Caulerpa spp. are siphonous green algae. They are common and ubiquitous and ecological important features of many tropical marine environments, including coral reefs, lagoons and seagrass beds (Clifton and Clifton, 1999; Collado-Vides and Robledo, 1999; Scrosati, 2001; Collado-Vides, 2002). They are widely distributed throughout tropical and subtropical seas (Taylor, 1960; Lüning, 1990). They have recently become subjected to considerable study as a result of species expansions of their ranges into more temperate environments and have become very successful invasive species in the Mediterranean sea (Piazzi et al., 1994; Olsen et al., 1998; Aussem and Hill, 2000; Benzie et al., 2000; Nodena et al., 2000; Ceccherelli et al., 2002; Fam et al., 2002; Renoncourt and Meinesz, 2002; Jaubert et al., 2003; Thake et al., 2003).

Despite its uni-cellularity, the Caulerpa plant shows a complex external morphology, differentiated into creeping stolon, rhizophores with rhizoid clusters, and erect assimilators. The assimilators usually bear numerous branchlets termed ramuli and showed highly species specific variability. The morphological variations (plasticity) of Caulerpa species seem to be related to substrate, light intensity, water exposure, currents, depth, seasons and grazing pressure (Calvert, 1976; Ohba et al., 1992; Carruthers et al., 1993; Gacia et al., 1996; Verlaque et al., 2000; de Senerpont Domis et al., 2003). This morphology variability could influence growth form, photosynthetic ability and ultimately, population dynamics of Caulerpa (Collado-Vides and Robledo, 1999; Collado-Vides, 2002).

Here we report: 1) the population dynamics of Caulerpa racemosa (Forsskål) J. Agardh., a common coral macroalga in shallow subtidal reefs and 2) the morphological plasticity of C. racemosa at different degrees of wave motion and seasons.

Materials and Methods

The population of C. racemosa studied are from the shallow subtidal reefs, 1-2 meters depth, at Koh Kham, Songkhla province, Southern Thailand (6° 71'N, 100° 20'E). The main oceananographic characteristics and the dynamics of the coral reef community of Koh Kham were reported in EIA study on gas separation and piping in Songkhla province (Prince of Songkla University, 2000), but macroalgae populations were not studied. Koh Kham is located on the Gulf of Thailand, nearly 2 kilometers from the coast, with little human activity in proximity to the study sites. Preliminary studies on diversity, distribution and abundance of macroalgae in Songkhla province, Thailand, were carried out during August 2002, which showed high abundance and many big thick meadows of C. racemosa at the site. C. racemosa grows together with corals and other algae on sandy, sea shells and rocky substrates near the coral reef flat.

To study the effect of wave motion on the population and morphological plasticity, C. racemosa was observed at two sites: on exposed and sheltered sites. The exposed site was on the northern coast of the Koh Kham, which directly opens to the sea. The sheltered site was on the western coast of Koh Kham, where lies parallel to the shore. Also, coral forms were used as biological indicators to measure the degrees of wave exposure. On the exposed site, the higher percentage cover of massive coral such as Platygyra sp., Porites lutea Milne-Edwards and Haime, 1860 and Goniastrea pectinata (Ehrenberg, 1834) were dominant, while foliose coral such as Turbinaria peltata (Esper, 1794) had greater percentage cover on the sheltered site.

Percentage cover, frond density, mat thickness and biomass (dry weight) of C. racemosa were determined at 3 months intervals from November 2002 to November 2003. Samples were monitored and recorded 4 times within the wet and dry seasons in Southern Thailand. The wet season is predominated by the SW monsoon and a dry season predominated by NE moonsoon. Snorkeling and SCUBA techniques were used for data and sampling collection. The wet season study was conducted during 16-17 November 2002 and 19-20 July 2003, and the dry season study during 15-16 February 2003 and 19-20 April 2003. Additional observations of C. racemosa population were made on 18 August 2003, 15 November 2003, 13 December 2003 and 27 August 2004. On each sampling dates, five 50 cm X 50 cm quadrats were utilized to randomly sample macroalgal communities at each site. Percentage cover and substrates of macroalgae were estimated visually and recorded at both sites. To investigate frond density, twenty-four 5 cm X 5 cm quadrats were sampled randomly at each site, a thin wooden rod was inserted into the C. racemosa mat to measure the mat thickness of the C. racemosa meadows at each site with a total of 25 replications. To study C. racemosa morphology and biomass, five 50 cm X 50 cm quadrats were randomly sampled at each site across the C. racemosa bed. All algal specimens were collected by scraping and then placed into plastic bags. They were placed in dark and cool conditions, immediately brought back to the laboratory and processed. C. racemosa thalli were washed; epiphytes and other benthic organisms were removed. Fronds were closely observed and dried at 60°C to constant weight. A few samples were preserved and voucher specimens were deposited at PSU herbarium, Thailand.

Statistical analysis

Two-way ANOVA was employed to test percentage cover, frond density, mat thickness and biomass against different sites and seasons. Multiple comparisons were tested when there were significant differences between treatments, following Zar (1984). Cochrans C- test was used before each analysis, to test whether variances were homogeneous and data transformations were applied when necessary. Friedman's ANOVA was employed where homogeneity of the data set was not achieved after transformations. Tukey multiple comparison was employed to test the differences between sites and seasons. Statistical results were presented based on the transformed analyses, but for clarity graphical output was based on the untransformed means.

Results

Percentage cover, frond density, biomass and mat thickness of C. racemosa varied among sites and seasons. Slightly greater percentage cover of C. racemosa occurred on the sheltered site compared to the exposed site, with significant differences among months ($\chi^2 = 27.11$; df = 7, N =5, P<0.001; Fig. 1). C. racemosa was very abundant at the site, the maximum percentage cover of C. racemosa was found on the sheltered shore during late rainy season and early wet season, around 80% of percentage cover at both sites. Subsequently, in the dry season the percentage cover of C. racemosa dropped to 50% when some unhealthy, yellowish fronds were observed. Surprisingly, disappearance of C. racemosa occurred in July, 2003. Also, there was no recovery or recruitment of C. racemosa population upon revisiting the site in August 2003, November 2003 and December 2003 and August 2004.

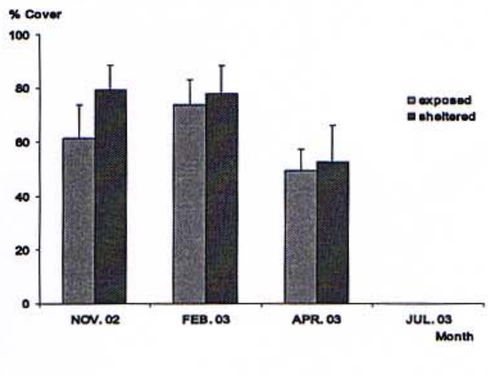

Fig. 1. Percentage cover of C. racemosa at different sites and seasons

Similar patterns were found in C. racemosa frond density. There was slightly greater frond density on the sheltered than on the exposed sites, with significant differences among months ($\chi^2 = 107.71$; df = 7, N =24, P<0.001; Fig. 2). C. racemosa patches contained very dense greenish fronds. The maximum densest fronds were found at the sheltered site during late rainy season and at the early wet season, 1.75 fronds/cm^2 in November 2002 and 1.85 fronds/ cm^2 in February 2003 respectively. It was worthwhile to note that there were some C. racemosa patches washed up on the shore both on the sheltered and exposed sites. Frond density dropped by 50% in dry season with more C. racemosa

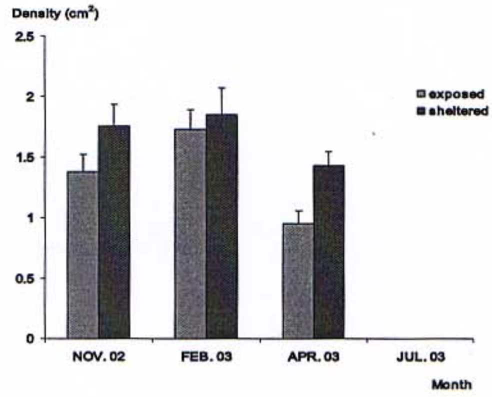

Fig. 2 Density of C. racemosa at different sites and seasons

In contrast, C. racemosa biomass was significantly greater during the dry seasons. Three hundred percent higher biomass was present in the dry season (April 2003), as compared to the wet season (November 2002) ($F_{(3,14)} = 21.44$, P<0.0001; Fig. 3), but there was no significant differecnes between different exposures ($F_{(1,14)} = 1.10$, P = 0.31). Due to the very strong wave action, C. racemosa stand could not be collected on the exposed site, thus no data was presented for the February, 2003 sampling event.

Similar patterns were found for the mat thickness of C. racemosa. There were significant differences in mat thickness among months ($F_{(1,24)} = 271.96$, P<0.01; Fig. 4). The thickness of C. racemosa mat was increased almost 300% in the early dry season compared to those in the wet season, however they became thinner in the middle of the dry season and no differences were found among sites ($F_{(1,192)} = 0.20$, P = 0.65).

