$$

where  $k$  ( $= 0, 1, 2, \dots$ ) is the time

lag in month;  $N$  ( $= 36$ ) is the total number of months in the time series;  $X_j$  and  $X_{j+k}$  are the rank of the litterfall component of the  $j$ th month and  $(j+k)$ th month, respectively; and  $\bar{X}_{1, N-k}$  and  $\bar{X}_{1+k, N}$  are the mean values of the rank of the component from the first to the  $(N-k)$ th month and from the  $(1+k)$ th to the  $N$ th month, respectively.

We performed a stepwise multiple regression analysis to determine the effects of five environmental factors (temperature, day length, rainfall, humidity, and maximum wind speed) on the litterfall of leaves, stipules, branches, flower buds, flowers, and mature propagules, using MA-MACRO/MRA software (ver. 3.0, Institute of Business Education, Tokyo, Japan). The stepwise multiple regression was continued until the adjusted  $R^2$  value showed a decreasing trend. A criterion of  $F$  value  $> 2.0$  was set to determine the minimum significance of a variable to be included in the equation. Multiple regression analysis of environmental factors on litterfall is difficult because the environmental factors often co-vary. A criterion of tolerance  $> 0.1$  was selected to avoid multicollinearity among the variables (Haga et al. 2004).

A one-way ANOVA was run to test significance differences in the annual masses of litterfall components, the numbers of flowers and propagules, and their conversion rates among the years. We performed Bonferroni's multiple comparison to

examine the pair-wise differences by using SPSS software (ver. 11.5, SPSS Inc., New York, USA).

The crosscorrelation coefficient,  $r_{xy}(l)$ , was calculated to identify the time lag,  $l$ , in maturation time between reproductive organs using their time series data:

$$r_{xy}(l) = \frac{\sum_{j=1}^{N-l} (X_j - \bar{X}_{1,N-l})(Y_{j+l} - \bar{Y}_{1+l,N})}{\sqrt{\sum_{j=1}^{N-l} (X_j - \bar{X}_{1,N-l})^2 \sum_{j=1}^{N-l} (Y_{j+l} - \bar{Y}_{1+l,N})^2}}, \text{ where } l (= 0, 1, 2, \dots) \text{ is the time lag}$$

in month;  $N (= 36)$  is the total number of months in the time series;  $X_j$  and  $Y_{j+l}$  are the masses of the reproductive organs for the  $j$ th month and  $(j+l)$ th month, respectively;  $\bar{X}_{1,N-l}$  is the mean mass of a reproductive organ from the first to the  $(N-l)$ th month; and  $\bar{Y}_{1+l,N}$  is the mean mass of the other reproductive organ from the  $(1+l)$ th to the  $N$ th month.

Mean annual leaf litterfall per tree was calculated by dividing annual leaf litterfall per plot by the number of trees in the plot. The relationship between mean annual leaf litterfall per tree ( $l$ , g yr<sup>-1</sup>) and population density ( $\rho$ , m<sup>-2</sup>) was described using the following power equation:  $l = k \cdot \rho^{-\alpha}$ , where  $k$  and  $\alpha$  are constants. Standard major axis regression was performed to determine the  $k$  and  $\alpha$  values using Microsoft Excel 2003 and KaleidaGraph (ver. 4.1, Synergy Software, USA).

### 6.3. Results

Figure 6-2 shows the monthly patterns of vegetative (leaf, stipule, branch) organ litterfall in the *B. gymnorhiza* stand. Leaf litterfall (Fig. 6-2a) and stipule litterfall (Fig. 6-2b) occurred continuously throughout the year, and each showed a clear monthly pattern. Leaf litterfall was highest in summer (June–August) and lowest in winter (December–February). Excessive leaf litterfall occurred in August and October 2010, May and August 2011, and August and September 2012 because of typhoons. Due to frequent typhoons, the rate in the last 2 years decreased distinctly in June and July (summer). Stipule litterfall, which is an indicator of new leaf production, was also highest in summer months (June–August) and lowest in winter months (December–February). Branch litterfall, including small twigs, bark, and large branches, also showed a clear monthly pattern, with the highest peak in August (Fig. 6-2c). As illustrated in Fig. 6-3, the autocorrelation coefficient revealed that leaf (Fig. 6-3a),

stipule (Fig. 6-3b), and branch (Fig. 6-3c) litterfall showed a clear 1-year cycle. Kendall's coefficient of concordance,  $W$ , also revealed that the monthly changes in leaf, stipule, and branch litterfall were strongly and significantly concordant among the study years.

Litterfall of flower buds, including both immature and mature buds, was highest in summer and lowest in autumn and winter (Fig. 6-4a). Flower litterfall was observed throughout the year, with the highest abundance in August–September (Fig. 6-4b). Unfertilized flowers aborted and fell quickly from trees, and some pollinated flowers also fell. *Bruguiera gymnorhiza* has no distinct fruiting stage, because propagule development immediately follows fertilization, with a single hypocotyl emerging from an attached mature calyx. Propagule litterfall including both mature and developing propagules was found throughout the year, but the abundance of immature propagules was highest in autumn and winter months (Fig. 6-4c), whereas that of mature propagules was highest in spring–summer (Fig. 6-4d). The autocorrelation coefficient revealed that flower bud (Fig. 6-5a) and mature propagule (Fig. 6-5c) litterfall each had a clear 1-year cycle, whereas flower (Fig. 6-5b) litterfall showed an around 1-year cycle. Kendall's  $W$  value also revealed that the monthly changes in flower bud, flower, and mature propagule litterfall were significantly concordant among years.

Table 6-2 presents the results of the stepwise multiple regression analyses for litterfall components with environmental factors. Leaf litterfall was significantly related to monthly maximum wind speed and monthly day length, whereas stipule litterfall was significantly related to monthly mean air temperature. Branch litterfall was correlated with monthly maximum wind speed and monthly rainfall. Flower bud litterfall was significantly influenced by monthly maximum wind speed, whereas flower litterfall was significantly associated with monthly mean air temperature. Mature propagule litterfall was significantly correlated with monthly day length and monthly mean air temperature.

As shown in Table 6-3, the annual mass of each litterfall component significantly differed among the years. However, there was no significant difference in the sum of vegetative organs litterfall among the years. Leaf litterfall (young, tender, green, and yellow leaves) contributed the most (65.8%) to the total litterfall, followed by branches (22.4%). The mean litterfall was made up of the vegetative organ of  $1092.8 \pm 92.8 \text{ g m}^{-2} \text{ yr}^{-1}$  and the reproductive organ of  $84.7 \pm 48.2 \text{ g m}^{-2} \text{ yr}^{-1}$ , corresponding to

92.8% and 7.2% to the total litterfall, respectively.

Table 6-4 shows the mean number of reproductive organs and their mean conversion rate. The numbers of flowers, propagules, immature propagules, and mature propagules significantly differed among the years. The conversion percentage of flowers to propagules including both immature and mature propagules was  $15.8 \pm 1.3\%$ , whereas the conversion rate from flowers to mature propagules was  $5.9 \pm 0.8\%$ .

As shown in Fig. 6-6a, the development of flower buds into flowers took 1 month. After fertilization, hypocotyls develop from flowers and then mature into propagules. Flowers took 7 months to develop into mature propagules (Fig. 6-6b); thus it took 8 months for flower buds to develop into mature propagules (Fig. 6-6c).

#### **6.4. Discussion**

The maximum leaf and stipule litterfall of *B. gymnorrhiza* was in summer and the minimum was in winter (Fig. 6-2a and 6-2b). Similar patterns for the same species have been reported in Ohura Bay, Okinawa Island, Japan (Hardiwinoto et al. 1989) and at Manko Wetland, Okinawa Island, Japan (Kamruzzaman et al. 2013). Duke et al. (1984) reported marked seasonal periodicity in both leaf and stipule litterfall for *B. gymnorrhiza* in northern Australia, with a peak in the summer wet season. In contrast to the present study, Shunula and Whittick (1999) reported that *B. gymnorrhiza* on Unguja Island, Zanzibar, Tanzania, produced litterfall throughout the year, with no significant seasonal differences in leaf production. Results similar to ours were observed in southern Thailand in the congeneric species *B. cylindrica* (L.) Blume, which showed unimodal patterns with maximum leafing and shedding rates during the tropical monsoon season with high air temperatures and heavy rainfalls (Wium-Andersen and Christensen 1978). Unimodal leaf and stipule litterfall peaks have been observed in Rhizophoraceae species in subtropical areas (Gill and Tomlinson 1971; Wilson and Saintilan 2012), whereas in tropical areas, unimodal, bimodal, trimodal patterns, and no distinct peak have been observed in species of the same family (Wium-Andersen and Christensen 1978; Wium-Andersen 1981; Leach and Burgin 1985; Shunula and Whittick 1999). The tropical climate could cause multimode peaks of leaf and stipule litterfall in mangroves.

Mangroves on Okinawa Island face frequent typhoons, which could be the

main reason for the higher litterfall, especially the high leaf and branch litterfall observed (Fig. 6-2a and 6-2c). During typhoons, green leaves are damaged and fall to the ground individually or on broken branches. These green leaves create excessive leaf litterfall in certain months. Figure 6 depicts the exponential relationship between branch litterfall and monthly maximum wind speed. Branch litterfall increased exponentially with increasing monthly maximum wind speed. High rates of branch litterfall in some months were also attributed to typhoons, which have wind speeds that exceed  $17.2 \text{ m s}^{-1}$ . Six strong typhoons (Kompasu, Chaba, Songda, Muifa, Bolaven, and Jelawat) occurred on 28 August and 27 October in 2010, 28 May and 5 August in 2011, and on 26 August and 29 September in 2012. Branch litterfall of *B. gymnorrhiza* was significantly concordant among the years and showed a clear 1-year cycle, possibly due to typhoons that frequently occurred in August. In contrast to the present study, Kamruzzaman et al. (2012, 2013) reported that typhoons disrupt the seasonality of mangrove branch litterfall, which showed no clear yearly cycle. Branch litterfall of this species varied primarily with monthly maximum wind speed. Similar observations were recorded on Okinawa Island by Hardiwinoto et al. (1989), who reported that typhoons had strong effects on branch litterfall of *B. gymnorrhiza*. Branch litterfall of *Avicennia marina* (Forssk.) Vierh. was also correlated with storms along the Brisbane River, Queensland, Australia (Mackey and Smail 1995).

The relationship between mean annual leaf litterfall per tree ( $l$ ,  $\text{g yr}^{-1}$ ) and population density ( $\rho$ ,  $\text{m}^{-2}$ ) was described as  $l = 745.2\rho^{-0.9774}$  (Fig. 6-8). The exponent (0.9774) was within the 95% confidence limits of 0.9310 and 1.0238; thus, the following approximation holds:  $l \cong k \cdot \rho^{-1.0}$ . This result indicates that annual leaf litterfall ( $k \cong l \cdot \rho$ ) was constant regardless of the number of trees in the plot. Similar findings were also observed by Sharma et al. (2012) for *Kandelia obovata* (S., L.) Yong stands at Manko Wetland. These results are generally consistent with the findings of Deshar et al. (2012), who found that leaf biomass was constant in self-thinning stands of *B. gymnorrhiza* on Okinawa Island.

The mean living leaf biomass of this *B. gymnorrhiza* stand was  $1.13 \pm 0.06 \text{ kg m}^{-2}$ , whereas the mean annual leaf litterfall of the stand was  $0.77 \pm 0.09 \text{ kg m}^{-2} \text{ yr}^{-1}$  (Table 2). Using these values, we estimated that mean leaf longevity was  $1.53 \pm 0.14 \text{ yr}$ , i.e., 18.4 months. The mean leaf longevity in the present study was longer than the

values reported for *B. gymnorrhiza* in Fujian Province, China (9–10 months, Wang and Lin 1999) and was almost identical to the 19 months reported for the same species at Manko Wetland (Kamruzzaman et al. 2013). Our value is also higher than the leaf longevity of *B. cylindrica* in southern Thailand (13 months, Wium-Andersen and Christensen 1978), but much shorter than that reported for *B. gymnorrhiza* in northeastern Australia (2–3 yr, Duke et al. 1984). These differences in leaf longevity might be influenced by methodological differences. Kikuzawa and Lechowicz (2006) observed that lifetime net carbon gain by a single leaf was rather constant across species, suggesting that lifetime net carbon gain by leaves of *B. gymnorrhiza* on Okinawa Island may be similar to that by leaves of the same species in Fujian Province or in northeastern Australia, regardless of leaf longevity.

New leaf production and leaf litterfall were related to increases in mean air temperature, and to monthly maximum wind speed and monthly day length, respectively (Table 6-1). It was likely that the main climatic factor of new leaf production of *B. gymnorrhiza* at the Okukubi River and also at Manko Wetland (Kamruzzaman et al. 2013) was monthly mean air temperature. Our results support the findings of Gill and Tomlinson (1971), who found that leaf production of *Rhizophora mangle* L. in Florida, USA, was most common in summer when solar radiation and temperature levels were highest. Similar findings were also reported by Gwada et al. (2000), who found that air temperature was the strongest environmental factor influencing leaf production in other species of Rhizophoraceae at Sashiki on Okinawa Island. Reproductive organs of *B. gymnorrhiza* along the Okukubi River were influenced by monthly mean air temperature (flowers), and monthly day length and monthly mean air temperature (mature propagules), in agreement with Duke's (1990) findings that day length and air temperature strongly affect *A. marina* flowering in Australia, Papua New Guinea, and New Zealand. Similar to the present study, monthly mean air temperature was also related to flower litterfall of the same species at Manko Wetland (Kamruzzaman et al. 2013). Borchert (2012) also found that expansion of dormant flower buds may be triggered by increasing exposure to sunlight or the first heavy rains of the wet season. Flowering phenograms of *B. gymnorrhiza* were relatively similar to leaf production phenograms and both were correlated with monthly mean air temperature. It may be concluded that air temperature and day length are the important

environmental clues that control the seasonality of vegetative and reproductive organ litterfall of *B. gymnorrhiza* in subtropical regions. In addition, monthly maximum wind speed is an important climatic factor in this area, because Okinawa Island is prone to seasonal typhoons.

