Tropical Natural History 24 (2024): 128-136

Changes in *Tetragnatha* Spider Abundance and Web Characteristics Throughout Rice Field Development

VENUS SAKSONGMUANG[1], BOOPPA PETCHARAD[2] AND SARA BUMRUNGSRI[1*]

[1] *Department of Biology, Faculty of Science, Prince of Songkla University, Songkhla 90110, THAILAND*
[2] *Department of Biotechnology, Faculty of Science and Technology, Thammasat University, Pathum Thani Province, 90112, THAILAND*
[*]Corresponding author. Sara Bumrungsri (*sarabumrungsri@gmail.com; sara.b@psu.ac.th*)
Received: 4 October 2023; Accepted: 19 March 2024

ABSTRACT. – Vegetation change is one of the major drivers affecting web-building spider species, causing them to vary in abundance and to adapt their web traits accordingly. Rice ecosystems are among the most important agricultural areas, and understanding the influence of vegetation complexity throughout rice development on common *Tetragnatha* spiders is crucial to developing sustainable management practices. Six sympatric species of *Tetragnatha* spiders, *T. javana, T. mandibulata, T. maxillosa, T. nitens, T. praedonia* and *T. virescens,* were found in rainfed lowland rice fields in southern Thailand. The abundance, web diameter and web height of each species were measured and compared across rice developmental stages. Overall, the number of *Tetragnatha* spiders was significantly higher in the tillering stage than the flowering stage, while abundance during the booting stage was not significantly different from either. The numbers of *T. javana, T. mandibulata* and *T. maxillosa* were higher than those of *T. nitens, T. praedonia,* and *T. virescens* during all rice stages. Throughout the rice growing season, vegetation complexity increased continuously while both web diameter and web height exhibited hump-shaped patterns for all spider species (i.e., webs were larger and built higher above ground level during the middle of the growing season). The diameter and height of *Tetragnatha* webs varied by species, but only web diameter was positively related to spider body length for almost all spider species. Our findings confirm that changes in vegetation complexity during rice development, as well as spider body length, affect the functional traits of *Tetragnatha* webs in rice ecosystems.

KEYWORDS: rice stage, *Tetragnatha* spider, vegetation complexity, web trait

INTRODUCTION

Web-building spiders are common generalist predators in agricultural ecosystems. They are highly diverse in agroecosystems and help limit prey populations, including those of insect pests (Takada et al. 2013; Michalko et al. 2019). For example, previous studies have reported that spiders were the main predators of lepidopteran and coleopteran pests (Tahir et al. 2009; Mishra et al. 2020). Additionally, they also trap small insect pests, such as thrips, planthoppers, and aphids (Kiritani et al. 1972; Landis et al. 2000). Therefore, many researchers have demonstrated the role of web-building spiders as important biological control agents for regulating insect pest populations, especially in rice ecosystems (Ludy, 2007; Tahir et al. 2009; Mishra et al. 2020).

Rice ecosystems are temporary wetlands that host high biodiversity (Lawler, 2001; Bambaradeniya et al., 2004; Leitão et al. 2007) and support complex interactions among multiple species, which help to suppress rice pests and thus enhance rice production (Settle et al., 1996; Altieri, 1999; Macfadyen et al., 2015). Vegetation complexity in rice ecosystems changes markedly during the growing season, which can affect spider abundance and composition (Bao et al. 2018). For instance, the abundance of *T. javana* decreased significantly as rice fields progressed from the reproductive stage to the ripening stage (Saksongmuang et al. 2020). However, there are no studies examining the effect of vegetation complexity on the web characteristics of web-building spiders in rice ecosystems. Therefore, it is important to study not only spider abundance but also web trait composition in order to gain basic knowledge on how habitat structure affects community and niche partitioning of web-building spiders in rice ecosystems.

Tetragnatha (Latreille, 1804) spiders are a dominant group of web-building spiders that are commonly found in rice ecosystems (Tahir and Butt, 2008; Rattanapun, 2012). Previous studies have reported that *Tetragnatha* spiders offer a potential value in pest control in rice fields (Baba et al. 2018; Tsutsui et al. 2018). They prefer wet habitats, especially during the rice growing season, and exhibit spatial and temporal dynamics (Tsutsui et al. 2016; Saksongmuang et al. 2020). Previous studies have reported that vegetation structure determines the availability of attachment substrates for web-building spiders to build webs (Langellotto and Denno, 2004; Glover, 2013; Ávila et al. 2017; Mithali and Pai, 2018). *Tetragnatha* spiders normally build large horizontal webs that requires optimal spacing between rice stems or the rice canopy to build webs of the appropriate size for catching prey; less complex vegetation early in the season may thus be more suitable for these species (Jayakumar and Sankari, 2010; Rattanapun, 2012).

Here, we examined changes in the abundance and web traits (specifically, web diameter and web height from the ground) of *Tetragnatha* spider communities throughout rice development in rainfed lowland rice fields in southern Thailand. We hypothesized that (i) the overall number of *Tetragnatha* spiders, as well as the numbers of each species, would change throughout rice development. We also predicted that (ii) different species of *Tetragnatha* spiders would change their web diameters and web heights as vegetation complexity changes during rice development. Specifically, we predicted that *Tetragnatha* spiders would maximize their web diameter and web height in the middle season of rice when vegetation complexity was moderate. Finally, we predicted that (iii) web diameter and web height would increase with increasing spider body length.