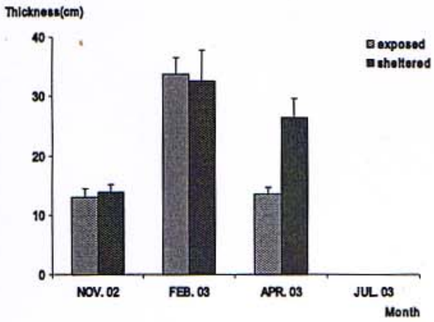

Fig. 3. Mat thickness of C. racemosa at different sites and seasons

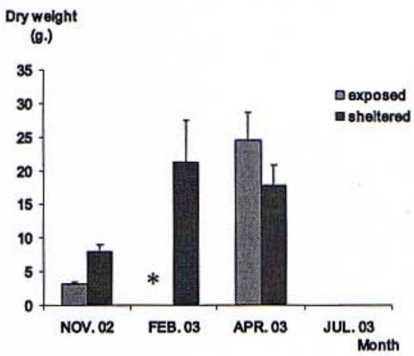

Fig. 4. Biomass of C. racemosa at different sites and seasons. *: Samples can not be collected because of strong wave

In addition, close observation on C. racemosa fronds showed no differences in frond morphology among sites and seasons. Similar shapes and size of ramuli were found at both sites. Also, C. racemosa fronds underneath the canopy were observed to be bigger and greener than those on the upper part of the patches during February and April 2003.

Discussion

Many studies have shown that there is significant morphological plasticity of C. racemosa due to various physical factors such as temperature, light, salinity and wave motions (Calvert, 1976; Ohba et al., 1992; Carruthers et al.; 1993, Gacia et al., 1996; Verlaque et al., 2000; de Senerpont Domis et al., 2003). Surprising, this study showed no differences in percentage cover, frond density, mat thickness, biomass and frond morphology of C. racemosa between exposed and sheltered sites. The large meadows of C. racemosa, dense compact stolons and fronds are similar to those known to form turf-forming communities in coral reef habitats. The turf-forming algae are known to be an adaptation against herbivory and desiccation (Hay, 1981) and against excessive irradiance which may cause bleaching in many algae (Hay, 1986; Beach and Smith, 1996 a, b). It is also known to reduce water velocities over the individual fronds (Hurd and Stevens, 1997). Thus, there might have been very little influence in such physical factors over C. racemosa turfs at both sites, hence similar patterns of C. racemosa population were found.

Temporal variations in percentage cover, frond density, mat thickness and biomass were found in the big thick mats of C. racemosa, that once covered areas of more than 1,625 m^2. Populations sharply declined by 50% in April, the middle of dry season. Also, C. racemosa fronds underneath the canopy were observed to be bigger and greener than those on the upper part of the patches. Greater exposure to high light could cause bleaching and die off in some other marine algae (Beach and Smith 1997; Scrosati and DeWreede, 1998). Thus, greater exposure to high light in February and April of C. racemosa may have caused yellowish unhealthy fronds and later died-off.

Although, seawater temperature of tropical sea is relatively constant (Scrosati, 2001), C. racemosa population inhabited at the shallow subtidal with only 1-2 meters depth and may be influenced by an increase of in seawater temperature and greater irradiance in the dry season when the tide was out. The long term monitoring data set of 12 years showed that February has the minimum rainfall and April was the month with the warmest air temperature at over 30 ° C (Prince of Songkla University, 2000), such condition during dry season may have caused the 50% dropped of C. racemosa population as shown in the results. The decline of C. racemosa populations reported here, therefore, may be a result of a combination of an increased seawater temperature and greater irradiance.

Surprisingly, the C. racemosa population disappeared in July 2003 at the beginning of wet season. Although, there was already a record of population dropping in previous sampling, it seemed unlikely to result in the disappearance of such massive populations of C. racemosa unless biomass removal was alternatively the result of a typhoon or an endemic pathogen. However, there was no any catastrophic tropical weather event reported during this period. Incidentally, no changes in other marine algae and fauna were noticed at the site. In addition, Caulerpa spp. are known to contain secondary compounds such as caulerpin, caulerpicin and caulerpenyne, which are known to deter fishes and other potential marine predators (Hatta, 2001). These toxins help to maintain and make Caulerpa population stable and are very successful in favorable conditions in the Mediterranean Sea (Meinesz et al., 1995; Ceccherelli and Cinelli, 1999). Our observations did not indicate the presence of grazing activity.

Some studies have shown population Caulerpa decline and died-off after releasing gametes both in the field (Clifton, 1997; Clifton and Clifton, 1999) and in laboratory (Panayotidis and Zuljevic, 2001; de Senerpont Domis et al., 2003). In the field, C. racemosa was found releasing their gametes in the early morning after sunrise, however which environmental or biological factors triggering the onset of the sexual reproduction remain unknown (Clifton, 1997). When the conditions become favorable for sexual reproduction, fronds became fertile within 12 hours and it would take only short period of time for gametes releasing. As a result, Caulerpa population may disappear in a very short period of time; as short as 3 hours depending on wave motion and currents (Clifton and Clifton, 1999).

The disappearance of such an expansive population of C. racemosa in the same period of time is suggestive of sexual reporoduction and resulting decline of the population in this study. Caulerpa have been classified as a clonal organism (Collado-Vides, 2002) due to their siphonous fronds connection, thus the population may be influenced by the effects of an environmental conditions throughout the clonal mat (de Kroon and Schieving, 1990). They also could have the same set of genetic materials as they could reproduce and increase their population size by asexual reproduction or fragmentation, which already has reported to have resulted in successful population increases in the Mediterranean sea (Panayotidis and Zuljevic, 2001). Therefore, the populations of Caulerpa at Koh Kham likely originated from the same parents cell with similar ages, resulting in simultaneous fertility, gamete release, and die-off during the same period of time.

Recruitment and recovering of new population of C. racemosa should be found within a few months after sexual reproduction (Clifton and Clifton, 1999). However, after revisiting at the study sites several times for over a year after the disappearance of C. racemosa, there has been no recruitment and recovery of C. racemosa population. There were only a few patches of small C. racemosa observed in the rock cracks or coral cervices. The unsuccessful recruitment of sexually produced gametes of C. racemosa in the early rainy season, may have been a result of greater wave motion, as increasing wave motion would dilute gametes and decrease fertilization success (Gordon and Brawley, 2004. The vegetative reproduction and fragmentation, therefore, might be an adaptation of this tropical green alga to maintain its population.

This study was the first to report population dynamics and the disappearance of C. racemosa in the tropical shallow subtidal reef in Southeast Asia and Thailand. The incidence of sexual reproduction in this invasive species is still poorly known, thus further studies on what triggers the onset of sexual reproduction would be very useful. Also, this information would be very useful for understanding the population dynamics of this genus of highly invasive macroalgae.

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Appendix 2

Editorial Manager(tm) for Journal of Applied Phycology
Manuscript Draft

Manuscript Number:

Title: A comparison of the growth form of Porphyra vietnamensis Tanaka et Pham-Hoang Ho between sheltered and exposed shores in Songkhla province, Thailand

Article Type: Original Research

Section/Category:

Keywords: Porphyra vietnamensis; growth; morphological variation; wave action

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Manuscript Region of Origin:

Abstract: The growth form of the red alga, Porphyra vietnamensis Tanaka et Pham- Hoang Ho, was investigated to answer the following questions: Are there variations in length, width, biomass and shape of P. vietnamensis between sheltered and exposed habitats? And, if so, what physical and chemical factors such as wave action, nutrients, salinity, and temperature influence such differences? The Porphyra populations from Suansongtalay (sheltered) and Kaoseng (exposed) in Songkhla Province, Thailand were monitored for 2 years from December 2002 to February 2004. Length (mm), width (mm) and dry weight (mg) of P. vietnamensis varied between the sites ($P<0.05$). Similar patterns in length, width and biomass were found in both years. The highest dry weight, 37.5+2.1 mg, was found in February 2003 at the sheltered habitat and in January 2004, 37.3+3.9 mg, at exposed site. The lowest, 3.2+0.4 mg, was found in November 2003, at the sheltered site. The shape varied with respect to the degrees of exposure. The narrower and thinner blades were found at the sheltered site, while the shorter and wider blades were found at the exposed habitat.

There is evidence that splashing waves could remediate the effects of exposure on the establishment of Porphyra populations.

A comparison of the growth form of *Porphyra vietnamensis* Tanaka et Pham-Hoang Ho between sheltered and exposed shores in Songkhla province, Thailand

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Abstract

The growth form of the red alga, *Porphyra vietnamensis* Tanaka et Pham- Hoang Ho, was investigated to answer the following questions: Are there variations in length, width, biomass and shape of *P. vietnamensis* between sheltered and exposed habitats? And, if so, what physical and chemical factors such as wave action, nutrients, salinity, and temperature influence such differences? The *Porphyra* populations from Suansongtalay (sheltered) and Kaoseng (exposed) in Songkhla Province, Thailand were monitored for 2 years from December 2002 to February 2004. Length (mm), width (mm) and dry weight (mg) of *P. vietnamensis* varied between the sites ($P<0.05$). Similar patterns in length, width and biomass were found in both years. The highest dry weight, 37.5 ± 2.1 mg, was found in February 2003 at the sheltered habitat and in January 2004, 37.3 ± 3.9 mg, at exposed site. The lowest, 3.2 ± 0.4 mg, was found in November 2003, at the sheltered site. The shape varied with respect to the degrees of exposure. The narrower and thinner blades were found at the sheltered site, while the shorter and wider blades were found at the exposed habitat. There is evidence that splashing waves could remediate the effects of exposure on the establishment of *Porphyra* populations.