The mean total litterfall of *B. gymnorrhiza* ( $11.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ) was higher than those recorded on Irimote Island, Okinawa, Japan ( $8.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ , Kishimoto et al. 1987), in Ohura Bay ( $7.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ , Hardiwinoto et al. 1989), and at Manko Wetland ( $10.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ , Kamruzzaman et al. 2013). This is less than  $16 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  reported for *B. gymnorrhiza* on Unguja Island (Shunula and Whittick 1999) and  $13 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  in Ohura Bay (Mfilinge et al. 2005), but identical to  $11.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  for *R. apiculata* Blume and *R. mucronata* Lam. in the central West Coast of India (Wafar et al. 1997). Our data suggest that litterfall production by *B. gymnorrhiza* at the northern limit of its biogeographical distribution may be comparable to those found in other mangrove species in tropical and subtropical regions. Similar to previous studies (Wafar et al. 1997; May 1999; Ochieng and Erftemeijer 2002; Mfilinge et al. 2005), leaves of *B. gymnorrhiza* were the major contributors to the total litterfall production. Flowers and propagules contributed 6.8% to the total litterfall. This value is lower than those recorded for the same species in Ohura Bay (7.4%, Hardiwinoto et al. 1989), in the estuary of the Geasashi River, Okinawa Island, Japan (13.1%, Mokolensang and Tokuyama 1998), and at Manko Wetland (42%, Kamruzzaman et al. 2013). The proportion of reproductive components to the total litterfall at the Okukubi River was also lower than those for *R. apiculata* (21.8%) and *R. mucronata* (23.2%) on the central West Coast of India (Wafar et al. 1997).

The mean conversion rate of flowers into mature propagules for *B. gymnorrhiza* (5.9%) was higher than the rate reported for *B. gymnorrhiza* in Fiji (3.2–4.9%, Tyagi 2003), but lower than those of *B. gymnorrhiza* in northeastern Australia (16.8%, Duke et al. 1984) and at Manko Wetland (10.3%, Kamruzzaman et al. 2012). The conversion rate of the same species on Okinawa Island varied from location to location, which may be due to variation in pollinators, nutrients, substrates, or internal conditions of the plants.

The period of flower bud maturation into flowers was 1 month (Fig. 6-6a), the same as that reported for this species on the Orissa Coast, India (Upadhaya and Mishra

2010) and at Manko Wetland (Kamruzzaman et al. 2013). It took 7 months for flowers to mature into propagules (Fig. 6-6b), similar to previous studies on the same species at Manko Wetland (Kamruzzaman et al. 2013) and on *B. cylindrica* in tropical regions (Wium-Andersen and Christensen 1978). Thus, *B. gymnorrhiza* growing at the northern limit of its biogeographical distribution appears to have a similar maturation period to congeneric species inhabiting tropical regions.

As shown in Fig. 6-9, litterfall made up of stipules increased as that consisting of reproductive organs increased. Generally, the production of flowers and propagules imposes a heavy burden on leaf recruitment. For example, *R. stylosa* and *K. obovata* tend to slow new leaf production with increasing production of reproductive organs (Kamruzzaman et al. 2012). Duke et al. (1984) suggested that coordination between the production of vegetative and reproductive organs may indicate resource partitioning within plants. Potential partitioning of resources within mangroves was observed by Coupland et al. (2005) for *Sonneratia alba* J. Smith, which showed a clear depression in leaf production at the time of peak flowering and fruiting. Duke (1990) also reported that leaf production was suspended in favor of propagule development in *A. marina* and subsequently leaf emergence accompanied propagule litterfall. However, in the present study, *B. gymnorrhiza* tended to increase leaf production with increasing reproductive organ production. Similar trends were observed by Kamruzzaman et al. (2012) for the same species at Manko Wetland. In *B. gymnorrhiza*, flower buds and flowers are reddish or yellow in color (Allen and Duke 2006) and contain red or yellow carotenoids, which contribute less to the photosynthetic output of the plants (Frank and Cogdell 1996). Therefore, it is assumed that *B. gymnorrhiza* requires more leaves for photosynthesis during the production of reproductive organs. High production of newly flushed leaves helps trees produce more energy, which is used to produce more reproductive organs.

## 6.5. Conclusion

In summary, our result showed that the very clear monthly pattern of each litterfall component except propagule litterfall and significant difference in amounts among the years. Branch litterfall depended on monthly maximum wind speed and increased exponentially with increasing monthly maximum wind speed. Annual leaf litterfall per plot was almost constant regardless of the tree density. The periodicity of flowering and

fruiting of all the species were restricted to the season. *Bruguiera gymnorrhiza* produced a large number of flowers but only a few of them were come into mature propagule.

## References

- Allen JA, Duke NC (2006) *Bruguiera gymnorrhiza* (large-leafed mangrove), ver. 2.1. In: Elevitch CR (ed) Species profiles for Pacific Island agroforestry. Permanent Agriculture Resources (PAR), Holualoa, Hawaii. <http://www.traditionaltree.org>. Accessed 10 June 2013
- Borchert R (2012). The phenology of tropical trees. KU Undergraduate Biology Program, University of Kansas Web. [http://www.biology.ku.edu/tropical\\_tree\\_phenology/](http://www.biology.ku.edu/tropical_tree_phenology/). Accessed 11 June 2013
- Chen L, Zan Q, Li M, Shen J, Liao W (2009) Litter dynamics and forest structure of the introduced *Sonneratia caseolaris* mangrove forest in Shenzhen, China. *Estuar Coast Shelf Sci* 85:241–246
- Clarke PJ (1994) Baseline studies of temperate mangrove growth and reproduction; demographic and litterfall measures of leafing and flowering. *Aust J Bot* 42:37–48
- Coupland GT, Paling EI, McGuinness KA (2005) Vegetative and reproductive phenologies of four mangrove species from northern Australia. *Aust J Bot* 53:109–117
- Deshar R, Sharma S, Mouctar K, Wu M, Hoque ATMR, Hagihara A (2012) Self-thinning exponents for partial organs in overcrowded mangrove *Bruguiera gymnorrhiza* stands on Okinawa Island, Japan. *Forest Ecol Manage* 278:146–154
- Duke NC (1990) Phenological trends with latitude in the mangrove tree *Avicennia marina*. *J Ecol* 78:113–133
- Duke NC, Bunt JS, Williams WT (1984) Observations on the floral and vegetative phenologies of north-eastern Australian mangroves. *Aust J Bot* 32:87–99
- Frank HA, Cogdell RJ (1996) Carotenoids in photosynthesis. *Photochem Photobiol* 63: 257–264
- Gill AM, Tomlinson PB (1971) Studies on the growth of red mangrove (*Rhizophora mangle* L.). 3. Phenology of the shoot. *Biotropica* 3:109–124
- Gwada P, Makoto T, Uezu Y (2000) Leaf phenological traits in the mangrove *Kandelia*

- candel* (L.) Druce. *Aquat Bot* 68: 1–14
- Haga T, Okuhara M, Nozawa M (2004) *Multivariate analysis by the Excel*. Vol. 2. Institute of Business Education, Tokyo (in Japanese)
- Hasegawa K (1997) *Formulas of statistical analysis by the Excel*. Kyouritsu-Shuppan, Tokyo (in Japanese)
- Hardiwinoto S, Nakasuga T, Igarashi T (1989) Litter production and decomposition of a mangrove forest at Ohura Bay, Okinawa. *Res Bull Coll Exp For, Hokkaido Univ* 46:577–594
- Imgraben S, Dittmann S (2008) Leaf litter dynamics and litter consumption in two temperate South Australian mangrove forests. *J Sea Res* 59:83–93
- Kamruzzaman M, Sharma S, Hoque ATMR, Hagihara A (2012) Litterfall of three subtropical mangrove species in the family Rhizophoraceae. *J Oceanogr* 68:841–850
- Kamruzzaman M, Sharma S, Kamara M, Hagihara A (2013) Vegetative and reproductive phenology of the mangrove *Bruguiera gymnorhiza* (L.) Lam. on Okinawa Island, Japan. *Trees-Struct Funct* 27:619–628
- Kikuzawa K, Lechowicz MJ (2006) Toward synthesis of relationships among leaf longevity, instantaneous photosynthetic rate, lifetime leaf carbon gain, and the gross primary production of forests. *Am Nat* 168:373–383
- Kishimoto T, Miyajima H, Nakasuga T, Baba S (1987) Zonation of mangrove forest (III) Litterfall and its seasonal change. *Trans Mtg Jpn For Soc* 98:301–302 (in Japanese)
- Leach GJ, Burgin S (1985) Litter production and seasonality of mangroves in Papua New Guinea. *Aquat Bot* 23:215–224
- Mackey AP, Smail G (1995) Spatial and temporal variation in litter fall of *Avicennia marina* (Forssk.) Vierh. in the Brisbane River, Queensland, Australia. *Aquat Bot* 52:133–142
- May JD (1999) Spatial variation in litter production by the mangrove *Avicennia marina* var. *australsica* in Rangaunu Harbour, Northland, New Zealand. *New Zeal J Mar Fresh Res* 33:163–172
- Metcalfe KN, Franklin DC, McGuinness KA (2011) Mangrove litterfall: Extrapolation from traps to a large tropical macrotidal harbour. *Estuar Coast Shelf Sci*

95:245–252

- Mfilinge PL, Meziane T, Bachok Z, Tsuchiya M (2005) Litter dynamics and particulate organic matter outwelling from a subtropical mangrove in Okinawa Island, South Japan. *Estuar Coast Shelf Sci* 63:301–313
- Mokolensang JF, Tokuyama A (1998) Litter production of mangrove forest at the Gesashi River. *Bull Coll Sci, Univ of the Ryukyus* 65:73–79
- Newbould PJ (1967) Methods for estimating the primary production of forests. IBP Handbook No. 2. Blackwell Scientific Publications, Oxford
- Ocheing CA, Erftemeijer PLA (2002) Phenology, litterfall and nutrient resorption in *Avicennia marina* (Forssk.) Vierh in Gazi Bay, Kenya. *Trees-Struct Funct* 16:167–171
- Robertson AI, Alongi DM, Boto KG (1992) Food chains and carbon fluxes. In: Robertson AI, Alongi DM (eds) *Tropical mangrove ecosystems*, American Geophysical Union, Washington, DC, pp 239–329
- Saito H (1977) Production process. In Shidei T, Kira T (eds) *Primary productivity of Japanese forests-productivity of terrestrial communities*. Univ of Tokyo Press, Tokyo, pp 65–93
- Sánchez-Andrés R, Sánchez-Carrillo S, Alatorre LC, Cirujano S, Álvarez-Cobelas M (2010) Litterfall dynamics and nutrient decomposition of arid mangroves in the Gulf of California: Their role sustaining ecosystem heterotrophy. *Estuar Coast Shelf Sci* 89:191–199
- Sharma S, Hoque ATMR, Analuddin K, Hagihara A (2012) Litterfall dynamics in an overcrowded mangrove *Kandelia obovata* (S., L.) Yong stand over five years. *Estuar Coast Shelf Sci* 98:31–41
- Shunula JP, Whittick A (1999) Aspects of litter production in mangroves from Unguja Island, Zanzibar, Tanzania. *Estuar Coast Shelf Sci* 49:51–54
- Spadling M, Kainuma M, Collis L (2010) *World atlas of mangroves*. Earthscan Publications, London
- Tyagi AP (2003) Location and interseasonal variation in flowering, propagule setting and propagule size in mangroves species of the family Rhizophoraceae. *Wetlands Ecol Manage* 11:167–174
- Upadhyay VP, Mishra PK (2010) Phenology of mangroves tree species on Orissa coast,

- India. Trop Ecol 51:289-295
- Wafar S, Untawale AG, Wafar M (1997) Litter fall and energy flux in a mangrove ecosystem. Estuar Coast Shelf Sci 44:111–124
- Wang W, Lin P (1999) Transfer of salt and nutrients in *Bruguiera gymnorrhiza* leaves during development and senescence. Mangroves Salt Marshes 3:1–7
- Waring RH, Running SW (1998) Forest ecosystems: analysis at multiple scales. Academic Press, San Diego, California
- Wilson NC, Saintilan N (2012) Growth of the mangrove species *Rhizophora stylosa* Griff. at its southern latitudinal limit in eastern Australia. Aquat Bot 101:8–17
- Wium-Andersen S (1981) Seasonal growth of mangrove trees in southern Thailand. III. Phenology of *Rhizophora mucronata* Lamk. and *Scyphiphora hydrophyllaceae* Gaertn. Aquat Bot 10:371–376
- Wium-Andersen S, Christensen B (1978) Seasonal growth of mangrove trees in southern Thailand. II. Phenology of *Bruguiera cylindrica*, *Ceriops tagal*, *Lumnitzera littorea* and *Avicennia marina*. Aquat Bot 5:383–390
- Zhou G, Guan L, Wei X, Zhang D, Zhang Q, Yan J, Wen D, Liu J, Liu S, Huang Z, Kong G, Mo J, Yu Q (2007) Litterfall production along successional and altitudinal gradients of subtropical monsoon evergreen broadleaved forests in Guangdong, China. Plant Ecol 188:77–89

**Table 6-1.** Adjusted  $R^2$  values from the stepwise multiple regression analysis of vegetative and reproductive litterfall components in relation to environmental factors. Significant probabilities are indicated by \* ( $p \leq 0.05$ ), \*\* ( $p \leq 0.01$ ), and \*\*\* ( $p \leq 0.001$ ).