MATERIALS AND METHODS

Study sites and sampling periods

We conducted this study in 12 rainfed lowland rice fields across Songkhla and Phatthalung provinces in southern Thailand (Supplement materials Table S1). In this study, we selected rice fields that were treated with chemical fertilizers, herbicides, and mechanical weed controls on the field bunds, but were not treated with insecticides. All selected rice fields were growing the same rice variety locally known as "Sang Yod Phatthalung - geographical indication [GI] variety" that was planted using the seed sowing method during the same period. The mean size of the study rice fields was 1.39 ha, ranging from 1.12 to 1.60 ha (Supplement materials Table S1). We collected data during a single rice-growing season from November 2020 to February 2021. The phenological stages of rice were classified following Guo et al. (2018) and Gong et al. (2021). Our sampling periods corresponded with the three different developmental stages of rice: tillering (40-50 Day After Planting; DAP), booting (65-75 DAP) and flowering (80-90 DAP) (Fig. 1, S. Venus, personal communication, January 4, 2021).

Vegetation measurements

To measure the vegetation complexity at each rice stage, we placed a 1.5-m measuring pole upright at 5 random points per field and then recorded vegetation height of rice plants and weeds as well as vegetation contacts (the number of points where vegetation touched the pole) (McNett and Rypstra, 2000; Malumbres-Olarte et al. 2012; Saksongmuang et al. 2024). The height and the number of contacts continuously increased from the tillering stage to the flowering stage (Supplement materials Table S2). Vegetation complexity defined as the vegetation height multiplied by the vegetation contacts, increased with the development of rice stages ($R = 0.94$, $p < 0.05$; Supplement materials Fig. S1). Whereas the water level in the fields decreased with the development of rice fields (Supplement materials Table S2).

Spider collection

At each site, we collected spiders following a standardized protocol (Diehl et al. 2013; Michalko et al. 2021). During each rice developmental stage, we collected data at each study site in the evening (6.30 pm – 8.30 pm) and morning (6.30 am – 8.30 am), as these times are when *Tetragnatha* spiders are most active (Kiritani et al., 1972; Herberstein and Elgar 1994). In each field, we established four 40-m transects along rice bunds. We collected *Tetragnatha* spiders by visually inspecting all rice plants, from ground level to the highest part of the rice plant, within 1 m on each side of the transect. We recorded web diameter and web height from the ground surface and also observed the angle of the web from horizontal plane - 0^o or nearly 0^o being horizontal and 90^o or nearly 90^o being vertical (Tew and Hesselberg, 2018; Kennedy et al. 2019). We spent 30 min per transect, resulting in two hours of observation in the morning and two hours of observation in the evening for each study rice field. During evening observations, we used a flashlight covered with dark red plastic to minimize disturbance to spiders (Herberstein and Elgar 1994). Specimens were euthanized following Cooper (2011). We measured the body length of all adult *Tetragnatha* spiders (from the front of the cephalothorax to the tip of the abdomen when they were stretched out). To identify adult vs juvenile, is by considering the genitalia whether it has been fully developed. All adult *Tetragnatha* spiders were identified to species level based on Vungsilabutr (1988) and Barrion and Litsinger (1995) and related taxonomic publications facilitated by the World Spider Catalog (2022), e.g. Song et al. 1999. Only adult spiders were used in the analyses while juvenile spiders were excluded.

Statistical analysis

To investigate the impact of rice stage or vegetation complexity on the abundance and web traits of *Tetragnatha* spiders, we conducted separate analyses for 1] the overall number of *Tetragnatha* spiders, 2] the number of each species of *Tetragnatha* spiders, 3] the web diameter of each species, and 4] web height from

FIGURE 1. The three developmental stages of "Sang Yod Phatthalung" rice during which data were collected: tillering (left), booting (middle) and flowering (right).

the ground for each species. We also investigated 5] the relationships between spider body length and web diameter and web height.

We used generalized linear mixed effects models (GLMM) for the abundance and web trait analyses. We treated rice stage or vegetation complexity, *Tetragnatha* spider species, and body length as fixed effects. We treated rice fields as a random effect. In all analyses, we used the information-theoretic approach to select an optimal model based on model probabilities, i.e. Akaike information criteria (AIC) or Akaike weights, as an alternative to backward or forward selection. The AIC or Akaike weights for each model can be computed based on how they support the data while correcting for biases that arise from model complexity (Garamszegi, 2011). We built several competing models and ranked the models following the highest Akaike weights (Supplement materials Table S3, S4 and S6). We based our inferences on the models that were strongly supported by the highest Akaike weights (Guthery et al. 2003; Cinar et al. 2021). To account for potential nonlinear relationships between response variables and explanatory variables as the response variable takes its maximum value at medium values of explanatory variable, we included quadratic terms of vegetation complexity in all models. We built models with all possible combinations of explanatory variables, including linear and quadratic terms of vegetation complexity, and the simplest model was the null model (Supplement materials Table S4). Depending on the response variable, the most complex models included interactions between quadratic terms of vegetation complexity and spider species (e.g., poly(vegetation complexity,2)*species) for vegetation complexity analyses and interactions between body length and spider species (e.g., body length*species) for body length analyses (Supplement materials Table S4 and S6).

To account for non-normal distributions of errors, we used various distributional families within the GLMMs depending on the distribution type of each response variable. For the overall number of *Tetragnatha* spiders and the number of *Tetragnatha* spiders of each species, we used GLMMs with negative binomial distributions and log link functions as the dependent variables were count data and overdispersed. We analyzed web diameter and web height using GLMMs with gamma distributions and log link functions as the dependent variables were positively continuous and heteroscedastic.