Key words: *Porphyra vietnamensis*, growth, morphological variation, wave action

Introduction

The red alga genus, *Porphyra*, popularly known as 'Nori' in Japan, 'Kim' in Korea and 'Zicai' in China, is an important economic seaweed because it is used as food. It contains high levels of protein (16.5% compared to 5.6% in Gracilaria salicornia, another common seaweed used as food); vitamins (430 IU g^{-1} d.wt beta-carotene compared with 15 IU g^{-1} d.wt in G. salicornia; higher vitamin C content than in oranges); trace minerals and dietary fibers (Noda, 1993; McDermid and Stuercke, 2003). Because of its economic importance and health benefits, *Porphyra* has been cultivated on a large scale in many countries such as Japan, Korea, and China.. In 1999, the combined production of *Porphyra* from these three countries was over 1,000,000 wet tonnes (FAO, 2003). Porphyra in Japan is a US$ 1.5 billion per year business (Ohno and Largo, 1998), at US$ 25 kg^{-1} (Lindsey Zemke-White and Ohno, 1999). Nearly 133 species of *Porphyra* have been reported worldwide (Sahoo et al., 2002) although only a few are cultivated commercially.

Porphyra vietnamensis Tanaka et Pham- Hoang Ho, one of the edible tropical seaweeds, is found on rocks in the upper littoral zone along the coasts of Northwest Pacific in Vietnam (Tanaka and Ho, 1962), China (Tseng, 1984) and Thailand (Lewmanomont and Ogawa, 1978) and also on the Indian Ocean coasts of India and Pakistan (Dhargalkar et al., 1981; Dinabandhu et al., 2007; Shameel and Aftab 1993). In Thailand, the algae are found along the coasts of Songkhla province (Ruangchuay and Notoya, 2003), Pattani and Narathiwas province (Lewmanomont and Chittpoolkusol, 1993). Many aspects of the life cycle and physiological responses of gametophytes and sporophytes (the conchocelis phase) of *P. vietnamensis* has been investigated (Lewmanomont and Chittpoolkusol, 1993; Ruangchuay and Notoya, 2003). However, little is known about its ecology. Such understanding would be useful and necessary for development of a mariculture program for *P. vietnamensis.*

Photoperiod, temperature, irradiance, salinity, and nutrients (nitrates and phosphates) are known to influence growth and reproduction of most species of *Porphyra* (Bird et al., 1972; Avila et al., 1986; Waaland et al., 1990; Notoya et al., 1993; Conitz et al., 2001; Orfanidis, 2001; Pereira et al., 2005). In *P. vietnamensis*, photoperiod and light intensity, however, are not the most important factors in contolling the life cycle but temperature and salinity are (Lewmanomont and Chittpoolkusol, 1993). Wave action is a crucial factor in the distribution and abundance of all intertidal organisms (Denny, 1995; Shaughnessy et al., 1996; Carrington, 2002). Moreover, it is known to limit the size of nearshore plants (Denny, 1999). Flexible organisms, like macroalgae, often experience lower drag than rigid organisms because their shape and size change as the velocity increases (Boller and Carrington, 2006). In calm water, the fronds can reach larger sizes than in extreme water velocity (Denny and Wethey, 2000; Boller and Carrington, 2006).

In this study we explored the following questions: 1.Are variations in length, width, biomass and shape of *P. vietnamensis* correlated with sheltered (Suansongtalay) and exposed (Kaoseng) habitats? 2. If so, what physical and chemical factors, such as wave exposure, nutrients, salinity, and temperature, influence such differences?

Materials and Methods

Porphyra vietnamensis grows on rocks in the upper littoral zone exposed to strong wave action. It seems to grow best fully exposed, moistened by the spray of the waves. The gametophyte blade of *P. vietnamensis*, appears in the months of November to February during the monsoon season. During this period water temperature decreases from 27-30°C to 24-27°C, salinity from 31-33%o to 18-26%o sometimes to 11%o. The light period in Songkhla during October to February is close to 12 hours, about 2-18 minutes shorter than the rest of the year. Photoperiod, therefore, does not vary much for the whole year in Songkhla province, Thailand (Lewmanomont and Chitpoolkusol, 1993). The sporophyte of *P. vietnamensis* appears on shells in the months of March to October during the dry season (Lewmanomont and Ogawa, 1978).

Suansongthalay (7°13’48’’N, 100°34’48’’E) and Kaoseng (7°10’57’’N, 100°37’22’’E) , Songkhla province, Southern Thailand were selected for this study due to the abundance of *P. vietnamensis* during the November to March period, which is a rainy season in the Gulf of Thailand (Fig. 1). The temperature and salinity ranges dropped from 28-31 °C and 8.17-30 %o respective. At Kaoseng, the site is exposed, facing toward the ocean and has a splash zone while at Suansongtalay, the site is sheltered by breakwater. The water velocity was measured at high tide in May, using MINI Current Meter model SD-6000 (Sensordata, Norway).

The *P. vietnamensis* populations were monitored for 2 years from December 2002 to February 2004. Fifty gametophyte thalli were collected randomly from both sites on 15 December 2002, 5 February 2003, 22 November 2003, 17 January and 29 February 2004. A total of five hundred thalli were gently removed and preserved in 4% seawater formalin for measurement in the laboratory. Length (mm) width (mm) and dry weight (mg) of each thallus were measured using the electronic caliper PD-151 (Pro'sKit, Taiwan) and electronic balance JP-3000 W (Chyo, Japan), respectively. Physical parameters such as salinity and temperature were recorded at each site. Phosphates and nitrates were provided by NICA (National Institute of Coastal Aquaculture), Songkhla. Wind speed and direction data were provided by Thai Meteorological Department.

Statistical analysis

Analysis of variance (ANOVA) was employed to test the effect of sites and times of collection on length, width and dry weight of Porphyra, PO_4, NO_3, seawater temperature and salinity. If necessary, data were transformed to meet the assumptions of the parametric test. Multiple comparisons were made following Zar (1984). Statistical results were presented based on the transformed analyses, but for clarity graphical output was based on the untransformed means. SPSS Version 15.0 was used for all analyses.

Results

Physical parameters

There were no significant differences in water temperature, salinity, nitrates and phosphates between the two sites ($P>0.05$). The average water temperature, salinity, nitrates and phosphates at both sites were 29.83$\pm$0.33 °C, 26.71$\pm$2.11‰, 0.0668$\pm$0.0107 mg/l, and 0.0145$\pm$0.0022 mg/l, respectively. Linear regressions of all parameters showed that there was no relationship between these factors on length, width, and dry weight of *P. vietnamensis* (Table 1). However, the average water motion at the exposed shore was higher than at the sheltered shore. Water splashing was also greater. The water velocity at Kaoseng was 3 times greater than at Suansongtalay, 0.106 ± 0.016 ms^{-1} and 0.034 ± 0.007 ms^{-1}, respectively. In addition, greater wave motion and water velocity are expected during the monsoon season and is on average 3.98 knots, compared to only 1.98 knots in dry season.

Growth and Shape of *P. vietnamensis*

Length (mm), width (mm) and dry weight (mg) of *P. vietnamensis* varied between sites ($p<0.05$) (Table 1, 2). The largest fronds at 37.5 ± 2.1 mg were found in February 2003 at the sheltered shore and 37.3 ± 3.9 mg in January 2004 at the exposed shore, while the lowest was found in November 2003, at 3.2 ± 0.4 mg at sheltered site (Table 2). In February 2004, *Porphyra* thalli were not found at Suansongtalay, the sheltered area (Table 2).

The shape of *P. vietnamensis* varied between sites and among the times of sampling. The thalli at exposed site, were shorter and wider than at the sheltered site. At both sites the blades were narrow and thin during the early sampling period (November and December), and wider and thicker at late sampling period (January and February) (Fig. 2).

Discussion

Life cycle

Porphyra vietnamensis gametophyte thalli were present on rocks at Kaoseng and Suansongtalay in the months of November to February, the rainy, coolest time of the year, as also reported by Lewmanomont and Ogawa (1978) and Ruangchuay and Notoya (2007). The smallest fronds of *P. vietnamensis* were found in November which is the first period of its development while the largest were found in the later period, January and February. During March to October, the conchocelis stage, the sporophyte, was found on the underside of shells. Temperature and salinity are known to be the major environmental factors inducing conchospore release of *P. vietnamensis* in Songkhla Province (Lewmanomont and Chittpoolkusol, 1993). Oyster shells and barnacles were collected from both sites; and the filamentous conchocelis phase was observed and then gametophytes later.

The heteromorphic life cycle of *Porphyra* is unique and complex. The gametophyte and sporophyte phases of *P. vietnamensis* develop at different times of the year. The different phenotypes have advantages by being able to inhabit different ecological niches which, besides other factors, may have different grazing pressures (Taylor and Hay, 1984; Thornber, 2006). Many species have complex life histories as for example, the brown algae, *Lessonia nigrescens*, *Macrocystis pyrifera*, and *Ecklonia radiata*; the brown crust *Ralfsia californica*; and the green alga Acrosiphonia spp (Dethier, 1981; Martinez and Santelices, 1998; Sussmann and DeWreede, 2001; Nelson and Schwarz, 2005). The heteromorphic life cycle of *P. vietnamensis* is useful in promoting cultivation because the conchochelis phase can be kept conveniently in small spaces as stock before putting it out into the larger scale cultivation of the marketable gamemtophyte.