Component	Monthly mean temperature °C ( $x_1$ )	Monthly length h month <sup>-1</sup> ( $x_2$ )	day	Monthly rainfall mm month <sup>-1</sup> ( $x_3$ )	Monthly mean relative humidity % ( $x_4$ )	Monthly maximum wind speed m s <sup>-1</sup> ( $x_5$ )	Equation
Leaf		0.76 (0.88)				0.75 (0.88)	$y = -182.6 + 8.1^{***} x_5 + 0.4^* x_2$
Stipule	0.49 (1.0)						$y = -14.8 + 0.4^{***} x_1$
Branch				0.75 (0.65)		0.66 (0.65)	$y = -58.6 + 3.8^{***} x_5 + 0.1^{**} x_3$
Flower bud						0.24 (1.00)	$y = -0.46 + 0.5^{**} x_5$
Flower	0.14 (1.00)						$y = -18.4 + 1.0^{**} x_1$
Mature propagule	0.25 (0.36)	0.04 (0.44)					$y = 6.5 + 0.04^{**} x_2 - 0.3^{**} x_1$

Numerals in parentheses are tolerances of the coefficients of the multiple regression for a component

**Table 6-2.** Annual amounts ( $\text{g m}^{-2} \text{ yr}^{-1} \pm \text{SE}$ ) of vegetative and reproductive litterfall components during the study period.

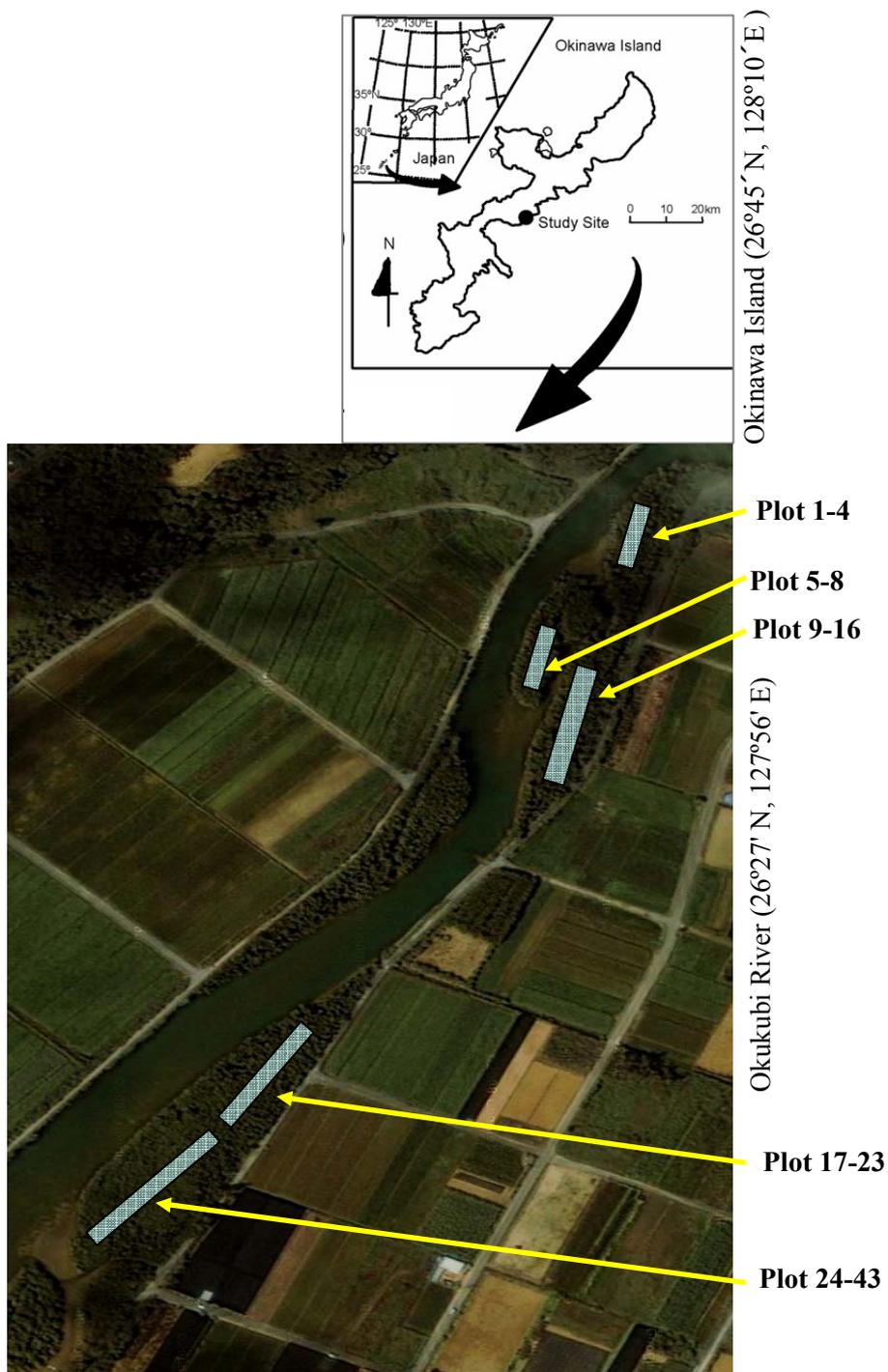
Litterfall components	1 <sup>st</sup> year	2 <sup>nd</sup> year	3 <sup>rd</sup> year	Mean
Leaf	953.4 $\pm$ 13.9 <sup>a</sup> (71.0)	745.5 $\pm$ 20.3 <sup>b</sup> (68.7)	625.5 $\pm$ 30.0 <sup>c</sup> (56.7)	774.8 $\pm$ 95.8 (65.8)
Stipule	71.0 $\pm$ 1.2 <sup>a</sup> (5.3)	45.2 $\pm$ 1.1 <sup>b</sup> (4.2)	47.6 $\pm$ 1.4 <sup>b,c</sup> (4.3)	54.6 $\pm$ 8.2 (4.6)
Branch	138.7 $\pm$ 9.0 <sup>a</sup> (10.3)	266.7 $\pm$ 14.5 <sup>b</sup> (24.6)	384.8 $\pm$ 36.3 <sup>c</sup> (34.9)	263.4 $\pm$ 71.1 (22.4)
Sum of vegetative organs	1163.2 $\pm$ 19.5 <sup>a</sup> (86.6)	1057.3 $\pm$ 30.4 <sup>a</sup> (97.4)	1057.9 $\pm$ 59.1 <sup>a</sup> (95.9)	1092.8 $\pm$ 35.2 (92.8)
Flower bud	2.1 $\pm$ 0.5 <sup>a</sup> (0.2)	8.5 $\pm$ 0.8 <sup>b</sup> (0.8)	1.8 $\pm$ 0.4 <sup>a,c</sup> (0.2)	4.2 $\pm$ 2.2 (0.4)
Flower	139.5 $\pm$ 4.8 <sup>a</sup> (10.4)	7.3 $\pm$ 0.7 <sup>b</sup> (0.7)	19.5 $\pm$ 1.2 <sup>c</sup> (1.8)	55.4 $\pm$ 42.2 (4.7)
Propagule	38.9 $\pm$ 5.4 <sup>a</sup> (2.9)	12.4 $\pm$ 1.4 <sup>b</sup> (1.2)	24.0 $\pm$ 4.7 <sup>b,c</sup> (2.2)	25.1 $\pm$ 7.7 (2.1)
Sum of reproductive organs	180.5 $\pm$ 8.4 <sup>a</sup> (13.4)	28.2 $\pm$ 1.9 <sup>b</sup> (2.6)	45.3 $\pm$ 5.1 <sup>b,c</sup> (4.3)	84.7 $\pm$ 48.2 (7.2)
Total	1343.7 $\pm$ 25.2 <sup>a</sup>	1085.5 $\pm$ 30.6 <sup>b</sup>	1103.2 $\pm$ 61.9 <sup>b,c</sup>	1177.5 $\pm$ 83.3

Values with the same letter were not statistically different among years at a 5 % level of significance using Bonferroni's multiple comparison. Numerals in parentheses represent percentages to the total litterfall.

**Table 6-3.** Mean numbers of reproductive organs ( $m^{-2} yr^{-1} \pm SE$ ) and their conversion rates ( $\% \pm SE$ ) during the study period.

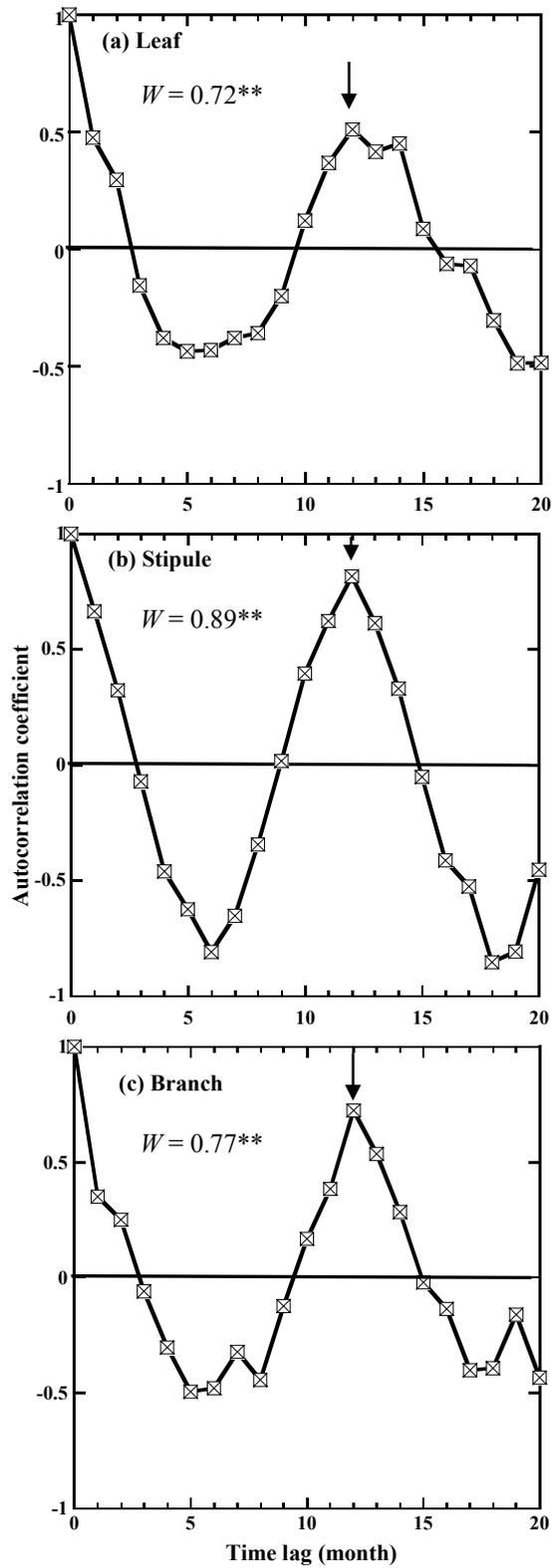
Reproductive organs	1 <sup>st</sup> year	2 <sup>nd</sup> year	3 <sup>rd</sup> year	Mean
Flower	372.2 $\pm$ 12.1 <sup>a</sup>	21.1 $\pm$ 2.1 <sup>b</sup>	51.6 $\pm$ 3.2 <sup>c</sup>	148.3 $\pm$ 14.7
Propagule	26.1 $\pm$ 2.9 <sup>a</sup>	6.7 $\pm$ 0.6 <sup>b</sup>	9.1 $\pm$ 1.4 <sup>b, c</sup>	14.0 $\pm$ 1.3
Immature propagule	23.1 $\pm$ 2.6 <sup>a</sup>	4.9 $\pm$ 0.6 <sup>b</sup>	3.4 $\pm$ 0.5 <sup>b, c</sup>	10.5 $\pm$ 1.2
Mature propagule	3.0 $\pm$ 0.6 <sup>a</sup>	1.8 $\pm$ 0.3 <sup>a, b</sup>	5.7 $\pm$ 1.4 <sup>a, c</sup>	3.5 $\pm$ 0.5
Flower to propagule	6.3 $\pm$ 0.6 <sup>a</sup>	26.5 $\pm$ 2.5 <sup>b</sup>	14.6 $\pm$ 1.8 <sup>c</sup>	15.8 $\pm$ 1.3
Flower to immature propagule	5.6 $\pm$ 0.5 <sup>a</sup>	18.1 $\pm$ 2.0 <sup>b</sup>	6.0 $\pm$ 1.0 <sup>a, c</sup>	9.9 $\pm$ 0.9
Flower to mature propagule	0.7 $\pm$ 0.1 <sup>a</sup>	8.4 $\pm$ 1.6 <sup>b</sup>	8.6 $\pm$ 1.6 <sup>b, c</sup>	5.9 $\pm$ 0.8

Values with the same letter were not statistically different among years at a 5 % level of significance using Bonferroni's multiple comparisons.