All statistical analyses were conducted within the R environment, version 4.1.2 (R Development Core Team, 2021). GLMMs were conducted within the R package "glmmADMB" (Skaug et al. 2018) and model selection within the package "MuMIn" (Barton, 2018).

RESULTS

Overall, we collected 613 adult *Tetragnatha* spiders comprising of six species namely *T. maxillosa (*32.1*%)*, *T. javana* (30.7%), *T. mandibulata (*27.7*%)*, *T. nitens* (4.6%), *T. pradonia* (3.0%) and *T. virescens* (1.9%). All species of *Tetragnatha* spiders built horizontal webs (0º - 30º from horizontal plane), but web diameter and web height from the ground differed by species.

The effect of rice stages on *Tetragnatha* spider abundance

Rice stage significantly affected the total number of *Tetragnatha* spiders (Akaike weights = 0.954; Supplement materials Table S3). Overall, the number of *Tetragnatha* spiders was significantly higher in the tillering stage compared to the flowering stage, while the booting stage was not significantly different from either (Fig. 2a).

When considering spider species, the most optimal model included the additive effect of rice stage and species of *Tetragnatha* spider (Akaike weights = 0.895; Supplement materials Table S3). The numbers of *T. javana*, *T. mandibulata,* and *T. maxillosa* were clearly

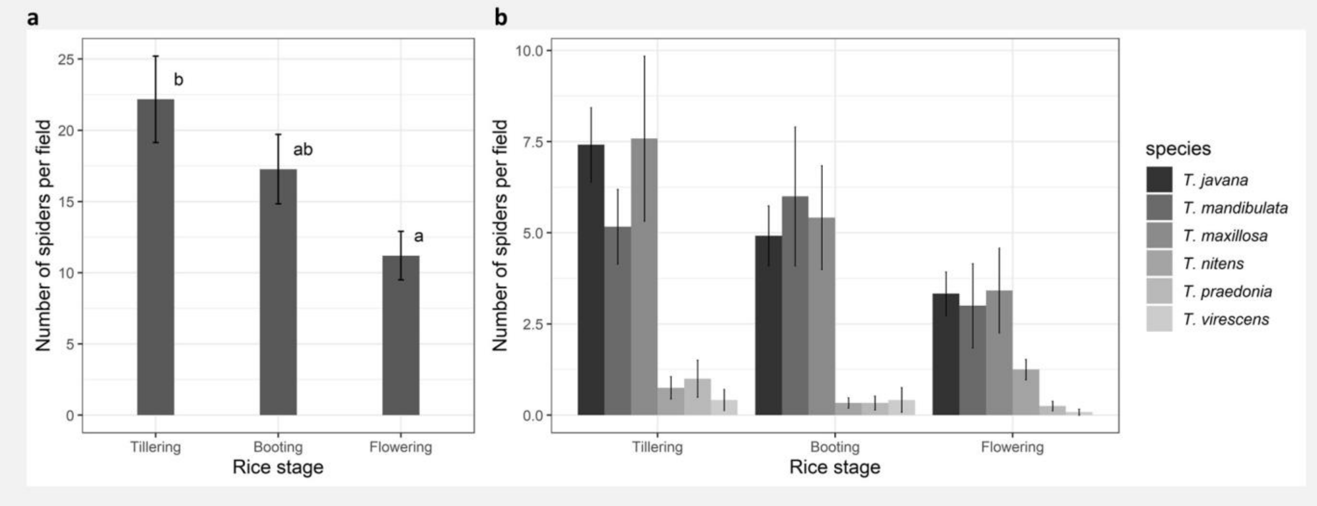

FIGURE 2. Mean (± SE) number of all *Tetragnatha* spiders per rice field (a) and for each *Tetragnatha* spider species (b) at each developmental stage of rice. Rice stages with different letters are significantly different (Tukey's honestly significant differences test, P<0.05).

higher than those of *T. nitens*, *T. praedonia* and *T. virescens* in all rice stages (Fig. 2b). The numbers of *T. javana*, *T. mandibulata*, *T. maxillosa* and *T. praedonia* were generally higher in the tillering stage than the flowering stage, while the numbers of *T. nitens* and *T. virescens* were not different among stages (Fig. 2b).

The effect of vegetation complexity on web diameter and web height

When examining web diameter, the best model included the additive effects of the quadratic terms of vegetation complexity and spider species (Akaike weights = 0.611; Supplement materials Table S4 and S5). The relationship between vegetation complexity and web diameter was hump-shaped for all species. All species built their webs with the largest sizes in middle complex vegetation (i.e., the booting stage) and built their webs at smaller sizes in more complex vegetation (i.e., the flowering stage) than compared to simple vegetation (i.e., the tillering stage) (Fig. 3a). Moreover, the six species of *Tetragnatha* differed in web diameter. *Tetragnatha mandibulata* built webs that were significantly larger than all other species, while *T. virescens* built the smallest webs (Fig. 3a).

When analyzing web height, the best model included the additive effects of the quadratic terms of vegetation complexity and spider species (Akaike weights = 0.684; Supplement materials Table S4 and S5). The relationship between vegetation complexity and web height was hump-shaped for all species. All species built their webs at the highest heights in middle complex vegetation and built their webs at lower heights in more complex vegetation than compared to simple vegetation (Fig. 3b). Furthermore, the six species of *Tetragnatha* built webs at different heights above ground level. *Tetragnatha virescens* webs were significantly higher than all other species, while *T. maxillosa* webs were significantly lower than all others (Fig. 3b).