Porphyra thalli at Suansongtalay, the more sheltered and less water-splashed area, disappeared earlier than at Kaoseng. The water splashing decreases desiccation, which increases in late February. In this study the higher temperature in February during 2004 could have caused greater desiccation and die off of gametophyte. Desiccation is known to limit the distribution and life span of many intertidal organisms including seaweeds (Tomanek and Helmuth, 2002)

Wave motion

The shape of *P. vietnamensis* differed at the two sites. The shorter and wider blades were found in exposed area, while the narrower and thinner blades were found at sheltered area. The adaptation of *Porphyra* might give an advantage for survival in the wave-swept rocky intertidal zone. This pattern is found in many marine algae such as *Chondrus crispus*, *Codium fragile*, *Mastocarpus papillatus*, and *Turbinaria ornata* (Kitzes and Denny, 2005; Boller and Carrington, 2006; Prathep et. al, 2006; D'Amours and Scheibling, 2007). However, the size of seaweed is influenced by other physiological and ecological factors, i.e. reproduction, photosynthesis, nutrient uptake and competition. Large macroalgae have more competitive and reproductive advantages than small macroalgae (Dudgeon and Johnson, 1992; Gaylord et al., 1994; Blanchette et al., 2002; D'Amours and Scheibling, 2007). Thus, variation in morphology could be a trade-off between the dislodgement of blade and these factors. Our study shows that wave action plays an important role in establishing the phenotype of *Porphyra* populations.

Cultivation

In 1978, Lewmanomont and Ogawa reported that *Porphyra* in Thailand was harvested and sold on a small scale at US$6 to 15 kg^{-1}, depending on the quality. An attempt to cultivate *Porphyra* at Kaoseng; was made in 1978. However, it was not successful due to the high water velocity. We suggest that *P. vietnamensis* cultivation should be promoted in Thailand, Vietnam, South East Asia and South Asia, since the of life cycle, biology and ecology of *P. vietnamensis* are now better understood. In addition, there are many techniques and technologies which have been used in the cultivation of *P. yezoensis*, *P. haitanensis* and *P. tenera* with great success in East Asia (Ayano et al., 1998; Han, 2006; Cultured Aquatic Species Information Programme, 2007; Monterey Bay Aquarium Research Institute, 2007).

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Figure 1. Study sites of *Porphyra vietnamensis* at Kaoseng and Suansongtalay, Songkhla, Thailand.

Figure 2. Blade shape of *Porphyra vietnamensis* Tanaka et Pham-Hoang Ho at November 2003 – December 2006 at exposed and shelted area. Site a: Kaoseng (exposed area), site b: Suansongtalay (sheltered area), I=Dec 02, II=Feb 03, III=Nov 03, IV=Jan 04, V-VIII= Jan 07.

Figure_1
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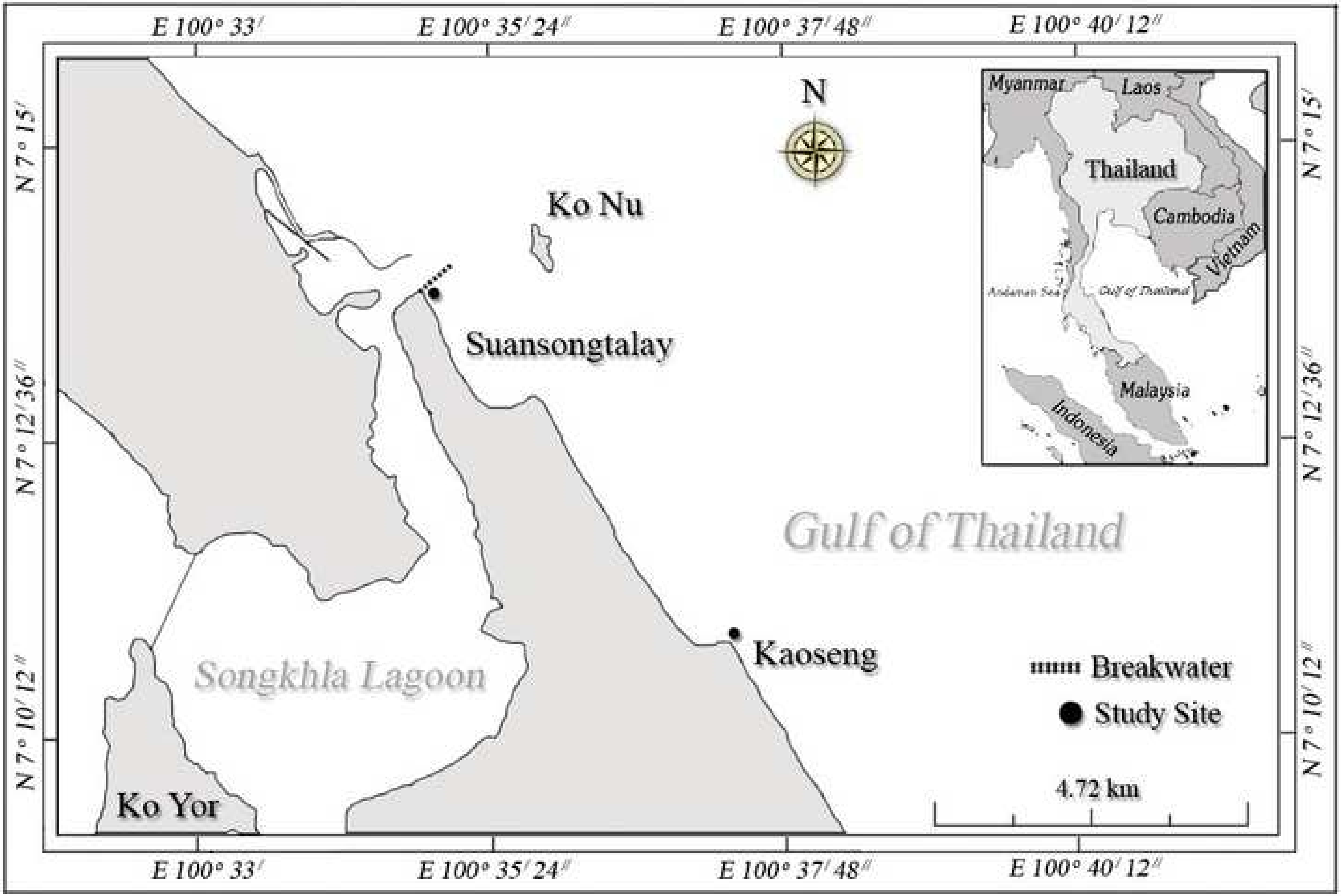

Figure_2
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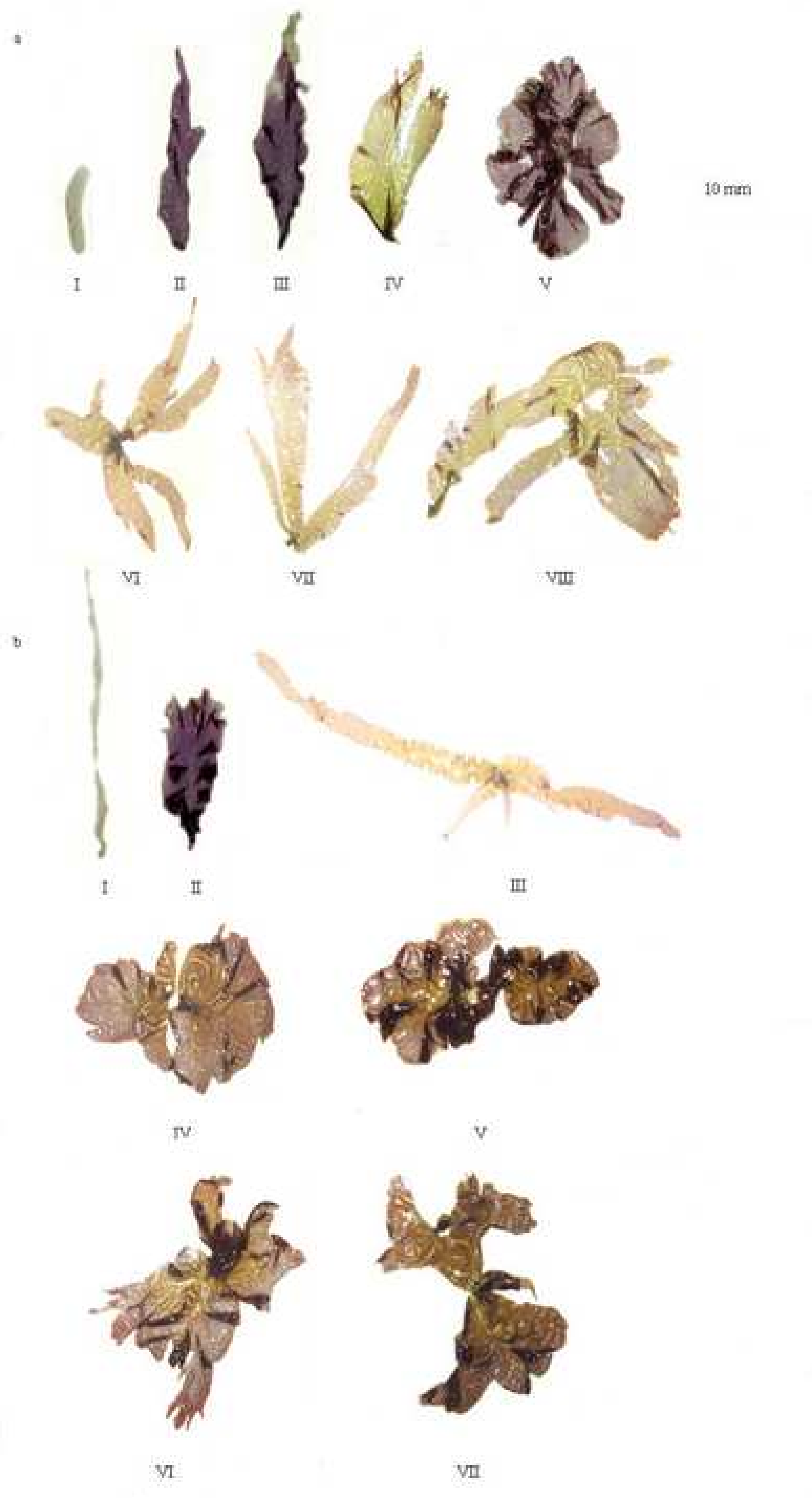