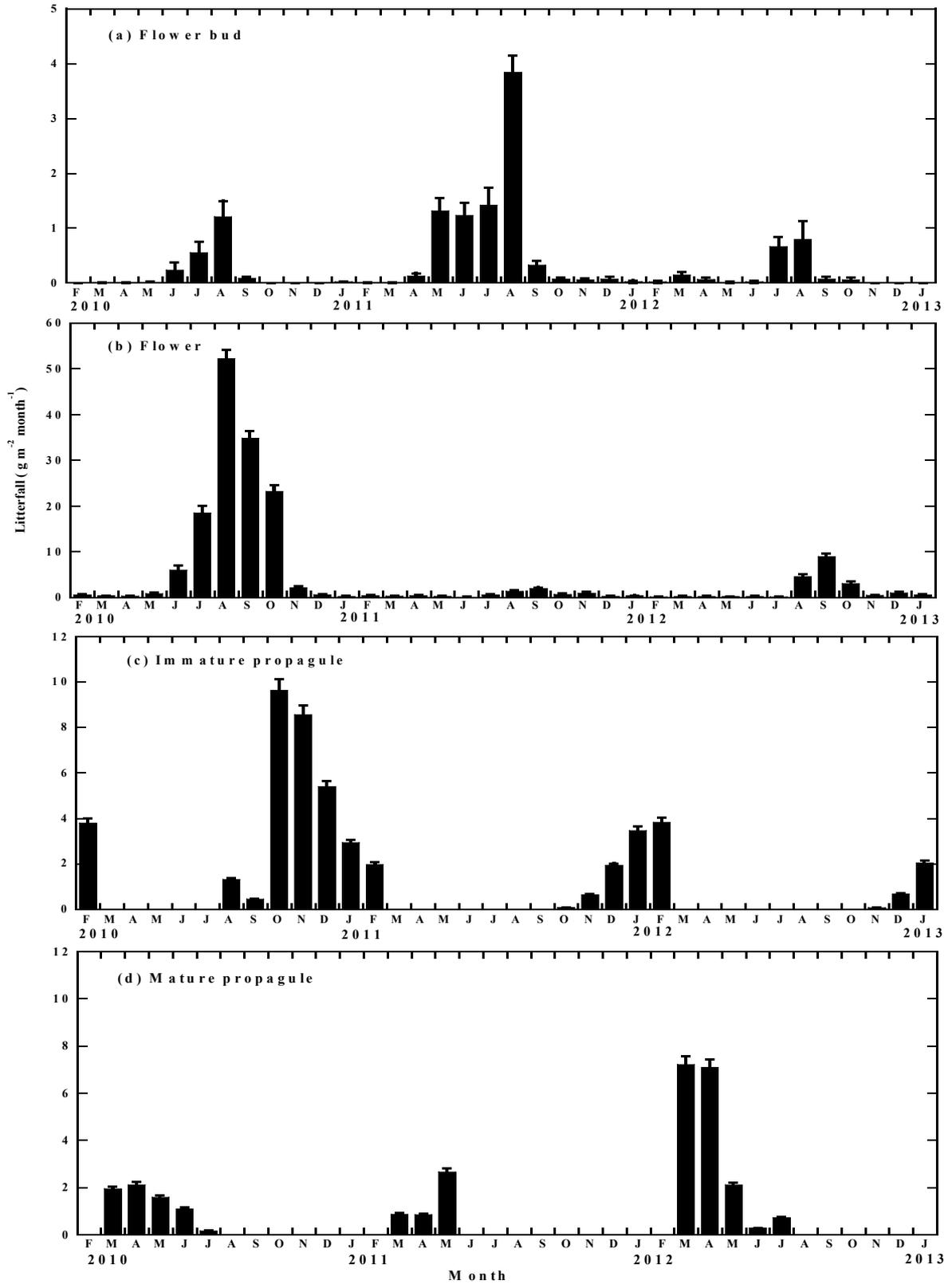


**Fig. 6-1.** Location of the study area. A non-continuous (215 m long, 5 m wide) belt-transect along the river was established and divided it into 43 plots.

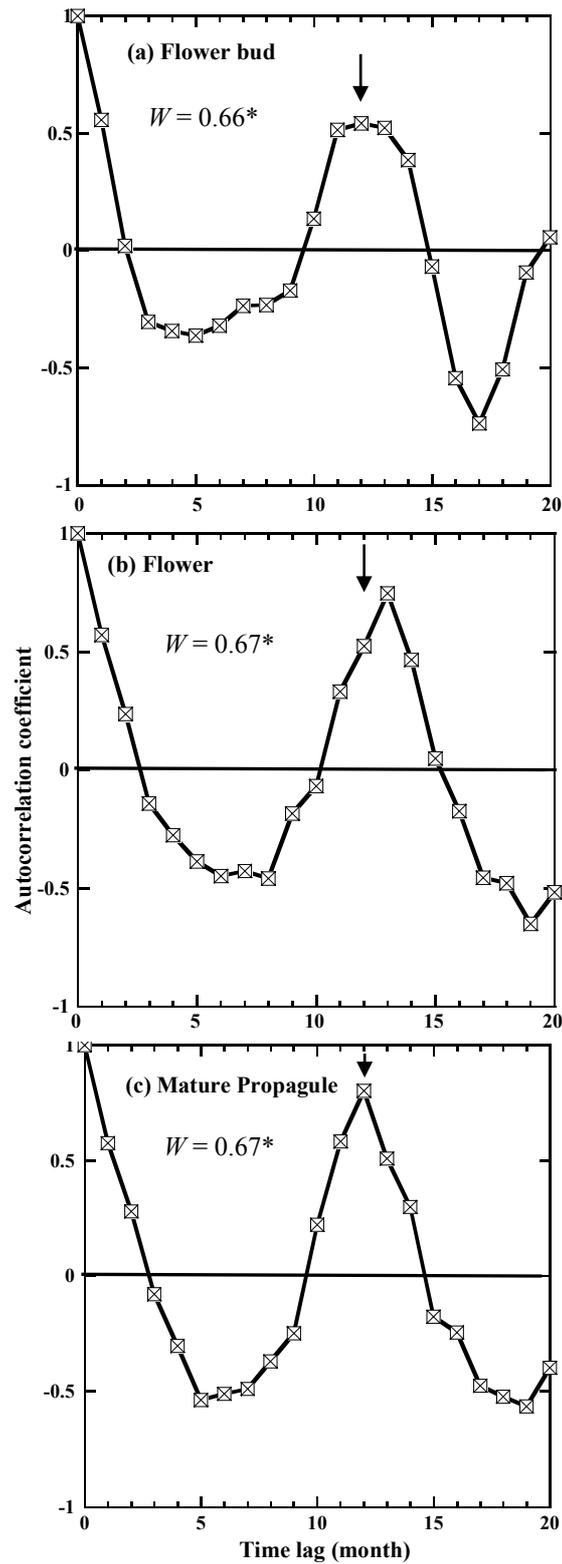




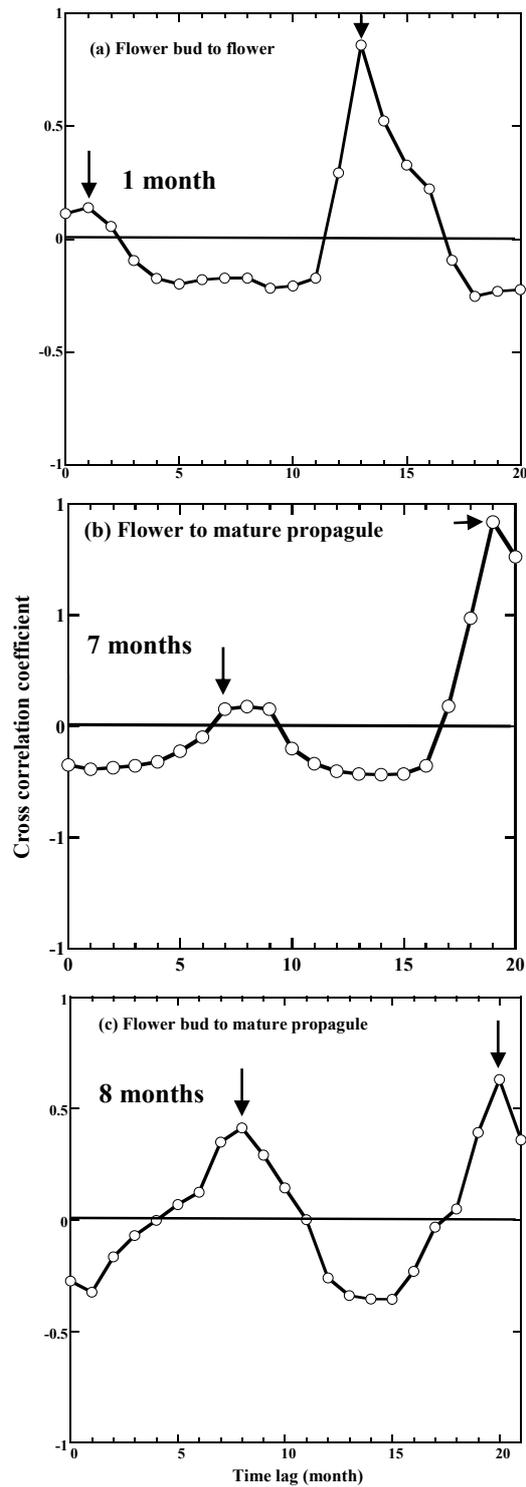
**Fig. 6-3.** Correlograms of vegetative litterfall components. Arrows indicate a 1-year cycle. \*\*, Kendall's  $W$  value with the significant probability of 0.01.



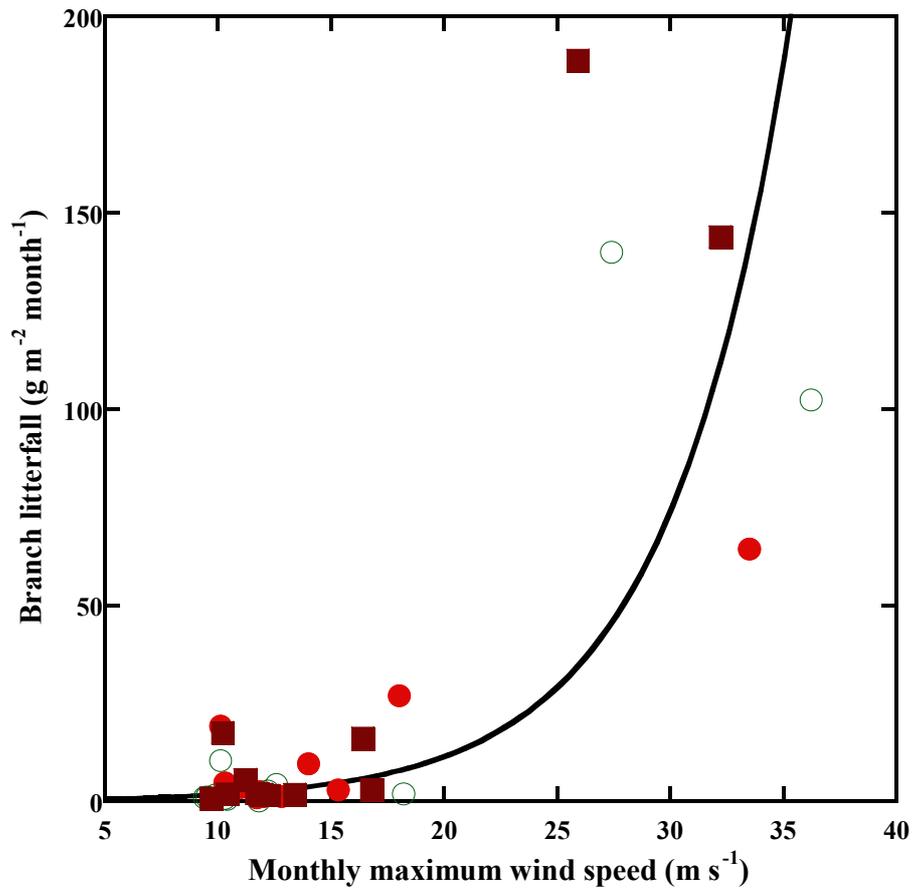
**Fig. 6-4.** Phenograms of reproductive litterfall. Vertical bars represent the standard errors of means ( $n = 43$ ).



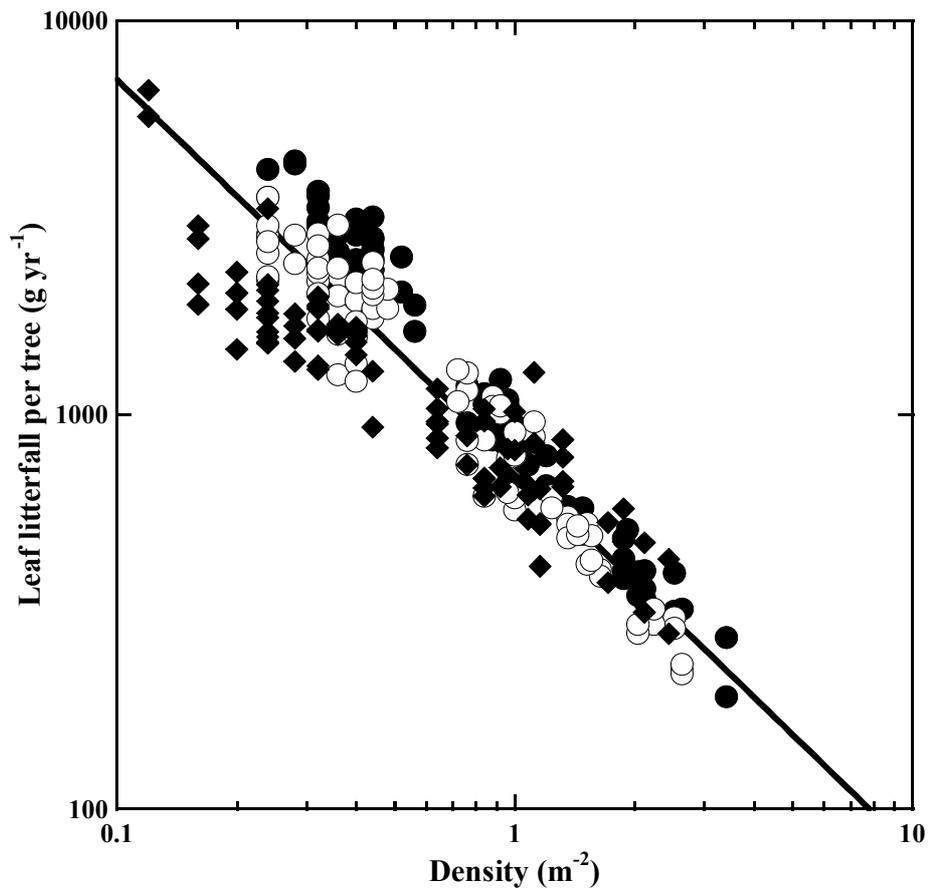
**Fig. 6-5.** Correlograms of reproductive litterfall components. Arrows indicate a 1-year cycle. \*, Kendall's  $W$  value with the significant probability of 0.05.