The effect of spider body length on web diameter and web height

When examining web diameter, the best model included the additive effects of body length and spider species (Akaike weights = 0.922; Supplement materials Table S6). Web diameter of *Tetragnatha* spiders tended to increase with their body length for almost all species, except *T. nitens* (Fig. 4a). However, the largest web diameter (web size) did not relate with the largest size of spider body length. *Tetragnatha javana* showed the highest body length, but they built the smallest web size. Whereas *T. mandibulata,* the second largest body length, built the largest web size (Fig. 4a).

When analyzing web height, the best model included only the spider species (Akaike weights = 0.520; Supplement materials Table S6). Web height did not relate to any of body length. The web height of *T. virescens* was the highest web from ground, but not significantly different from *T. javana*, *T. mandibulata* and *T. praedonia*. Whereas web height of *T. maxillosa* and *T. nitens* were significantly lower than other species, except *T. praedonia* (Fig. 4b).

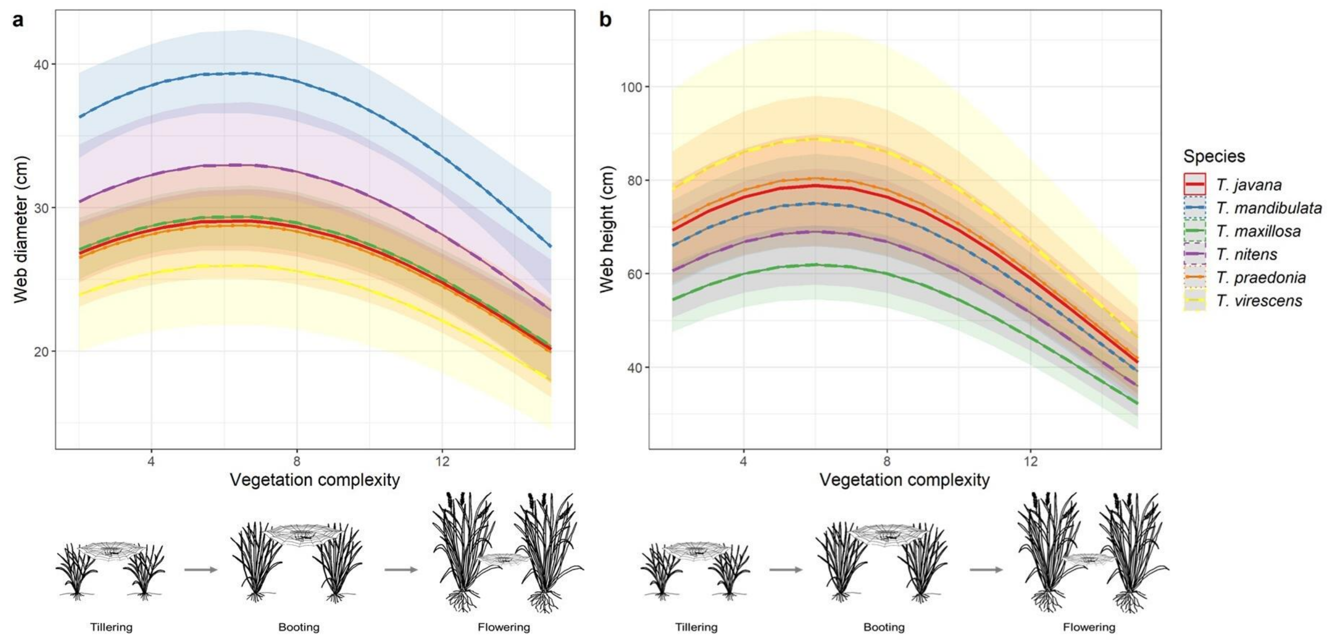

FIGURE 3. The effect of vegetation complexity on web diameter (a) and on web height (b) for six *Tetragnatha* spider species during rice field development. Thick lines show the estimated relationships and shaded bands show 95% confidence intervals.

DISCUSSION

The decreasing abundance of *Tetragnatha* spiders from the tillering stage to the flowering stage can be explained by two reasons. First, *Tetragnatha* spiders are orb-weavers that exhibit high dispersal ability and can quickly reach new habitats (Bell et al. 2005; Cotoras et al. 2017; Candek et al. 2021). They prefer wet habitats that can support high numbers of prey, including midge flies and mayflies, so they were high abundance by occupying rice canopies and rice stems above water level to build horizontal webs for catching prey during the early rice growing season (Rattanapun, 2012; Tsutsui et al. 2016; Radermacher et al., 2020). Then, *Tetragnatha* spider abundance decreases when the number of their main prey decreases due to the draining out of water in the late rice growing season (Saksongmuang et al. 2024). Second, the observed decline in spider abundance is likely due to the relationship between vegetation structural complexity and spider web characteristics. Many studies have reported that the webs of web-building spiders strongly depend on vegetation structure, which determines the availability of attachment substrates (McNett and Rypstra, 2000; Glover, 2013; Ávila et al. 2017). In the tillering stage or early growing season, lower vegetation complexity creates optimal gaps between rice stems and within the rice canopy to support the preferred web sizes of *Tetragnatha* spiders. These spiders are therefore abundant during this period (Blackledge et al. 2003; Saksongmuang et al. 2020). On the other hand, in the flowering stage, the vegetation may become too dense and complex for *Tetragnatha* spiders to build their large webs. The abundance of *Tetragnatha* spiders in rice fields therefore decreases during the late growing season as they move to other habitats that provide more suitable conditions, such as levees or ditches (Bambaradeniya and Edirisinghe, 2008; Tsutsui et al., 2016).