	N	Sheltered area	Exposed area	P	Temperature (°C)		Salinity (ppt)		Nitrate (mg/l)		Phosphate (mg/l)	
		Mean±SE	Mean±SE		R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*
Length (cm)	320	39.55±2.19	29.12±1.42	0.00	0.217	0.174	0.372	0.061	0.004	0.862	0.007	0.815
Width (cm)	150	5.8±0.34	9.9±0.78	0.00	0.125	0.316	0.129	0.308	0.001	0.918	0.016	0.729
Dry weight (mg)	320	17.4±1.4	24.4±2.8	0.00	0.043	0.566	0.005	0.85	0.022	0.682	0.508	0.021

	N	Sheltered area					Exposed area				
		Dec-02	Feb-03	Nov-03	Jan-04	Feb-04	Dec-02	Feb-03	Nov-03	Jan-04	Feb-04
		Mean±SE					Mean±SE				
Length (mm)	320	60.54±3.86	44.88±1.89	62.57±3.06	30.30±2.16	x	30.32±1.38	27.94±0.89	26.23±1.52	32.08±1.47	29.04±1.81
Width (mm)	150	-	-	4.92±0.26	24.1±1.46	x	-	-	12.74±0.85	20.48±2.04	16.33±0.99
Dry weight (mg)	320	17.8±1.6	37.5±2.1	3.2±0.4	28.5±2.8	x	23.6±2.2	26.6±2.6	13.9±1.5	37.3±3.9	20.6±3.8

Appendix 3

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Manuscript Draft

Manuscript Number:

Title: Effects of wave exposure on population and reproductive phenology of an algal turf, Gelidium pusillum (Gelidales, Rhodophyta), Songkhla, Thailand

Article Type: Research Paper

Section/Category:

Keywords: algal turf; Gelidium pusillum; life phase; population; Thailand; wave exposure

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First Author: Anchana Prathep, Ph.D.

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Manuscript Region of Origin:

Abstract:

Suggested Reviewers: Robert DeWreede Ph.D.
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He has been working on the life history and ecology of this group for sometime. He has a lot of publications in this kind of research.

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Opposed Reviewers:

TITLE: Effects of wave exposure on population and reproductive phenology of an algal turf, *Gelidium pusillum* (Gelidales, Rhodophyta), Songkhla, Thailand

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Abstract

The effect of wave exposure on the population and reproductive phenology of the common red alga, *Gelidium pusillum* (Stackhouse) le Jolis, was investigated between July 2003 and June 2004, at Suan Song Tha Le, Songkla Province, Thailand. Lengths of thalli, percentage cover, percentage of reproductive fronds and the number of reproductive structures were examined monthly in relation to different degrees of wave exposure (sheltered vs exposed), temperature and rainfall. Frond length and percentage cover of *G. pusillum* were different among sites and seasons. Shorter fronds were found on the exposed shore which had a greater percentage cover. Fronds bleached and died off during the summer months (April and May), which resulted in shorter fronds and reduced percentage cover in June. The thalli reproduced throughout the year, with a predominance of tetrasporophytes. The highest percentage of tetrasporophytic fronds was 33% in February 2004 and 13.33% of cystocarpic fronds in April 2004, but male gametophytic fronds were never observed. Rainfall showed a strongly negative influence on

reproduction since no reproductive fronds were observed during the rainy season (R^2 =0.49, P<0.01). The dominance of *Gelidium pusillum* at this study site and throughout the world might be a function of persistent vegetative growth which forms dense clumps of turf and its ability to reproduce almost throughout the entire year.

Key words: algal turf; *Gelidium pusillum*; life phase; population; Thailand; wave exposure

Introduction

Exposure to wave action is generally considered to be an important factor in the distribution and abundance of intertidal organisms (Lewis, 1964; Stephenson and Stephenson, 1972; Denny, 1998). It is also well known to influence size, morphology and distribution patterns. Organisms on wave swept shores are often much smaller than those in more wave protected habitats (Lewis, 1968; Menge, 1976; Blanchetter, 1997, Prathep et al., 2007). Wave exposure also influences the community structure via water motion (Lobban and Harrison, 1994). Propagule dispersal, fertilization, settlement and recruitment (Vadas et al., 1990; Serra˜o et al., 1996) are all affected. Recent studies on the red alga, *Mazzaella oregona (*Mudge and Scrosati, 2003) have shown an inverse relationship between G:T (gametophyte:tetrasporophyte) ratio and the degree of wave exposure although this is not the case in *M. parksii* (Scrosati and Mudge, 2004).

The taxonomy of red algae is based on the nature of reproductive structures and details of life histories. In the family Gelidiaceae (Order Gelidiales) gametophytes and tetrasporophytes are isomorphic. Various investigators have reported that tetrasporophytic fronds predominate over gametophytic fronds in natural populations

(Akatsuka, 1986; Santelices, 1988; Santos and Duarte,1996). *Gelidium pusillum* (Stackhouse) le Jolis has a very wide geographic range throughout UK, Europe, Chile and Australia (Dixon and Irvine, 1977; Santelices, 1988; Rueness and Fredriksen, 1998; Millar and Freshwater, 2005). It is an intertidal turf-forming alga with a stoloniferous growth form. The clump erect fronds could be more influenced by seasons, due to the increased degree of exposure, desiccation at the upper shore level as well as grazing pressure (Dixon and Irvine, 1977; Santelices, 1988). Intensive studies have been carried out on *G. sesquipedale* (Clem.) Born. et Thur. because of its economic value as an agarophyte (Santos, 1994; 1995; Santos and Duarte, 1996; Santos and Nyman, 1998). However, very little research has been done on *G. pusillum.*

In this study we examined 1) the effects of wave exposure, temperature and rainfall on percentage cover, length of thalli, life phase and degree of reproduction on populations of *G. pusillum* and 2) its reproductive phenology throughout the year.

Materials and Methods

Preliminary observations revealed that *G. pusillum* is a dominant red alga on many intertidal shores in Southern Thailand, it can form a vast area of monospecific stand. In Songkhla province, at Suan Song Tha Le (7°13´N, 100°34 ´W), a high abundance of *G. pusillum* was found over a 1 km long artificial rocky wall, on the intertidal rage between 0.4-1.5 m. *G. pusillum* is directly exposed to the wave motion which is especially high during the monsoon season (October-March). Sheltered area, thallus does not directly face the ocean and therefore are less exposed to wave splashes. The water velocity was measured at high tide in May, using MINI Current Meter model SD-6000 (Sensordata, Norway). The water velocity at the exposed site was 2 times greater than at sheltered, 0.034±0.007 ms^{-1} 0.016±0.006 ms^{-1} and, respectively.

Each month between July 2003 and June 2004, three hundred fronds were sampled from ten 50 cm X 50 cm quadrats on both the sheltered and exposed areas of the rocky wall. Fifteen fronds from each quadrat were measured for length and examined for reproductive status. Razor blade cross sections were stained using 1% aniline blue and examined for spermatangia, cystocarps and tetrasporic sori (Fredriksen et al., 1994).

Temperature and rainfall were monitored to test for whether there was any correlation with percentage cover, length of thalli, percentage of reproductive fronds and number of different reproductive phases. Physical parameters were provided by Thai Meteorological Department and NICA (National Institute of Coastal Aquaculture), Songkhla.

Two way ANOVA was employed to test the differences in percentage cover, length of thalli, life phase and numbers of each reproductive phase among sites and seasons using STATISTICA, version 5.0. When necessary, data were transformed to meet the assumptions of the parametric test. Multiple comparisons were made following Zar (1984) when there were significant differences between treatments. Statistical results are presented based on the transformed analyses, but for clarity, graphical output was based on the untransformed means. Regression analysis was employed to assess the relationship between temperature and rainfall on percentage cover, length, percentage of reproductive fronds, life phase and number of each reproductive phase.