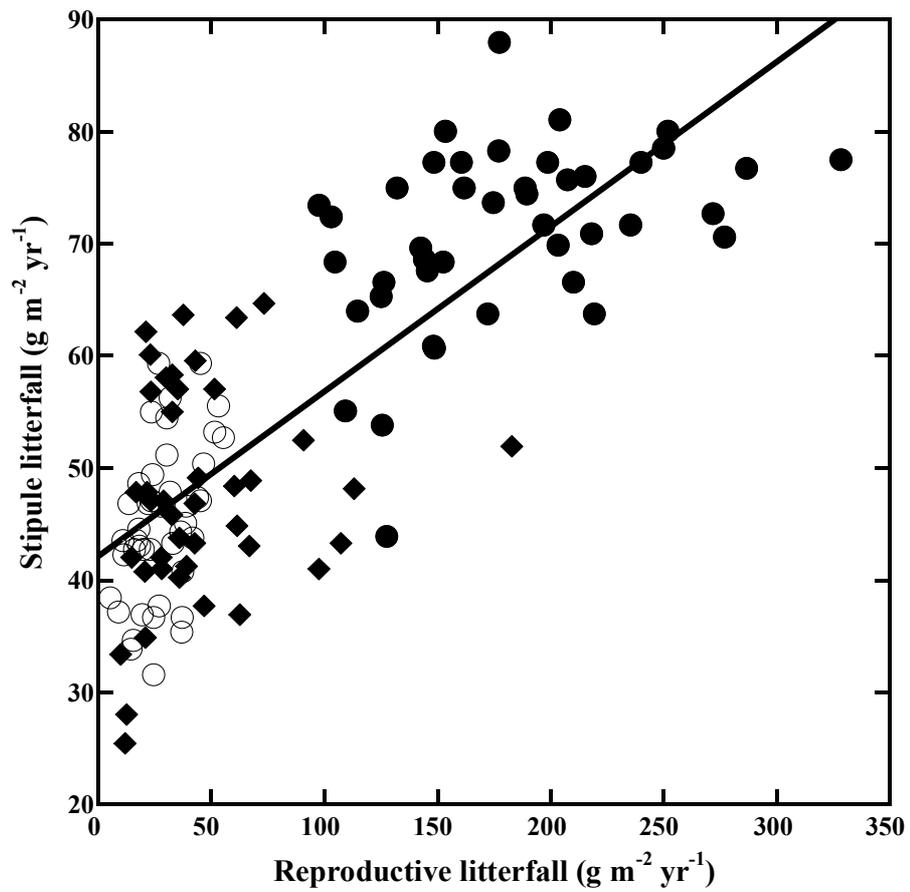
**Fig. 6-6.** Crosscorrelation coefficients between pairs of reproductive components. Arrows indicate maturation periods.



**Fig. 6-7.** Exponential relationship between monthly branch litterfall of *B. gymnorrhiza* and monthly maximum wind speed. ●: 1st year; ○: 2nd year; ■: 3rd year.



**Fig. 6-8.** Relationship between leaf litterfall per tree ( $l$ ) and population density ( $\rho$ ) on a log-log scale. The straight line is fit with  $l = 745.2\rho^{-0.9774}$ . ●:1st year; ○:2nd year; ◆:3rd year.



**Fig. 6-9.** Relationship between stipule litterfall and reproductive litterfall ( $r = 0.80$ ,  $p < 0.001$ ). ●:1st year; ○:2nd year; ◆:3rd year.

## CHAPTER VII

### General Discussion and Conclusion

---

#### 7.1. Discussion

In subtropical regions, leaf fall and leaf production are low during winter months and high in summer months (Gill and Tomlinson 1971); the same was true for the studied species at Manko Wetland and along the Okukubi River, Okinawa Island, Japan. *Bruguiera gymnorrhiza*, *Kabdelia obovata*, and *Rhizophora stylosa* grow in intertidal area and show distinctly unimodal pattern, in contrast to tropical rain forests with a bimodal or multimodal pattern. High species diversity and appropriate humidity in tropical rain forests could cause multi-mode peaks of litterfall. The diversity and water condition in tropical rain forests differ substantially from mangrove ecosystems. Unimodal leaf and stipule litterfall peaks have also been observed in Rhizophoraceae species in subtropical areas (Gill and Tomlinson 1971; Steinke 1988; Wilson and Saintilan 2012), whereas in tropical areas, unimodal, bimodal, and trimodal patterns have been observed in the species of the same family (Wium-Andersen and Christensen 1978; Wium-Andersen 1981; Leach and Burgin 1985). The tropical climate may cause multimode peaks of leaf and stipule litterfall in mangroves.

Saenger and Moverley (1985) suggested that leaf production in mangroves was closely tied to changes in temperature, with seasonal increases in temperature associated with leaf initiation. New leaf production and leaf litterfall of all the studied species were mainly related to increases in mean air temperature, monthly day length, monthly rainfall, and monthly maximum wind speed (Table 7-1). Similar findings were also reported by several authors (e.g., Gill and Tomlinson 1971; Leach and Burgin 1985; Nakagoshi and Nehira 1986; Gwada et al. 2000), who found that leaf production and litterfall was significantly correlated with mean maximum air temperature and solar radiation. Rainfall was an important factor for new leaf production, which is generally consistent with the findings of Borchert (2012), who reported that heavy rains of the wet season cause bud break and rapid shoot growth in tropical forests. Most species in a tropical evergreen mountain rainforest show a good correlation with leaf shedding and precipitation (Bendix et al. 2006) and also display a bimodal peak in leaf production

that is correlated with the rainy periods (Medway 1972). Temperature, day length, rainfall, and relative humidity may be the important external controlling factors of *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* leaf initiation in subtropical regions. In addition with this monthly maximum wind speed is an important climatic factor for this area, because Okinawa Island is within the typhoon prone area.

The mean total litterfall of *B. gymnorrhiza* ( $10.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ) was higher than those recorded on Irimote Island, Okinawa, Japan ( $8.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ , Kishimoto et al. 1987) and in Ohura Bay ( $7.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ , Hardiwinoto et al. 1989). Litterfall was lower than  $16 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  reported for *B. gymnorrhiza* on Unguja Island, Zanzibar, Tanzania (Shunula and Whittick 1999). Litterfall of *K. obovata* ( $9.9 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ) was within the range reported in other studies ( $8.7\text{--}11.01 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ; Hardiwinoto et al. 1989; Lee 1989; Khan et al. 2009). The mean total litterfall of *R. stylosa* ( $12.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ) was higher than  $7.77 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  recorded at Vaitupu, Tuvalu, South Pacific (Woodroffe 1984). Litterfall was lower than  $14.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  reported for this species on Motupore Island (Leach and Burgin 1985) and was similar to  $11.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  measured for *R. apiculata* Blume and *R. mucronata* Lamk. in the central west coast of India (Wafar et al. 1997). Compared to previous studies, the present study may indicate that productivity of these mangrove species is relatively high in Manko Wetland. This study suggests that litterfall production by *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* at the northern limit of their biogeographical distribution may be comparable to that found in other mangrove species in tropical regions. Similar to other studies (Wafar et al. 1997; May 1999; Ochieng and Erftemeijer 2002), the leaves of *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* were the major contributors to total litterfall production. Flower and propagule litterfall of the subtropical mangrove *B. gymnorrhiza* contributed 7.2–38 % to the total litterfall. This range is higher than the 13.1 % found by Mokolensang and Tokuyama (1998) for *B. gymnorrhiza* in the estuary of the Geasashi River, Okinawa Island. The contribution of the reproductive components of *K. obovata* (18.8 %) to the total litterfall was very similar to other mangrove species reported by Wafar et al. (1997). The portion of reproductive organ litterfall to the total litterfall of *R. stylosa* (21.5 %) was more than 2% higher than reported for the same species (Woodroffe 1984) and was almost identical with those of *R. apiculata* (21.8 %) and *R. mucronata* (23.2 %) in the central west coast of India (Wafar et al. 1997).

The great diversity of phenological patterns found at Manko Wetland, Okinawa, Japan agreed with the literature (Newstrom et al. 1994). Reproductive irregularities have been reported in all long-term phenological studies of the species of the family Rhizophoraceae, but the causes are still open to discussion. The flowering in mangrove species occurs throughout the year with majority of flowering during the rainy season (FAO 1994; Upadhyay and Mishra 2010). Many mangrove species growing in tropical regions have one reproductive peak a year (Shunula and Whittick 1999; Ochieng and Erftemeijer 2002; Coupland et al. 2005) and their flowering and fruiting occur in summer months, similarly to as in the present study (Clark 1994; May 1999). At Manko Wetland, reproductive organs were associated mainly with long monthly day length and monthly mean air temperature (Table 7-1). Borchert (2012) found that expansion of dormant flower buds may be triggered by increasing exposure to sunlight or the first heavy rains of the wet season. In tropical moist forests, ripening of the fruits takes place in a single peak before monsoon suggesting that survival of seeds and seedlings is critically dependent on moisture availability (Bhat and Murali 2001). However, no such event is seen in mangroves which indicate that rainfall is not the only source of moisture for all the species. Since most of the propagules and seeds of mangroves directly fall into the river systems or marshy ground below, the moisture need may be met from there. Chapman (1976) observed that mangroves do not rely absolutely on rainfall for survival because they can extract fresh water from the sea through salt excreting glands (Upadhyay and Mishra 2010).

In case of *B. gymnorrhiza* at Manko Wetland and along the Okukubi River, the relationship between mean annual leaf litterfall per tree ( $l$ , g yr<sup>-1</sup>) and tree density ( $\rho$ , m<sup>-2</sup>) was described as  $l = 701.48\rho^{-0.9905}$  (Fig. 7-1). The exponent (-0.9905) did not significantly differ from -1.0 ( $t = 0.299$ ,  $df = 152$ ,  $p = 0.0624$ ). In case of *K. obovata*, the relationship between mean annual leaf litterfall per tree and tree density was described as  $l = 484.71\rho^{-0.9099}$  (Fig. 7-2). The exponent (-0.9099) was also not significantly differ from -1.0 ( $t = 1.979$ ,  $df = 123$ ,  $p = 0.149$ ). In case of *R. stylosa*, the relationship between mean annual leaf litterfall per tree and tree density was described as  $l = 850.91\rho^{-1.2813}$  (Fig. 7-3). The exponent (-1.2813) was also not significantly differ from -1.0 ( $t = 0.8619$ ,  $df = 23$ ,  $p = 0.398$ ). Thus, the following approximation holds:

$l \propto \rho^{-1.0}$  for the three species. The present study showed that annual leaf litterfall per plot of *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* were constant regardless of the number of trees in the plot. Similar findings were also observed by Sharma et al. (2012) on *K. obovata* stands at Manko Wetland. These data are generally consistent with the findings of Deshar et al. (2012), who found that leaf biomass was constant in self-thinning stands of *B. gymnorrhiza* on Okinawa Island.

There was a variation in leaf longevity among the species of the same family in the study area. The average leaf longevity of subtropical mangrove *B. gymnorrhiza* was ranged from 18 to 19 months. This range was longer than those reported for *B. gymnorrhiza* in Fujian Province, China (9–10 month, Wang and Lin 1999) and *B. cylindrica* in southern Thailand (13 month, Wium-Andersen and Christensen 1978), but much shorter than that reported for *B. gymnorrhiza* in north-eastern Australia (2–3 yr, Duke et al. 1984). The leaf longevity of *B. gymnorrhiza* did not increased with increasing latitude, which contradicts suggestions by Wilson and Saintilan (2012) for *R. stylosa* in Australia. These differences in leaf longevity might be influenced by methodological differences. Kikuzawa and Lechowicz (2006) observed that lifetime net carbon gain by single leaf was rather constant across species, suggesting that lifetime net carbon gain by the leaves of *B. gymnorrhiza* at Manko Wetland may be similar to that by the leaves of the same species in Fujian Province or in the north-eastern Australia, regardless of the leaf longevity. According to Sharma et al. (2012), mean leaf longevity was 12.1 months for *K. obovata* and 13.9 months for *R. stylosa*. Variations in leaf longevity are likely to reflect differences in species morphology, solar radiation and tidal inundation.