Different species of *Tetragnatha* spiders showed differences in abundance throughout the rice growing season. The numbers of *T. javana*, *T. mandibulata*, and *T. maxillosa* were dominant in all rice stages. These three species are the most common *Tetragnatha* spiders found across tropical Asian countries (Okuma, 1988a, b) and correspond with the results of studies in India (Jayakumar and Sankari, 2010; Anis Joseph and Premila, 2016a) and Pakistan (Tahir and Butt, 2008). These three species were highly abundant during every stage of rice development and much more dominant than the other three species throughout the rice growing season.

Rice development affected not only the abundance of *Tetragnatha* spiders, but also web trait composition. The web diameters and web heights of all *Tetragnatha* spider species were found to have hump-shaped relationships with vegetation complexity throughout rice development. This finding can be explained by the fact that vegetation structure is an important determinant of web trait composition (McNett and Rypstra, 2000; Langellotto and Denno, 2004; Mithali and Pai, 2018). Lower vegetation complexity during

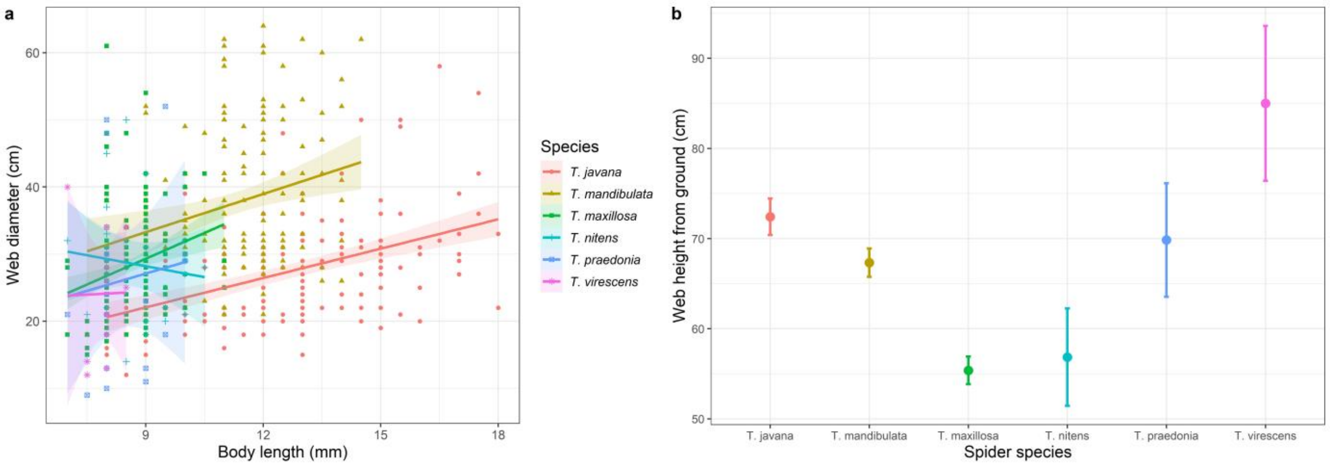

FIGURE 4. The effect of *Tetragnatha* spider body length on web diameter (a) and on web height (b) for six *Tetragnatha* spider species. Thick lines show the estimated relationships and shaded bands show 95% confidence intervals. Spider species with different letters are significantly different (Tukey's honestly significant differences test, P<0.05).

the early growing season or tillering and booting stages created larger spaces between rice plants, which allowed *Tetragnatha* spiders to build larger webs. However, these *Tetragnatha* spiders were found to build webs with smaller diameters when vegetation was more complex during the flowering stage. During the late growing season, the density of rice plants and weeds impeded the ability of spiders to build large webs and thus forced them to build smaller webs (Blackledge et al. 2003; Jayakumar and Sankari, 2010; Saksongmuang et al., 2020).

The six species of *Tetragnatha* spiders were also found to build webs closer to the ground during the flowering stage when vegetation complexity was higher. This finding might be due to the effect of dense vegetation near the rice canopy formed by the leaves and flowers of rice and weeds together with the draining out of water in the field. Therefore, *Tetragnatha* spiders that normally build large horizontal webs likely had to move closer to the ground or place that have enough space in order to build their horizontal webs of the optimal size in gaps for catching prey (Bambaradeniya and Edirisinghe, 2008; Anis Joseph and Premila, 2016b; Dzulhelmi et al. 2017).

Different species of *Tetragnatha* spiders showed differences in web diameter and web height throughout rice development. *T. mandibulata* built the largest webs but did not construct webs at the greatest heights. This result can be explained by the large body size and the high abundance of this species, allowing them to build larger webs and outcompete other species (Henaut et al., 2006; Tahir et al., 2010; Sensenig et al., 2011). However, the web diameter and height of *T. mandibulata* decreased in more complex vegetation because the density of rice plants and weeds inhibited the formation of large webs, so spiders were forced to build smaller webs closer to the ground. On the other hand, the smallest webs were constructed by *T. virescens* and they also built webs that were the highest above ground level. As this species occupies sites that are closer to the rice canopy and that have a denser microhabitat, they build smaller webs than those of other species that live at lower sites and build larger webs (Blackledge et al. 2003; Jayakumar and Sankari, 2010). This study confirms that some species construct larger webs at lower heights, while other species construct smaller webs at greater heights, which is in response to vegetation complexity. Such findings correspond to previous studies demonstrating that different spider species co-occurring within the same microhabitat may exhibit niche partitioning to minimise competition by building webs of different sizes and at different heights (Richardson and Hanks 2009; Tahir et al. 2012; Dzulhelmi et al. 2017) and this may turn to enhance pest control effects through multiple-predator effects (Losey and Denno, 1998; Michalko et al. 2019).