Results

There were variations in length of *G. pusillum* frond among sites and time of year ($F_{2,18}$ =15.30, $P < 0.05$). Specimens from the sheltered shore were taller than those on the exposed shore (Fig. 1a). The average longest frond was 1.04 ± .03 cm (mean ± S.E.) on the sheltered shore during July 2003. On the exposed shore the average shortest frond was 0.6 ± .01 cm during May 2004 ($F_{2,18}$ =7.52, P<0.05). Many bleached tips in late April and beginning of May were observed.

There were variations in percentage cover of *G. pusillum* both among sites and time of year ($F_{2,18}$=5.02, $P < 0.05$). The highest percentage cover was 82.8± 2.3 (Mean ± S.E.) during July 2003 on the exposed area (Fig. 1b). Significant greater percentage cover of *G. pusillum* was found on the exposed area throughout the study ($F_{2,18}$ =99.86, $P < 0.001$). The lowest percentage cover was 39.7±6.06 in October on the exposed shore; and the lowest percentage cover of the sheltered shore was 7.8± 2.49 in June 2004, after the bleaching phenomenon observed.

Seasonal variation in percentage of reproduction was striking. *G. pusillum* reproduced throughout the year, except for November and December 2003, the beginning of the rainy season (Fig. 2a). Both tetraspores and carpospores were observed, but spermatangia were never found in this study. There was greater percentage of tetrasporophytic plants in this population. For example, more than 33% of tetrasporophytic plants were found in July 2003 and Febuary 2004. But also only a few cystocarpic plants were found.

There were variations in number of tetrasporic sori of *G. pusillum* among sites and months ($F_{2,18}$ =4.49, $P < 0.001$). In general the thalli produced great numbers of tetraspores. The highest number of tetrasporic sori was 31.91 ± 6.01 sori /frond in January 2004, however, as mentioned above, there were no reproductive fronds in

November and December 2003, (Fig. 2b). There were variations of number of cystocarpic specimens among sites and months ($F_{2,18}$ =22.97, $P < 0.001$). The highest number was 3.52 ± 0.089 cystrocarps/ frond in April 2004 at the exposed shore site (Fig. 2c). This suggests that there were male gametophytes in the previous months.

Percentage cover and length of *G. pusillum* were not significantly influenced by temperature or rainfall (Table 1). However, increased temperature during summer months could decrease the frond length and some bleaching was observed. The bleached fronds later died off and washed away during the rainy season. Then, the percentage coverage declined.

Reproduction and the number of reproductive structures were significantly influenced by temperature and rainfall (Table 1). High temperature not only stressed reproduction but also caused the plants to die off. However, an increase in temperature was correlated with a fewer cystrocarphytic fronds (Fig. 3). Rainfall, caused a decrease in salinity to <10 psu during the rainy season. This low salinity is also correlated with low reproduction as expressed in percentage of reproductive fronds (Fig. 4). No reproductive fronds were observed during the mid-rainy season in November-December 2003.

DISCUSSION

The presence of a greater number of tetrasporophytic fronds than cystocarpic fronds, and only a few male or female gametophytic fronds was common in *G. pusillum*. This conforms to the reports for the family Gelidaceae (Akatsuka, 1986; Santelices, 1988; Servie`re-Zaragoza and Scrosati, 2002). However in the closely related order, Gigartinales, gametophytes are the dominant life phase (DeWreede and Green, 1990; Hommersand et al., 1993; Scrosati et al., 1994). In this study the number of cystrocarps was influenced by wave exposure. The cystocarps observed were on thalli from the exposed area just after the rainy season, a situation that might be caused by the greater water motion which could increase the success of fertilization by enhancing the ability of the nonmotile spermatia to encounter the trichogyne of the carpogonium.

Plants reproduced throughout the year, a condition which, together with the vegetative reproduction, accounts for the great percentage cover of this species in the study sites. The dense stand of algal-forming turf can persists under high stress along the intertidal shore (Hay, 1981; Guiry and Womersley, 1993). Since fronds could grow into 2 directions both as creeping axes and as uprights, the former withstands the high wave motion and provides as base for the shorter upright axes such as were found in the wave-exposed area. Although, this species is known as a perennial plant, the upright fronds bleached during summer months, when the apical tips became weak, the fronds became shorter and died, decreasing the coverage of the plants two months shortly after. This is similar to the pattern of many other turf forming red algae (Beach and Smith, 1996; Scorsati and DeWreede, 1998).

The onset of tetraspore and carpospore production did not reflect a physiological trade-off between resource allocation to vegetative growth and allocation to reproduction as suggested by Harper and Ogden (1970). *G. pusillum* reproduced spores throughout the year, except in November and December, without any decline of length, density or die off. Although known to be perennial, reproduction was not reduced as hypothesized (Bell 1984a) by the idea that plants reduce allocation to individual growth or general maintenance (Bell, 1984b; Obeso, 2002) in favor of reproductive cell formation or vice versa. It is possible that resources at the site exceed the requirements. Nutrient levels were high throughout the year. The highest was found during the rainy season, NO_3^{-1} was 0.12 mg/l and PO_4^{-3} was 0.024 mg/l. High concentrations of nutrients from urban runoff as well as from agriculture and aquaculture around the basin (Panapitukkul et al., 2005; Chevakidagarn, 2006) are well-known.

The rainfall, which decreased the salinity, might be expected to inhibit reproduction. Although increased temperature caused bleaching and later die off, the decline of reproduction might be due to lower salinity, which was < 10 psu at the site during the rainy season. The salinity stress lower than 15 psu was reported to reduce growth rate to almost 5 times in some *Gelidium* spp. (Oliger and Santelices, 1981).This is known to cause a decrease in productivity and reproduction in many red algae and now in *G. pulsillum* as well.

There were no shifts of life phase between seasons and sites in *G. pusillum* as has been observed in *Mazzaella* spp. (Mudge and Scrosati, 2003; Scrosati and Mudge, 2004). A predominance of tetrasporophytes is a common feature in *Gelidium* (Montalva and Santelices, 1981; Carter, 1985; Akatsuka, 1986; Macler and West, 1987; Santelices, 1990; Melo and Neushul, 1993; Sosa et al., 1993). Carmona and Santos (2006) have recently tested the advantages of tetrasporophytes over the gametophytes in *G. sesquipedale* through their ecophysiological performance. They found that there were no significant differences either in the photosynthesis rate, nitrogen uptake, nitrate reductase activity, or biochemical composition of phases, but there was an advantage in vegetative recruitment and spore production. The dominance of tetrasporophytes of *G. sesquipedale* cannot be explained but it does reflect the nature of the success of this turf-forming alga throughout the world.

The G:T ratio of *G. pulsillum* in our study was 1:14; the G:T ratio in *Geliduim* may be as high as 1:20. Abbott (1980) suggested that this might be because of the failure in the viability of tetraspores, which are the sources of gametophytes and/or the enhanced capability of carpospores to produce tetrasporophytes. Although, we found some mature red tetraspores and carpospores in our study, newly recruited plants were rarely observed. After release spores could be washed away or trapped within the turf, which form new thalli within the patch. Further investigation of spore settlement, recruitment and development both in laboratory and field would allow us to have a better understanding of the population structure and its maintenance in what appears to be a unique red algal species.

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Table 1. Summarize of length, percentage cover, percentage of reproductive fronds and number of reproductive organs of *G. pulsillum* at the sheltered and exposed areas; and its relations to temperature and rainfall during July 2003-June 2004 at Songkhla province, Thailand.

		Sheltered area	Exposed area	Temperature (•C)		Rainfall (mm)	
	N	Mean ± S.E.	Mean ±S.E.	R^2	*P*	R^2	*P*
Length (cm)	1800	0.759±0.007	0.736±0.005	0.18	0.52	0.001	0.85
% cover	150	35.14±1.65	63.01±1.87	0.07	0.22	0.10	0.131
% Reproductive fronds	12	15.66±3.22	15.88±4.81	0.22	0.13	0.49	<0.01
% Tetrasporic frond	12	14.61±3.01	12.92±4.04	0.08	0.18	0.36	<0.001
% Cystrocarpic frond	12	1.05±0.44	2.97±2.01	0.18	<0.05	0.05	0.31
No. of tertrasporic sori/ frond	1800	7.38±0.06	9.62±0.96	0.07	0.23	0.27	<0.001
No. of cystocarps/frond	1800	0.06±0.02	0.36±0.08	0.16	0.05	0.03	0.38

Figure_captions

Fig. 1 *Gelidium pusillum* population. Effects of wave exposure on length (1a) and % coverage (1b) throughout the year .

Fig. 2 *Gelidium pusillum* population. Effects of wave exposure on % reproduction (2a), No. of tetrasporic sori/ frond (2b) and No. of cystrocarps/ frond (2c) throughout the year.

Fig.3 Significant correlation between temperature and % cystrocarphytic frond and No. of cystrocarps/ frond of *Gelidium pusillum*.