Severe wind disturbance (i.e., typhoons or hurricanes) have a significant impact in changing the timing of litterfall input in temperate and tropical forests (Sato 2004; Lin et al. 2003). Mangroves at Manko Wetland and along the Okukubi River faces frequent typhoons, which disrupt the seasonality of litterfall production and could be the main reason for the higher litterfall of all the three species, especially the high branch litterfall (Table 7-1). In a typhoon month, branch litterfall was excessive compared with the litterfall in other months because all dead branches including broken living branches fell to the ground. This phenomenon shows the strong effect of the typhoon. High rates of branch litterfall in some months are attributed to typhoons which have wind speeds

that exceed  $17.2 \text{ m s}^{-1}$ . During the typhoons, green leaves were damaged and fell to the ground individually or attached to living broken branches. Similar observations were recorded on Okinawa Island by Sharma et al. (2012) for *K. obovata* in Manko Wetland and Hardiwinoto et al. (1989) for *K. obovata* and *B. gymnorrhiza* in Ohura Bay. Mackey and Smail (1995) also reported that branch litterfall of *Avicennia marina* (Forssk.) Vierh. was correlated with storms on the Brisbane River, Queensland, Australia. The frequent typhoons in Okinawa could be the main reason for the higher total branch litterfall rate of *K. obovata*, when compared to *R. stylosa* and *B. gymnorrhiza*. This is due to *K. obovata*'s incompact stem structure, which may weaken in strong wind (Chen et al. 2009).

In *B. gymnorrhiza* (9.8 %) of the flowers developed into propagules and the mean conversion rates of flowers to propagules for *K. obovata* (6.1 %). According to Primack et al. (1981), the high rates of the conversion rates of flowers to propagules in *K. obovata* and *B. gymnorrhiza* indicate self-compatibility, as in *Sonneratia alba* J. Simth. The mean conversion rate of flowers to mature propagules for *R. stylosa* (2.2 %) at Manko Wetland, Okinawa Island, was higher than those reported for the same species at tropical and subtropical areas (Duke et al. 1984; Leach and Burgin 1985; Tyagi 2003; Coupland et al. 2006). Coupland et al. (2006) reported that lower rate of fertilization might be due to limiting maternal resources and the lack of flower adaptation to either animal or wind pollination. *Rhizophora stylosa* has the largest propagules among the three species in this study and this could have resulted in the low rate of the conversion from flowers to propagules. Duke et al. (1984) noted that the low conversion of flowers to comparatively large fruits is a feature common in tropical areas. The conversion rates of flowers to propagules in the present study varied from species to species, which may be due to variation in pollinators, nutrients, substrates, or internal conditions of the plants. Another possibility is that the present rate of successful fertilization and subsequent propagule production were higher because of the availability of effective pollinators in the study area.

Litterfall data for the three mangroves of this study have also enabled me to compile a detailed sequence of progressive component maturation stages. This is the first study to report the maturation periods of reproductive organs of *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* at the northern limit of their biogeographical distribution.

Developmental rates of flower buds to flowers and mature propagules of *B. gymnorrhiza* (Fig. 7-4) were faster than *K. obovata* (Fig. 7-5), and *R. stylosa* (Fig. 7-6) in Manko Wetland, Okinawa Island, Japan. In *B. gymnorrhiza*, flower buds took one month to form flowers, which is consistent with results reported by Upadhyay and Mishra (2010). At Manko Wetland, flowers took eight months to form mature propagules, similarly to the findings of Wium-Andersen and Christensen (1978), who reported that *B. cylindrica* in tropical regions needed 6–8 months to form flower and mature propagules. In *K. obovata*, the developmental phase of flower bud initiation to mature propagules took 11 months, similar to the species of the same family, e.g., *R. mangle* L. in Florida was 8–13 months (Gill and Tomlinson 1971). *Rhizophora stylosa* needed 11–12 months to complete its reproductive cycle, which agrees with 10–11 months reported by Juliana et al. (2011) for *R. stylosa* in Peninsular Malaysia and 8–13 months reported by Gill and Tomlinson (1971) for *R. mangle* in Florida, USA. At Manko Wetland, flowers took 9–10 months to form mature propagules, in agreement with 11 months and 11–12 months respectively recorded for this species in northern (Coupland et al. 2005) and northeastern (Duke et al. 1984) Australia. The present reproductive cycle was shorter than that reported for *R. apiculata* in Malaysia (14–16 months) by Akmar and Juliana (2012) but almost identical to Farihah's (2011) findings (11–12 months). In comparison with previously reported data, *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* growing at the northern limit of their biogeographical distribution appear to have a similar maturation period to the same or congeneric species inhabiting tropical and subtropical regions.

There is some coordination between production of reproductive organs and leaves of all the studied species. Figures 7-7 and 7-8 show the correlation between stipule litterfall and reproductive organ litterfall of the studied species. In case of *B. gymnorrhiza*, stipule litterfall increased with increasing reproductive organ litterfall (Figs. 7-7a, 7-8), whereas *K. obovata* and *R. stylosa* exhibited a decreasing tendency in new leaf production, when the productions of reproductive organ were in maximum (Figs. 7-7b, 7-7c). Leaf production often occurs in the months proceeding or following flower and fruit production, generally with overlap. This may be because the production of flowers and propagules imposes a heavy burden on leaf recruitment. Wium-Andersen and Christensen (1978) observed the same pattern in *B. cylindrica* and *Ceriops tagal* in

southern Thailand. Duke et al. (1984) suggested that coordination between vegetative and reproductive organ production may indicate resource partitioning within plants. Potential partitioning of resources within mangroves was observed by Coupland et al. (2005) for *S. alba*, which showed a clear depression in leaf production at the time of peak flowering and fruiting. Duke (1990) also reported that leaf production was suspended in favor of propagule development in *A. marina* and subsequently leaf emergence accompanied propagule litterfall. In *B. gymnorrhiza*, flowering occurred throughout the year and propagules were produced for more than half of the year. Flower buds and flowers of *B. gymnorrhiza* are reddish or yellow in color (Allen and Duke 2006) and contain red or yellow carotenoids, which contribute less to photosynthetic output of the plants (Frank and Cogdell 1996). It is therefore assumed that *B. gymnorrhiza* requires more leaves for photosynthesis during reproductive organ production. High production of newly flushed leaves helps trees produce more energy, which is used to produce more reproductive organs.

## 7.2. Conclusion

Vegetative phenology, reproductive phenology, and litterfall dynamics of the mangrove *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* growing at the northern limit of their biogeographical distribution were evaluated and compared at Manko Wetland and along the Okukubi River, Okinawa Island, Japan.

- The periodicity of leaf initiation and leaf abscission of the studied species in subtropical regions showed unimodal patterns. Both new leaf production and leaf litterfall of these species were lowest in winter and highest in summer.
- Monthly mean air temperature and monthly day length may be the important environmental factors that control the seasonality of new leaf production of these three mangrove species in the subtropical regions.
- Branch litterfall of all three species depended on monthly maximum wind speed and increased exponentially with increasing monthly maximum wind speed.
- All the studied species showed that annual leaf litterfall per plot was almost constant regardless of the tree density.
- The average leaf longevity of subtropical mangrove *B. gymnorrhiza* ranged from 18 to 19 months.

- The periodicity of flowering and fruiting of all the species were restricted to the season. Monthly mean air temperature, monthly day length, monthly rainfall, and monthly air relative humidity are the environmental clues that control the seasonality of reproductive organ production of all three species.
- All the species produced a large number of flowers, but only a few of them were come into mature propagule. The mean conversion rates of flowers to mature propagules were 2.2 % for *R. stylosa*, 6.1 % for *K. obovata*, and 9.8 % for *B. gymnorrhiza*.
- This is the first study to report the maturation periods of reproductive organs of *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* at the northern limit of their biogeographical distribution. The period of reproductive organ development of all the three species in the subtropical region appears to have a similar maturation period to congeneric species inhabiting tropical regions.
- The annual total litterfall production of these three species followed the increasing trend (*K. obovata* < *B. gymnorrhiza* < *R. stylosa*). Leaves constituted over 50 % of the total litterfall for all three species. The contributions of reproductive organ litterfall to the total litterfall observed in this study were 38 % for *B. gymnorrhiza*, 18.8 % for *K. obovata*, and 21.5 % for *R. stylosa* at Manko Wetland.
- *Bruguiera gymnorrhiza* exhibited an increasing tendency in new leaf production, when the production of reproductive organs was at a maximum, while *K. obovata* and *R. stylosa* exhibited a decreasing tendency in stipule litterfall with reproductive organs litterfall.

## References

- Akmar NZ, Juliana WAW (2012) Reproductive phenology of two *Rhizophora* species in Sungai Pulai Forest Reserve, Johor, Malaysia. *Malays Appl Biol* 41:11–21
- Allen JA, Duke NC (2006) *Bruguiera gymnorrhiza* (large-leafed mangrove), ver. 2.1. In: Elevitch CR (ed) Species profiles for Pacific Island Agroforestry. Permanent Agriculture Resources (PAR), Holualoa, Hawaii. <http://www.traditionaltree.org>
- Bendix J, Homeier J, Cueva Ortiz E, Emck P, Breckle WS, Richter M, Beck E (2006) Seasonality of weather and tree phenology in a tropical evergreen mountain rain forest. *Int J Biomet* 50:370–384

- Borchert R (2012). The phenology of tropical trees. KU Undergraduate Biology Program, University of Kansas Web. [http://www.biology.ku.edu/tropical\\_tree\\_phenology/](http://www.biology.ku.edu/tropical_tree_phenology/). Accessed 05 October 2012
- Bhat DM, Murali KS (2001) Phenology of under storey species of tropical moist forests of Western Ghats regions of Uttara Kannada district in South India. *Curr Sci* 91:799–805
- Chapman VJ (1976) Mangrove vegetation. J. Cramer Verlag, Vaduz Liechtenstein
- Chen L, Zan Q, Li M, Shen J, Liao W (2009) Litter dynamics and forest structure of the introduced *Sonneratia caseolaris* mangrove forest in Shenzhen, China. *Estuar Coast Shelf Sci* 85:241–246
- Clarke PJ (1994) Baseline studies of temperate mangrove growth and reproduction; demographic and litterfall measures of leafing and flowering. *Aust J Bot* 42:37–48
- Coupland GT, Paling EI, McGuinness KA (2005) Vegetative and reproductive phenologies of four mangrove species from northern Australia. *Aust J Bot* 53:109–117
- Coupland GT, Paling EI, McGuinness KA (2006) Floral abortion and pollination in four species of tropical mangroves from northern Australia. *Aquat Bot* 84:151–157
- Duke NC (1990) Phenological trends with latitude in the mangrove tree *Avicennia marina*. *J Ecol* 78:113–133
- Duke NC, Bunt JS, Williams WT (1984) Observations on the floral and vegetative phenologies of north-eastern Australian mangroves. *Aust J Bot* 32:87–99
- FAO (1994) Mangrove Forest Management Guidelines. FAO Forestry Paper No. 117, Food and Agricultural Organization of the United Nations, Rome.
- Farihah AB (2011) Fenologi pembiakan *Rhizophora* di Tanjung Tuan dan Pantai Morib. Master of Science (MSc) Thesis. Universiti Kebangsaan Malaysia, Bangi (after Akmar NZ and Juliana 2012)
- Frank HA, Cogdell RJ (1996) Carotenoids in photosynthesis. *Photochem Photobiol* 63: 257–264
- Gill AM, Tomlinson PB (1971) Studies on the growth of red mangrove (*Rhizophora mangle* L.). 3. Phenology of the shoot. *Biotropica* 3:109–124
- Gwada P, Makoto T, Uezu Y (2000) Leaf phenological traits in the mangrove *Kandelia candel* (L.) Druce. *Aquat Bot* 68: 1–14