However, in this study, there was considerable overlap in web height between some spider species. For instance, *T. praedonia*, *T. javana* and *T. mandibulata* constructed their webs at similar heights. The observed overlap in web heights among these species possibly implies that there are differences in web diameter between these species. For example, *T. mandibulata* built larger webs than *T. javana* and *T. praedonia*, so they might target prey of different sizes. Corresponding to previous studies, sympatric web-building spider species also partition their niche through mesh size and mesh quality (Tahir et al. 2012;

Dzulhelmi et al., 2018a). In the present study, we did not study the quality and size of the mesh, so it remains to be addressed in further studies.

In addition, the web diameters of *Tetragnatha* spiders were also influenced by spider body length. In each species, body length was positively correlated with web diameter (Henaut et al., 2006; Tahir et al., 2010). These correlations are possibly due to larger spiders targeting larger prey that can be captured by larger webs, which also reduces competition with smaller spiders (Uetz et al. 1978; Richardson and Hanks, 2009; Dzulhelmi et al., 2018b). It is also possible that larger spiders need to construct larger webs than smaller spiders in order to support their heavier bodies (Sensenig et al., 2011; Dzulhelmi et al. 2018b). Moreover, when comparing between species, we found that the largest size of spider body length did not build the largest web diameter. This is possibly due to the web diameter positively related to carapace width more than body length of spider (Tahir et al., 2010). However, this study did not quantify carapace width of different species of *Tetragnatha* spiders. Therefore, further work should investigate the sizes of webs to determine whether they change in response to changes in carapace width of spiders.

CONCLUSIONS

This study shows that *Tetragnatha* spider abundance and web characteristics change throughout the rice growing season in response to the changing availability of support structures to construct their webs. Higher vegetation complexity decreased spider abundance and resulted in *Tetragnatha* spiders building smaller webs or closer to the ground. However, different spider species exhibited differences in web diameter and web height throughout the rice growing season in response to both vegetation complexity and body length. It can be concluded that different spider species exhibit niche partitioning with other congeners by using web characteristics, which promotes co-existence of *Tetragnatha* species within the same rice field habitats. The findings obtained from this study provide basic knowledge of niche partitioning and co-existence among different species of *Tetragnatha* spider. Our findings can be linked to the role of web-building spiders as important biological control agents and can help lead to sustainable management in rice ecosystems.

ACKNOWLEDGMENTS

This study was funded by the Thailand Agricultural Research Development Agency (ARDA) (grant number: HRD6305063) and Science Achievement Scholarship of Thailand (SAST). Our special thanks are extended to all of the farmers in Songkhla and Phatthalung provinces who permitted us to conduct fieldwork in their rice fields. We would like to thank Dr. Radek Michalko from Mendel University, Czech Republic for valuable suggestions that helped improve our work and Dr. Alyssa B. Stewart for English language revision. This research could not have been completed without the fieldwork assistance provided by members of the Department of Biology, Division of Biological Science at Prince of Songkla University. We also thank the editors and reviewers whose suggestions improved this work.

LITERATURE CITED

Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems. Invertebrate Biodiversity as Bioindicators of Sustainable Landscapes, 19–31.

Anis Joseph, R. and Premila, K.S. 2016a. A study on the richness of spider fauna in rice ecosystem. Journal of Entomology and Zoology Studies, 4(2): 425–430.

Anis Joseph, R. and Premila, K. S. 2016b. Species Composition and Quantitative Analysis of *Tetragnathid* Spiders, Tetragnathidae (Araneae) in Rice Fields. International Journal of Fauna and Biological Studies 2016, 3(3): 158–160.

Ávila, A.C., Stenert, C., Rodrigues, E.N.L. and Maltchik, L. 2017. Habitat structure determines spider diversity in highland ponds. Ecological Research, 32(3): 359–367.

Baba, Y. G., Kusumoto, Y. and Tanaka, K. 2018. Effects of agricultural practices and fine-scale landscape factors on spiders and a pest insect in Japanese rice paddy ecosystems. BioControl, 63 (2): 265–275.

Bambaradeniya, C. N. B., Edirisinghe, J. P., De Silva, D. N., Gunatilleke, C.V.S., Ranawana, K.B. and Wijekoon, S. 2004. Biodiversity associated with an irrigated rice agro-ecosystem in Sri Lanka. Biodiversity and Conservation, 13 (9): 1715–1753.

Bambaradeniya, C.N. and Edirisinghe, J.P. 2008. Composition, structure and dynamics of arthropod communities in rice agroecosystem. Ceylon Journal of Science, 37(1): 23–48.

Bao, L., Ginella, J., Cadenazzi, M., Castiglioni, E. A., Martínez, S., Casales, L., Caraballo, M. P., Laborda, Á. and Simo, M. 2018. Spider assemblages associated with different crop stages of irrigated rice agroecosystems from eastern Uruguay. Biodiversity data journal, 6: e24974.

Barrion, A.T. and Litsinger, J.A. 1995. Riceland Spiders of South and Southeast Asia. CABI and IRRI, Manila, Philippines, 700 pp.

Barton, K. 2018. MuMIn: Multi-Model Inference. R package version 1.40.4. Available from: https://CRAN.R-project.org/package=MuMIn (accessed 20 June, 2023)

Bell, J.R., Bohan, D.A., Shaw, E.M. and Weyman, G.S. 2005. Ballooning dispersal using silk: World fauna, phylogenies, genetics and models. Bulletin of Entomological Research, 95: 69–114.