Fig.4 Significant correlation between rainfall and % reproductive fronds, % tertasporophytic fronds and No. of tetrasporic sori/ frond of *Gelidium pusillum.*

Figure1

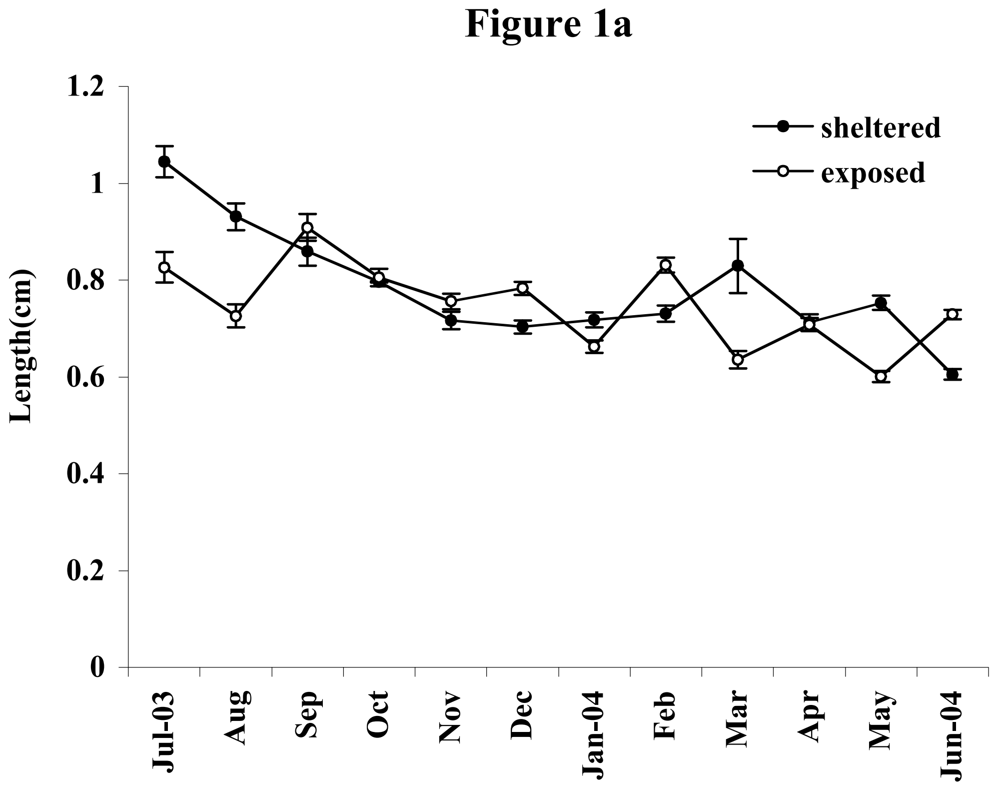


Figure 1a
Length(cm)
1.2
1
0.8
0.6
0.4
0.2
0
sheltered
exposed
Jul-03
Aug
Sep
Oct
Nov
Dec
Jan-04
Feb
Mar
Apr
May
Jun-04

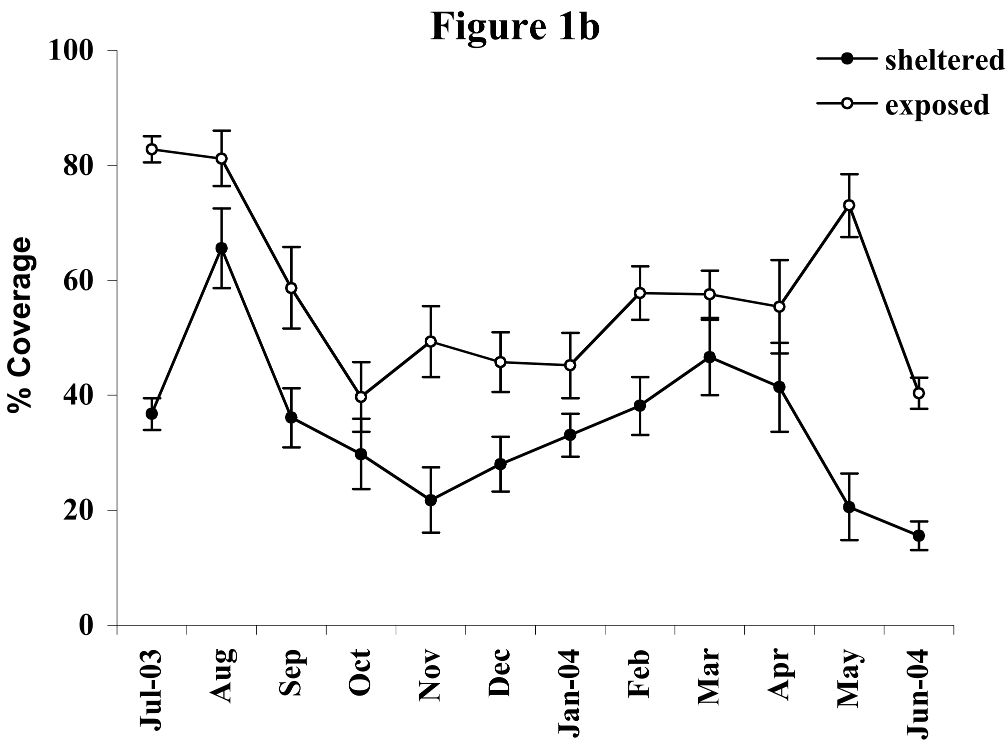


Figure 1b
% Coverage
100
80
60
40
20
0
sheltered
exposed
Jul-03
Aug
Sep
Oct
Nov
Dec
Jan-04
Feb
Mar
Apr
May
Jun-04

Figure2

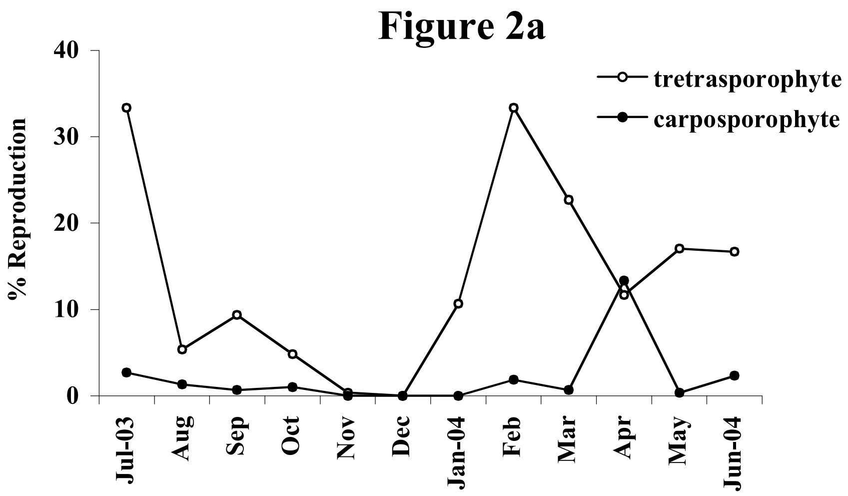


Figure 2a
40
30
20
10
0
% Reproduction
tretrasporophyte
carposporophyte
Jul-03
Aug
Sep
Oct
Nov
Dec
Jan-04
Feb
Mar
Apr
May
Jun-04

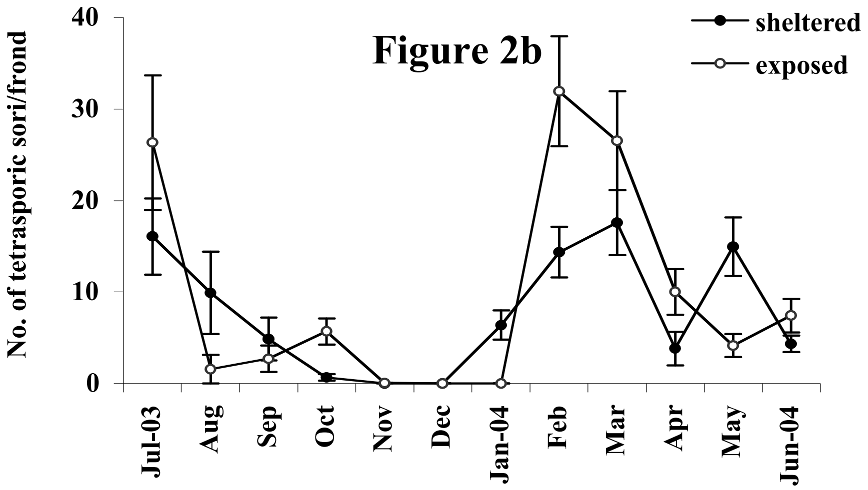


Figure 2b
40
30
20
10
0
No. of tetrasporic sori/frond
sheltered
exposed
Jul-03
Aug
Sep
Oct
Nov
Dec
Jan-04
Feb
Mar
Apr
May
Jun-04