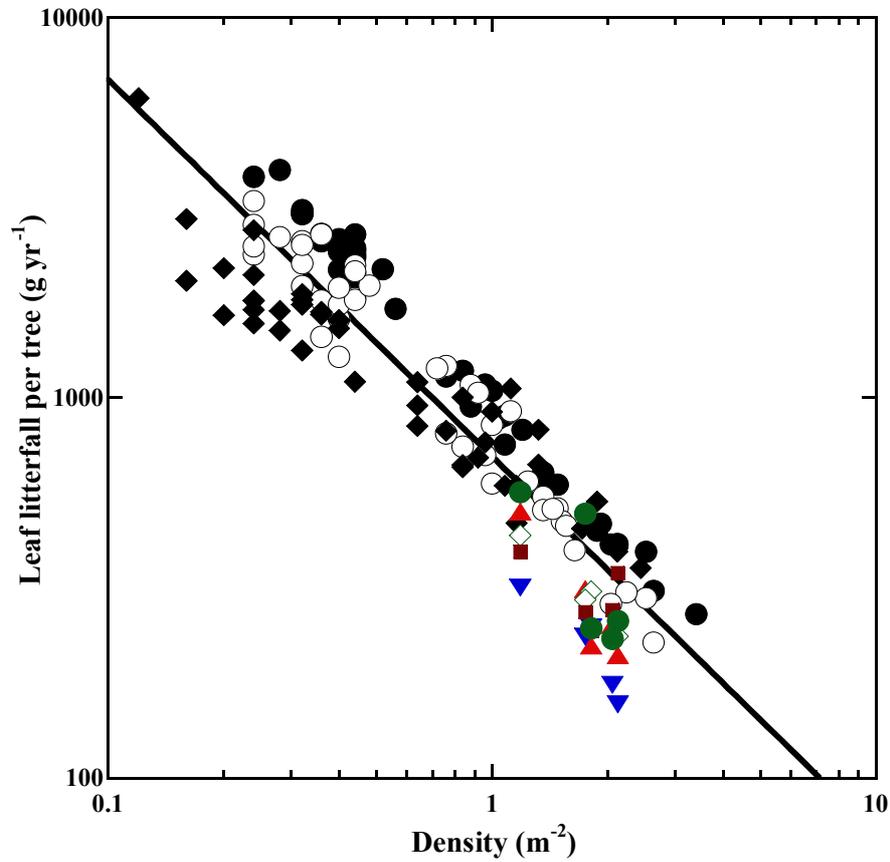
- Hardiwinoto S, Nakasuga T, Igarashi T (1989) Litter production and decomposition of a mangrove forest at Ohura Bay, Okinawa. *Res Bull Coll Exp For, Hokkaido Univ* 46:577–594
- Juliana WAW, Farihah AB, Akmar ZN, Razali SM, Nuhanim MN (2011) Phenology of *Rhizophora* species at three Peninsular Malaysia mangrove forests. Proceedings of the 10<sup>th</sup> International Annual symposium (UMTAS 2011), Universiti Malaysia Terengganu, pp12–17
- Khan MNI, Suwa R, Hagihara A (2009) Biomass and aboveground net primary production in a subtropical mangrove stand of *Kandelia obovata* (S., L.) Yong at Manko Wetland, Okinawa, Japan. *Wetl Ecol Manage* 17:585–599
- Kikuzawa K, Lechowicz MJ (2006) Toward synthesis of relationships among leaf longevity, instantaneous photosynthetic rate, lifetime leaf carbon gain, and the gross primary production of forests. *Am Nat* 168:373–383
- Kishimoto T, Miyajima H, Nakasuga T, Baba S (1987) Zonation of mangrove forest (III) litterfall and its seasonal change. *Trans Mtg Jpn For Soc* 98:301–302 (in Japanese)
- Leach GJ, Burgin S (1985) Litter production and seasonality of mangroves in Papua New Guinea. *Aquat Bot* 23:215–224
- Lee SY (1989) Litter production and turnover of the mangrove *Kandelia candel* (L.) Druce in a Hong Kong tidal shrimp pond. *Estuar Coast Shelf Sci* 29:75–87
- Lin KC, Hamburg SP, Tang S, Hsia Y, Lin T (2003) Typhoon effects on litterfall in a subtropical forest. *Can J For Res* 33:2184–2192
- Mackey AP, Smail G (1995) Spatial and temporal variation in litter fall of *Avicennia marina* (Forssk.) Vierh. in the Brisbane River, Queensland, Australia. *Aquat Bot* 52:133–142
- May JD (1999) Spatial variation in litter production by the mangrove *Avicennia marina* var. *australasica* in Rangaunu Harbor, Northland, New Zealand. *NZ J Mar Freshwat Res* 33:163–172
- Medway L (1972) Phenology of a tropical rain forest in Malaya. *Biol J Linn Soc* 4:117–146
- Mokolensang JF, Tokuyama A (1998) Litter production of mangrove forests at the Gaesashi River. *Bull Coll Sci, Univ Ryukyus* 65:73–79

- Nakagoshi K, Nehira K (1986) Growth and mortality of mangrove seedlings transplanted to Hiroshima. *Hikobia* 9:439–449
- Newstrom LE, Frankie GW, Baker HG (1994) A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica* 2:141–159
- Ochieng CA, Erftemeijer PLA (2002) Phenology, litterfall and nutrient resorption in *Avicennia marina* (Forssk.) Vierh in Gazi Bay, Kenya. *Trees* 16:167–171
- Primack RB, Duke NC, Tomlinson PB (1981) Floral morphology in relation to pollination ecology in five Queensland coastal plants. *Austrobaileya* 4:346–355
- Saenger P, Moverley J (1985) Vegetative phenology of mangroves along the Queensland coastline. *Proc Ecol Soc Aust* 13:257–265
- Sato T (2004) Litterfall dynamics after a typhoon disturbance in a *Castanopsis cuspidata* coppice, southwestern Japan. *Ann For Sci* 61:431–438
- Sharma S, Hoque ATMR, Analuddin K, Hagihara A (2012) Litterfall dynamics in an overcrowded mangrove *Kandelia obovata* (S., L.) Yong stand over five years. *Estuar Coast Shelf Sci* 98:31–41
- Shunula JP, Whittick A (1999) Aspects of litter production in mangroves from Unguja Island, Zanzibar, Tanzania. *Estuar Coast Shelf Sci* 49:51–54
- Steinke TD (1988) Vegetative and floral phenology of three mangrove in Mgeni Estuary. *S Afr J Bot* 54:97–102
- Tyagi AP (2003) Location and interseasonal variation in flowering, propagule setting and propagule size in mangroves species of the family Rhizophoraceae. *Wetlands Ecol Manage* 11:167–174
- Upadhyay VP, Mishra PK (2010) Phenology of mangroves tree species on Orissa coast, India. *Trop Ecol* 51:289–295
- Wafar S, Untawale AG, Wafar M (1997) Litter fall and energy flux in a mangrove ecosystem. *Estuar Coast Shelf Sci* 44:111–124
- Wang W, Lin P (1999) Transfer of salt and nutrients in *Bruguiera gymnorrhiza* leaves during development and senescence. *Mangroves Salt Marshes* 3:1–7
- Wilson NC, Saintilan N (2012) Growth of the mangrove species *Rhizophora stylosa* Griff. at its southern latitudinal limit in eastern Australia. *Aquat Bot* 101:8–17

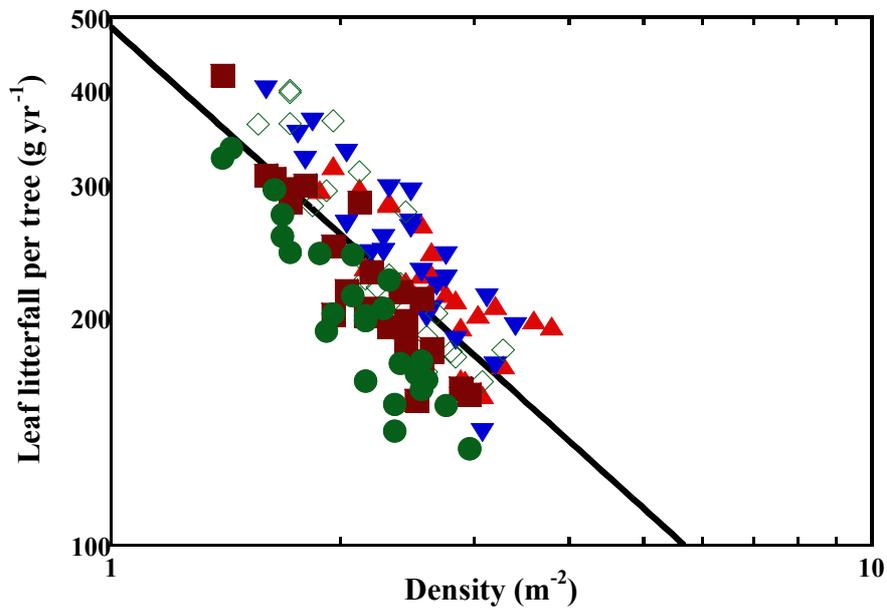
- Wium-Andersen S, Christensen B (1978) Seasonal growth of mangrove trees in southern Thailand. II. Phenology of *Bruguiera cylindrica*, *Ceriops tagal*, *Lumnitzera littorea* and *Avicennia marina*. *Aquat Bot* 5:383–390
- Wium-Andersen S (1981) Seasonal growth of mangrove trees in southern Thailand. III. Phenology of *Rhizophora mucronata* Lamk. and *Scyphiphora hydrophyllaceae* Gaertn. *Aquat Bot* 10:371–376
- Woodroffe CD (1984) Litter fall beneath *Rhizophora stylosa* Griff., Vaitupu, Tuvalu, South Pacific. *Aquat Bot* 18:249–255

**Table 7-1.** Adjusted  $R^2$  values from the stepwise multiple regression analysis of vegetative and reproductive litterfall components of *B. gymnorrhiza*, *K. obovata*, and *R. stylosa* in relation to environmental factors. Significant probabilities are indicated by \* ( $p \leq 0.05$ ), \*\* ( $p \leq 0.01$ ), and \*\*\* ( $p \leq 0.001$ ). Numerals in parentheses are tolerances of the coefficients of the multiple regression for a component.

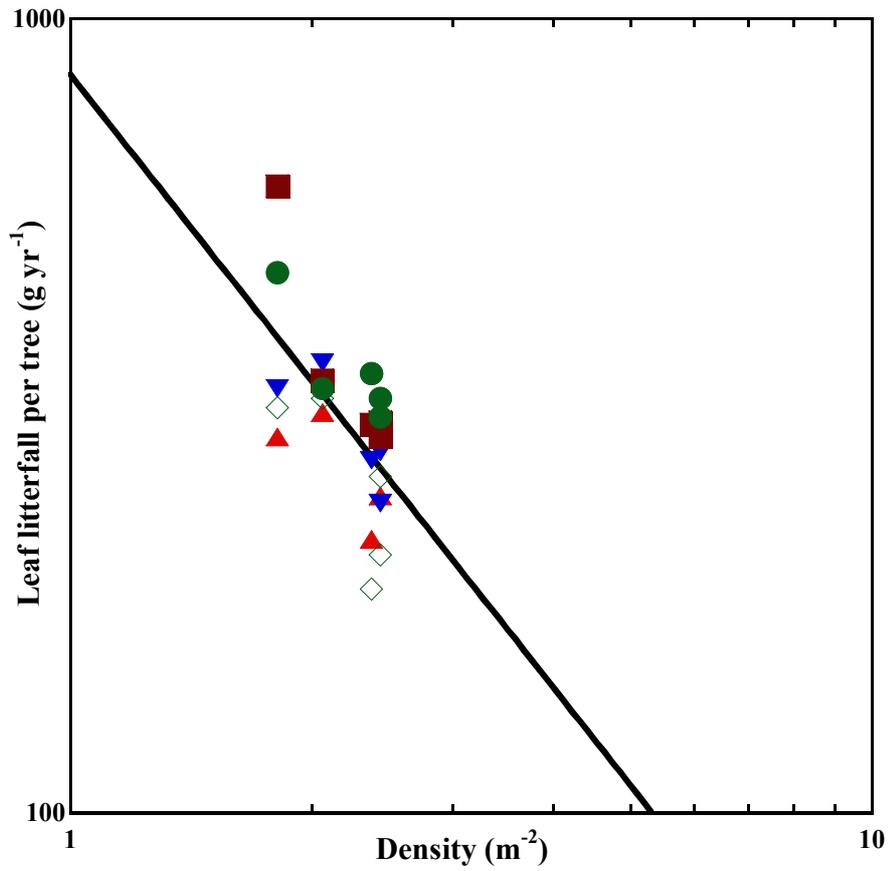
Species	Component	Monthly temperature °C	mean Monthly length h month <sup>-1</sup>	day Monthly rainfall mm month <sup>-1</sup>	Monthly relative humidity %	mean Monthly maximum wind speed m s <sup>-1</sup>
<i>B. gymnorrhiza</i>	Leaf		0.65*** (0.97)			0.57*** (0.97)
<i>K. obovata</i>		0.31*** (0.88)		0.57*** (0.86)		0.48*** (0.93)
<i>R. stylosa</i>			0.76*** (0.97)			0.57*** (0.97)
<i>B. gymnorrhiza</i>	Stipule	0.20** (0.85)		0.27* (0.76)		0.22* (0.83)
<i>K. obovata</i>			0.37*** (0.99)			0.41* (0.99)
<i>R. stylosa</i>		0.44** (0.53)			0.49** (0.53)	
<i>B. gymnorrhiza</i>	Branch					0.76*** (1.00)
<i>K. obovata</i>		0.56* (0.96)				0.53*** (0.96)
<i>R. stylosa</i>						0.65*** (1.00)
<i>B. gymnorrhiza</i>	Flower bud		0.12** (1.00)			
<i>K. obovata</i>		0.45*** (0.44)	0.31*** (0.89)		0.55*** (0.42)	
<i>R. stylosa</i>		0.31** (0.40)	0.36* (0.40)		0.27*** (0.42)	0.30** (0.87)
<i>B. gymnorrhiza</i>	Flower	0.40*** (0.53)		0.48* (0.60)	0.44*** (0.41)	
<i>K. obovata</i>		0.28*** (1.00)				
<i>R. stylosa</i>			0.39** (1.00)			
<i>K. obovata</i>	Fruit	0.20*** (0.50)	0.03*** (0.50)			
<i>R. stylosa</i>		0.19*** (1.00)				
<i>B. gymnorrhiza</i>	Propagule		0.11** (0.97)			0.18* (0.97)
<i>K. obovata</i>		0.44*** (0.50)	0.11*** (0.50)			
<i>R. stylosa</i>		0.20*** (1.00)				



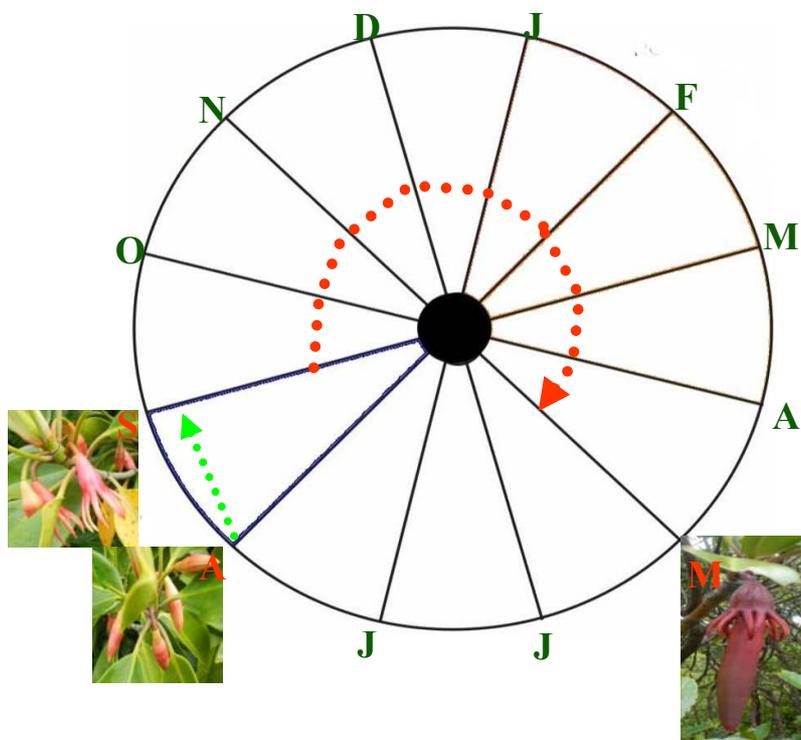
**Fig. 7-1.** Relationship between leaf litterfall per tree ( $l$ ) and tree density ( $\rho$ ) of *B. gymnorrhiza* at Manko Wetland and along the Okukubi River on log-log coordinates. The straight line is fit with  $l = 701.48\rho^{-0.9905}$  ( $R^2 = 0.87$ ).  $\blacktriangle$ : 1st year-Manko;  $\blacktriangledown$ : 2nd year-Manko;  $\diamond$ : 3rd year-Manko;  $\blacksquare$ : 4th year-Manko;  $\bullet$ : 5th year-Manko;  $\bullet$ : 1<sup>st</sup> year-Okukubi;  $\circ$ : 2<sup>nd</sup> year- Okukubi;  $\blacklozenge$ : 3<sup>rd</sup> year-Okukubi.