Blackledge, T.A., Binford, G.J. and Gillespie, R. G. 2003. Resource use within a community of Hawaiian spiders (Araneae: Tetragnathidae). Annales Zoologici Fennici, 40: 293–303.

Candek, K., Agnarsson, I., Binford, G.J. and Kuntner, M. 2021. Biogeography of Long-Jawed Spiders Reveals Multiple Colonization of the Caribbean. Diversity. 13: 622.

Cinar, O., Umbanhowar, J., Hoeksema, J.D. and Viechtbauer, W. 2021. Using information-theoretic approaches for model selection in meta-analysis. Research Synthesis Methods, 12(4): 537–556.

Cooper J. E., 2011. Anesthesia, Analgesia, and Euthanasia of Invertebrate. ILAR journal, 52(2): 196–204.

Cotoras, D. D., Murray, G. G. R., Kapp, J., Gillespie, R. G., Griswold, C.E., Simison, W.B., Green, R.E. and Shapiro, B. 2017. Ancient DNA resolves the history of *Tetragnatha* (Araneae, Tetragnathidae) spiders on Rapa Nui. Genes, 8: 403.

Diehl, E., Mader, V. L., Wolters, V. and Birkhofer, K. 2013. Management intensity and vegetation complexity affect web building spiders and their prey. Oecologia, 173(2): 579–589.

Dzulhelmi, M.N., Goh, T.G., Bakri, A., Rahim, F., Mohamed, Z. and Yusoff, N.R. 2017. Web characteristics determine niche partitioning for orb-web spiders (Araneae, Tetragnathidae) in Malaysia. Oriental Insects, 51(3): 262–275.

Dzulhelmi, M. N., Goh, T. G. and Suriyanti, S. N. P. 2018a. Coexistence of four orb-web spiders in an oil palm plantation in Peninsular Malaysia. Turkish Journal of Entomology, 42(4): 295–303.

Dzulhelmi, M.N., Goh, T.G., Zulqarnain, M. and Norma-Rashid, Y. 2018b. Relationships between morphology and web characteristics of four spider species (Araneae: Tetragnathidae) in Malaysia. Taiwanese Journal of Entomology Study, 3 (1): 1–11.

Garamszegi, L. Z. 2011. Information-theoretic approaches to statistical analysis in behavioural ecology: an introduction. Behavioral Ecology and Sociobiology, 65: 1–11.

Glover, N. 2013. The habitat preferences of web building spiders. The Plymouth Student Scientist, 6(1): 363–375.

Gong, T., Yang, K., Lin, Z., Fang, S., Wu, X., Zhu, R. and Peng, Y. 2021. Remote estimation of leaf area index (LAI) with unmanned aerial vehicle (UAV) imaging for different rice cultivars throughout the entire growing season. Plant Methods, 17(88). https://doi.org/10.1186/s13007-021-00789-4

Guo, X., Li, K., Shao, Y., Wang, Z., Li, H., Yang, Z., Long, L. and Wang, S. 2018. Inversion of Rice Biophysical Parameters Using Simulated Compact Polarimetric SAR C-Band Data. Sensors. 18(7): 2271.

Guthery, F.S., Burnham, K.P. and Anderson, D.R. 2003. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. The Journal of Wildlife Management, 67(3): 655.

Henaut, Y., Garcia-Ballinas, J.A. and Alauzet, C. 2006. Variations in web construction in *Leucauge venusta* (Araneae, Tetragnathidae). Journal of Arachnology, 34 (1): 234–240.

Herberstein, M.E. and Elgar, M.A. 1994. Foraging strategies of *Eriophora transmarina* and *Nephila plumipes* (Araneae: Araneoidea) : nocturnal and diurnal orb-weaving spiders. Austral Ecology, 19: 451–457.

Jayakumar, S. and Sankari, A. 2010. Spider population and their predatory efficiency in different rice establishment techniques in Aduthurai, Tamil Nadu. Journal of Biopesticides, 3: 20–27.

Kennedy, S., Lim, J.Y., Clavel, J., Krehenwinkel, H. and Gillespie, R.G. 2019. Spider webs, stable isotopes and molecular gut content analysis: Multiple lines of evidence support trophic niche differentiation in a community of Hawaiian spiders. Functional Ecology, 33: 1722–1733.

Kiritani, K.S., Kawahara, S., Sasaba, T. and Nakasuji, F. 1972. Quantitative evaluation of predation by spiders on the green rice leafhopper *Nephotettix cincticeps* Uhler, by a sight count method. Researches on Population Ecology, 13(2): 187–200.

Landis, D. A., Wratten, S. D. and Gurr, G. M. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology, 45: 175–201.

Langellotto, G. A. and Denno, R. F. 2004. Responses of invertebrate natural enemies to complex structured habitats: a meta analytical synthesis. Oecologia, 139(1): 1–10.

Lawler, S.P. 2001. Rice fields as temporary wetlands: A review. Israel Journal of Zoology, 47(4): 513–528.

Losey, J.E. and Denno, R.F. 1998. Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. Ecology, 79(6): 2143–2152.

Ludy, C. 2007. Prey selection of orb web spiders (Araneidae) on field margins. Agriculture, Ecosystems and Environment, 119(3-4): 368–372.

Leitão, S., Pinto, P., Pereira, T. and Brito, M.F. 2007. Spatial and temporal variability of macroinvertebrate communities in two farmed Mediterranean rice fields. Aquatic Ecology, 41(3): 373–386.