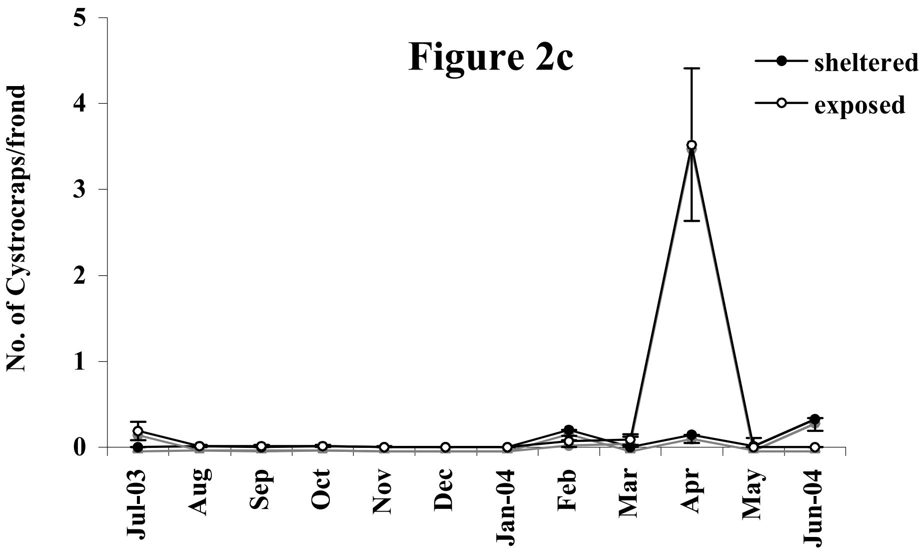
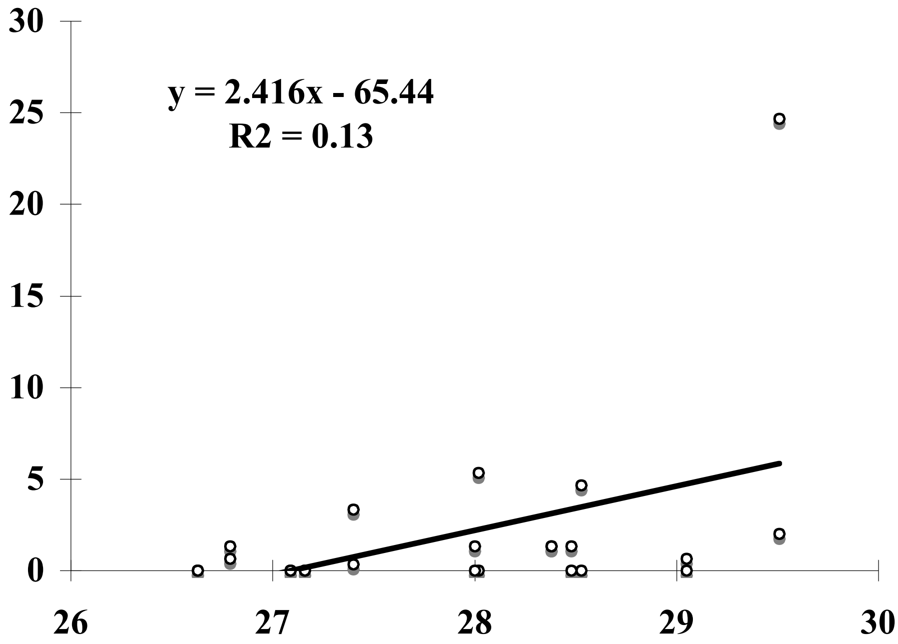


Figure 2c
5
4
3
2
1
0
No. of Cystrocraps/frond
sheltered
exposed
Jul-03
Aug
Sep
Oct
Nov
Dec
Jan-04
Feb
Mar
Apr
May
Jun-04

Figure3


y = 2.416x - 65.44
R2 = 0.13
30
25
20
15
10
5
0
26
27
28
29
30

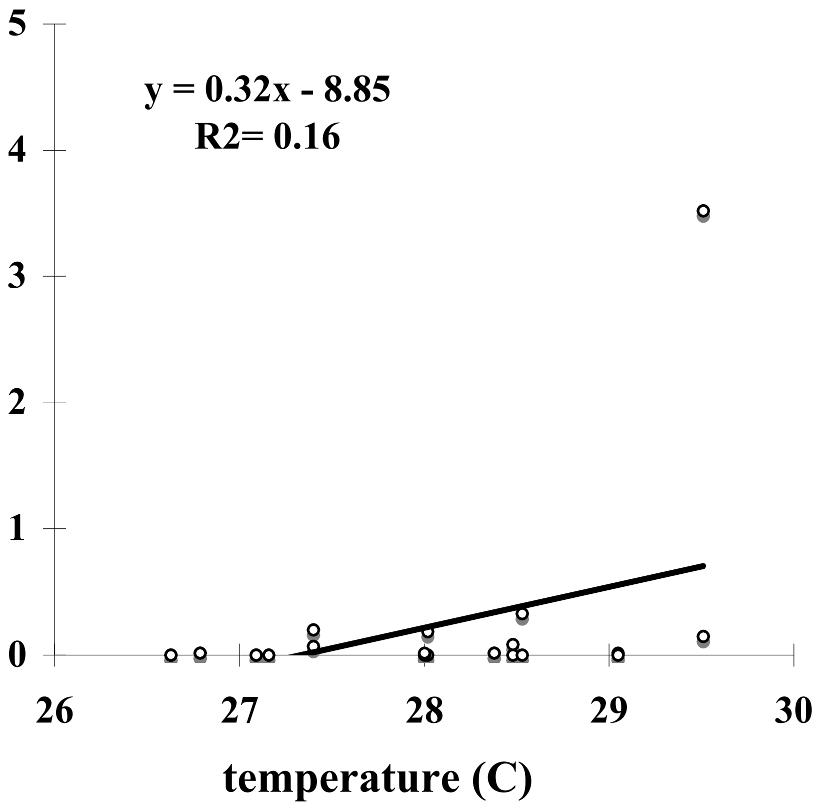
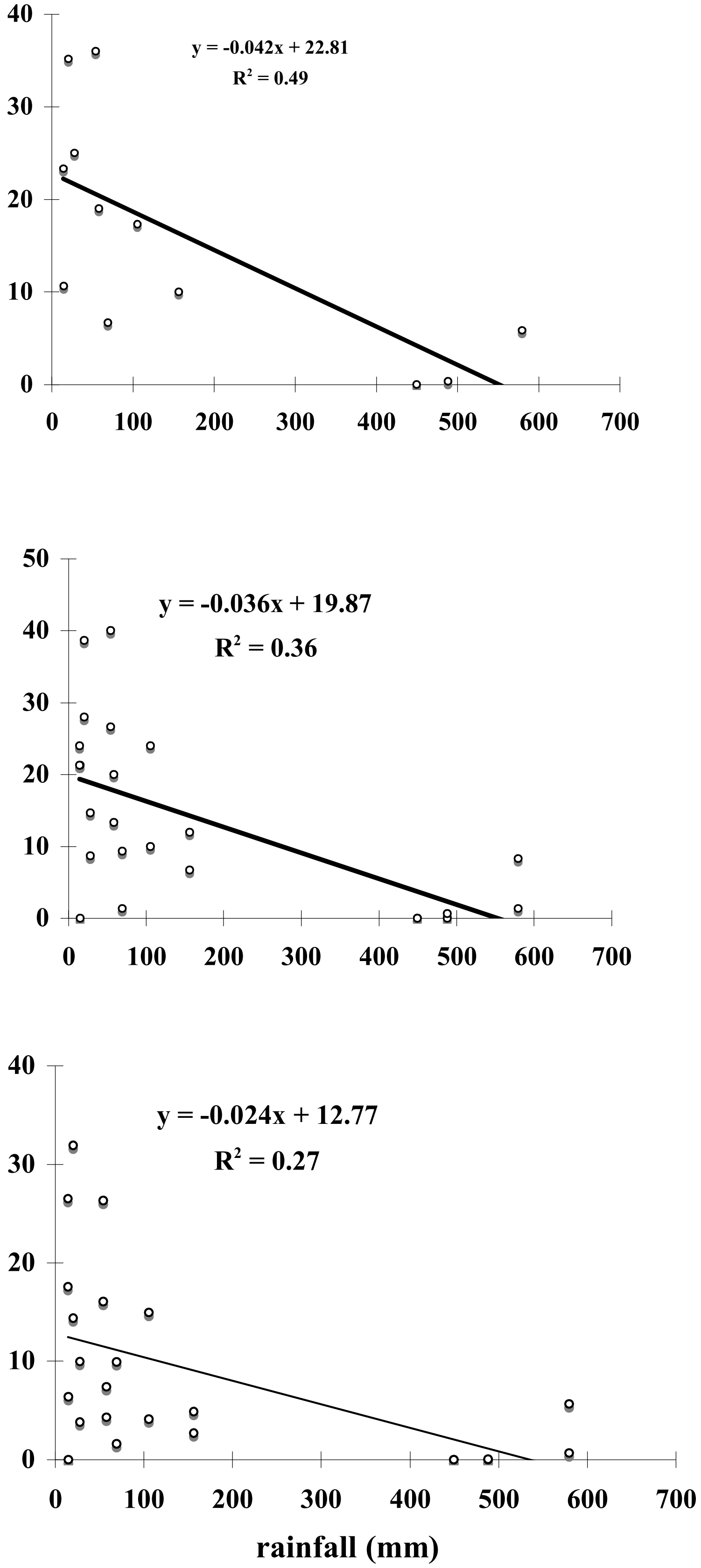

y = 0.32x - 8.85
R2= 0.16
5
4
3
2
1
0
26
27
28
29
30
temperature (C)

Figure4



y = -0.042x + 22.81
R^2 = 0.49
40
30
20
10
0
0 100 200 300 400 500 600 700
y = -0.036x + 19.87
R^2 = 0.36
50
40
30
20
10
0
0 100 200 300 400 500 600 700
y = -0.024x + 12.77
R^2 = 0.27
40
30
20
10
0
0 100 200 300 400 500 600 700
rainfall (mm)