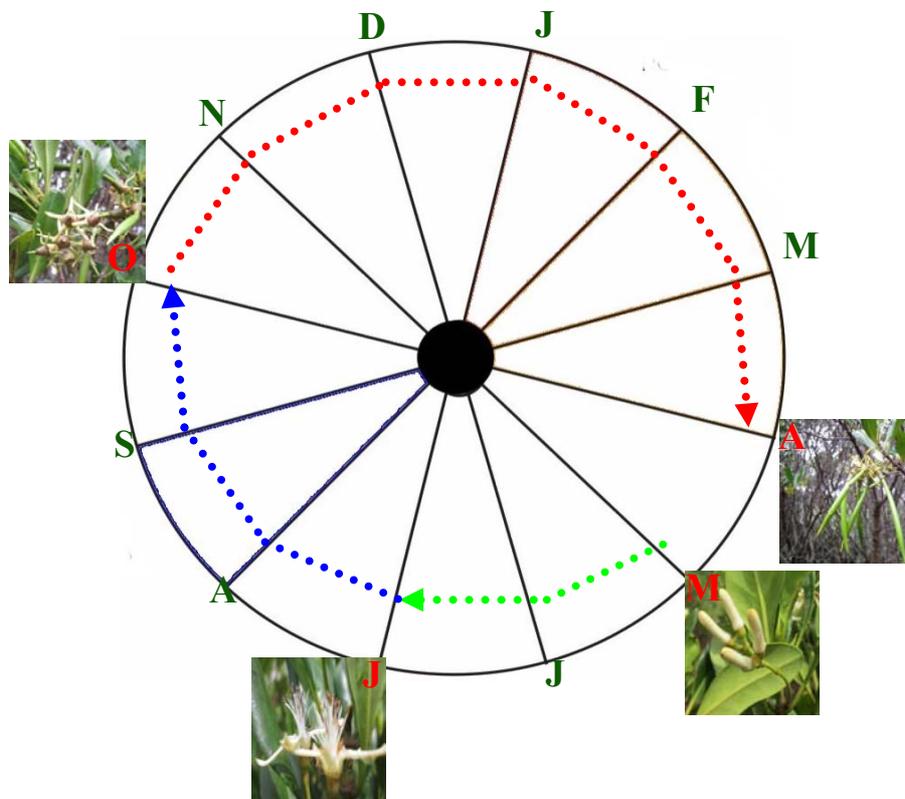
**Fig. 7-2.** Relationship between leaf litterfall per tree ( $l$ ) and tree density ( $\rho$ ) of *K. obovata* at Manko Wetland on log-log coordinates. The straight line is fit with  $l = 484.71\rho^{-0.9099}$  ( $R^2 = 0.54$ ).  $\blacktriangle$ : 1st year;  $\blacktriangledown$ : 2nd year;  $\blacklozenge$ : 3rd year;  $\blacksquare$ : 4th year;  $\bullet$ : 5th year.



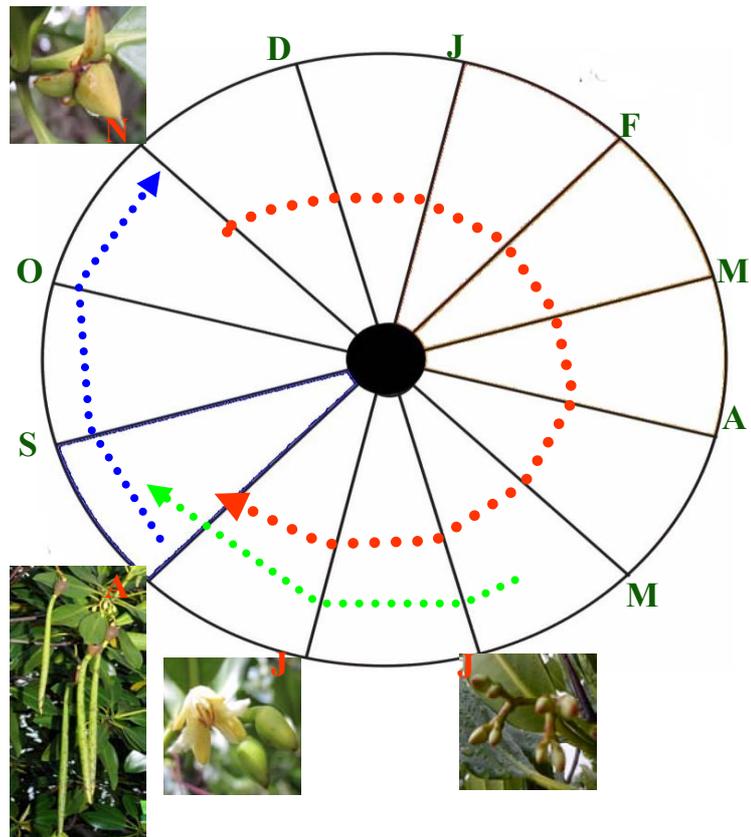
**Fig. 7-3.** Relationship between leaf litterfall per tree ( $l$ ) and tree density ( $\rho$ ) of *R. stylosa* at Manko Wetland on log-log coordinates. The straight line is fit with  $l = 850.91\rho^{-1.2813}$  ( $R^2 = 0.40$ ). ▲: 1st year; ▼: 2nd year; ◇: 3rd year; ■: 4th year; ●: 5th year.



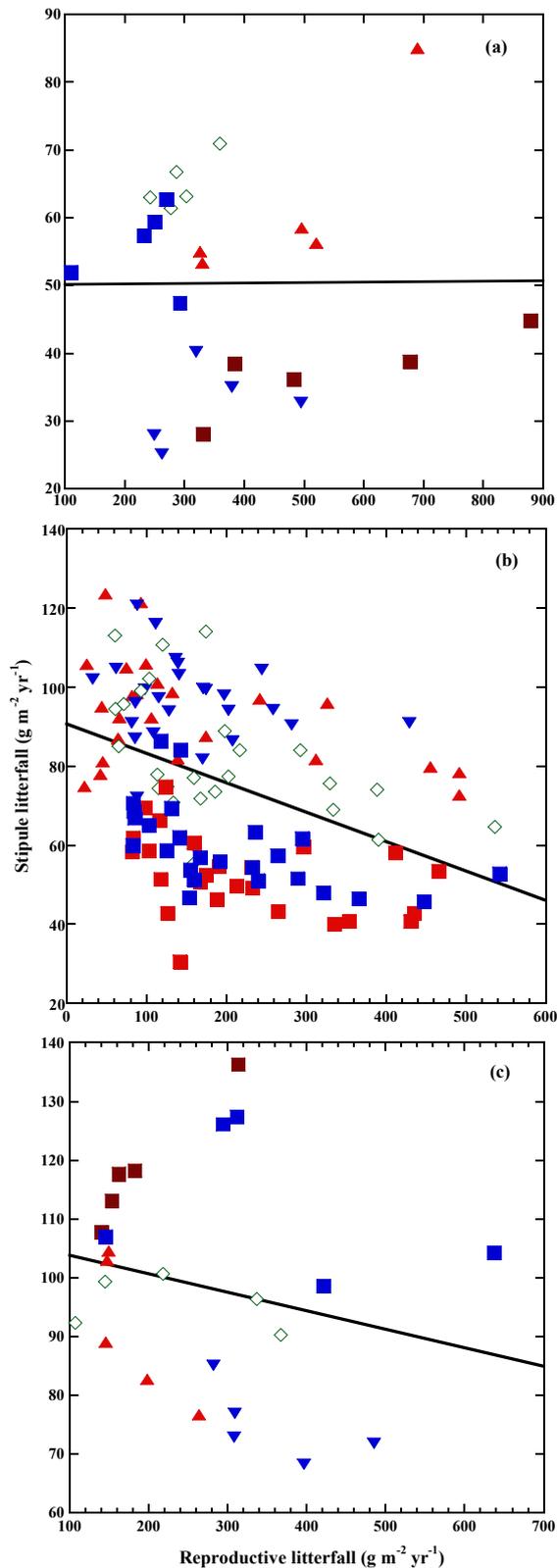
**Fig. 7-4.** Phenology of reproductive organs of *B. gymnorrhiza*.



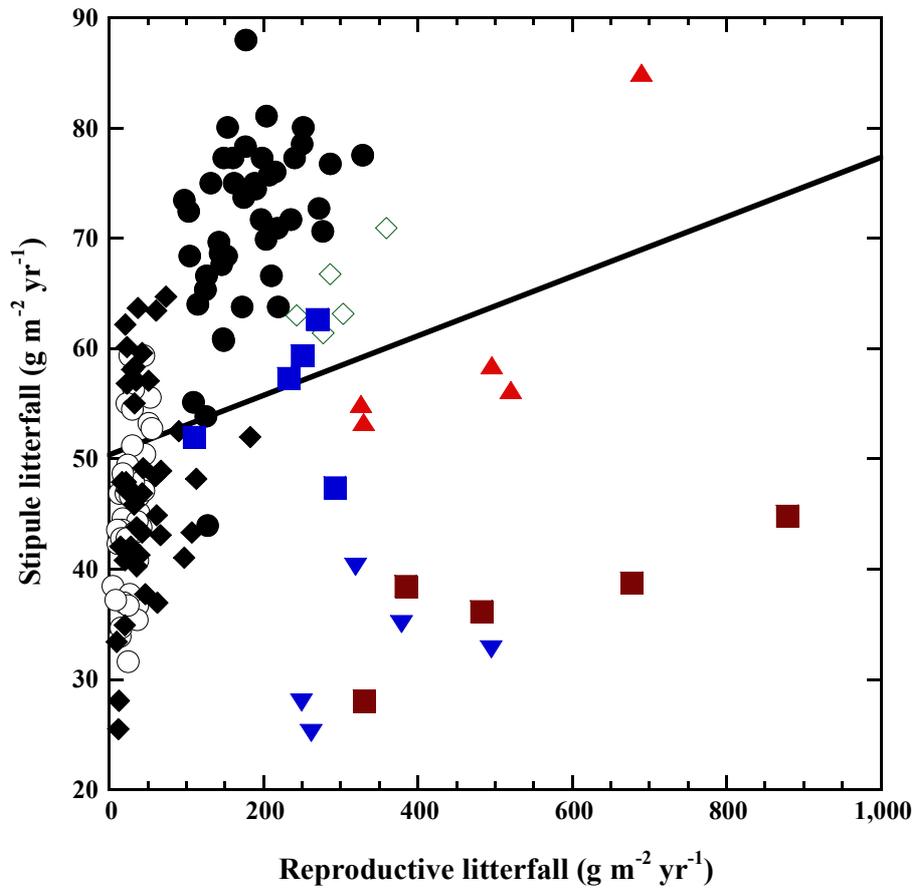
**Fig. 7-5.** Phenology of reproductive organs of *K. obovata*.



**Fig. 7-6.** Phenology of reproductive organs of *R. stylosa*.



**Fig. 7-7.** Relationships between stipule litterfall and reproductive litterfall for *B. gymnorrhiza* ( $r = 0.007$ ,  $p = 0.972$ ) (a), *K. obovata* ( $r = -0.42$ ,  $p = 1.2 \times 10^{-06}$ ) (b), and *R. stylosa* ( $r = -0.22$ ,  $p = 0.286$ ) (c) at Manko Wetland.  $\blacktriangle$ : 1st year;  $\blacktriangledown$ : 2nd year;  $\diamond$ : 3rd year;  $\blacksquare$ : 4th year;  $\blacksquare$ : 5th year.



**Fig. 7-8.** Relationship between stipule litterfall and reproductive litterfall for *B. gymnorhiza* at Manko Wetland and along the Okukubi River ( $r = 0.27$ ,  $p = 0.0006$ ). ▲: 1st year- Manko; ▼: 2nd year- Manko; ◇: 3rd year- Manko; ■: 4th year- Manko; ■: 5th year- Manko; ●: 1st year- Okukubi; ○: 2nd year- Okukubi; ◆: 3rd year- Okukubi.