Macfadyen, S., Kramer, E.A., Parry, H.R. and Schellhorn, N.A. 2015. Temporal change in vegetation productivity in grain production landscapes: linking landscape complexity with pest and natural enemy communities. Ecological Entomology, 40: 56–69.

Malumbres-Olarte, J., Vink, C.J., Ross, J.G., Cruickshank, R.H. and Paterson, A.M., 2012. The role of habitat complexity on spider communities in native alpine grasslands of New Zealand. Insect Conservation and Diversity, 6(2): 124–134.

McNett, B.J. and Rypstra, A.L. 2000. Habitat selection in a large orb weaving spider: vegetation complexity determines site selection and distribution. Ecological Entomology, 25(4): 423–432.

Michalko, R., Pekar, S. and Entling, M. H. 2019. An updated perspective on spiders as generalist predators in biological control. Oecologia, 189: 21–36.

Michalko, R., Košulič, O., Wongprom, P., Songsangchote, C., Saksongmuang, V. and Trisurat, Y., 2021. Reforestations of Tropical Forests Alter Interactions Between Web-Building Spiders and Their Prey. Ecosystems, 24(8): 1962–1975.

Mishra, A., Kumar, B. and Rastogi, N. 2020. Predation potential of hunting and web-building spiders on rice pests of Indian subcontinent. International Journal of Tropical Insect Science, 41(2): 1027–1036.

Mithali, M.H. and Pai, I. 2018. Distribution, Diversity and Ecology of Spider Species at Two Different Habitats. International Journal of Environmental Sciences and Natural Resources 0164. 8(5): 555–747.

Okuma, C. 1988a. A Revision of the Genus *Tetragnatha* Latreille (Araneae, Tetragnathidae) of Asia, Part I. Journal of the Faculty of Agriculture Kyushu University, 32(3.4): 165–181.

Okuma, C. 1988b. A Revision of the Genus *Tetragnatha* Latreille (Araneae, Tetragnathidae) of Asia, Part II. Journal of the Faculty of Agriculture Kyushu University, 32(3.4): 183–213.

Radermacher, N., Hartke, T. R., Villareal, S. and Scheu, S. 2020. Spiders in rice-paddy ecosystems shift from aquatic to terrestrial prey and use carbon pools of different origin. Oecologia, 192(3): 801–812.

Rattanapun, W. 2012. Diversity and population dynamics of pests and predators in irrigated rice fields with treated and untreated pesticide. Communications in agricultural and applied biological sciences, 77(4): 601–609.

Richardson, M.L. and Hanks, L.M. 2009. Partitioning of Niches Among Four Species of Orb-Weaving Spiders in a Grassland Habitat. Environmental Entomology, 38(3): 651–656.

Saksongmuang, V., Miyashita, T., Maneerat, T. and Bumrungsri, S. 2020. Population dynamics and prey composition of *Tetragnatha* spiders (Araneae: Tetragnathidae) in semi-organic rice fields, Songklanakarin Journal of Science and Technology, 42(4): 725–733.

Saksongmuang, V., Michalko, R., Petcharad, B. and Bumrungsri, S. 2024 Changes in vegetation complexity during the development of rice ecosystems affect orb-weaving spider-prey trophic networks. Agricultural and Forest Entomology, 1–13.

Sensenig, A.T., Agnarsson, I. and Blackledge, T. A. 2011. Adult spiders use tougher silk: ontogenetic changes in web architecture and silk biomechanics in the orb-weaver spider. Journal of Zoology, 285: 28-38.

Settle, W.H., Ariawan, H., Astuti, E.T., Cahyana, W., Hakim, A.L. amd Hindayana, D., 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology, 77(7): 1975–1988.

Skaug, H., Fournier, D., Nielsen, A., Magnusson, A.and Bolker, B., 2018. glmmADMB: Generalized linear mixed models using AD model builder. R package version 0.8.3.4 Available from: http://glmmadmb.r-forge.r-proje ct.org/ (accessed 20 June, 2023).

Song, D.X., Zhu, M.S. and Chen, J. 1999. The spiders of China. Hebei Science and Technology Publishing House Shijiazhuang, 640 pp.

Takada, M. B., Kobayashi, T., Yoshioka, A., Takagi, S. and Washitani, I. 2013. Facilitation of ground dwelling wolf spider predation on mirid bugs by horizontal webs built by *Tetragnatha* spiders in organic paddy fields. Journal of Arachnology, 41(1): 31–35.

Tahir, H. M. and Butt, A. 2008. Activities of spiders in rice fields of central Punjab, Pakistan. Acta Zoologica, 54(4):701–711.

Tahir, H. M., Butt, A. and Sherawat, S. M. 2009. Foraging strategies and diet composition of two orb web spiders in rice ecosystems. Journal of Arachnology, 37(3): 357–362.

Tahir, H. M., Butt, A. and Alam, I. 2010. Relationships of web characteristics and body measures of *Leucauge decorate* (Araneae: Tetragnathidae). Pakistan Journal of Zoology, 42(3): 261–265.

Tahir, H. M., Butt, A., Mukhtar, M. K., Bilal, M. and Khan, S. Y. 2012. Co-existence of Four Orb Weaving Spiders in the Rice Ecosystem. Pakistan Journal of Zoology, 44(6): 1521–1528.

Tew, N. E. and Hesselberg, T. 2018. Web asymmetry in the tetragnathid orb spider *Metellina mengei* (Blackwell, 1869) is determined by web inclination and web size. Journal of Arachnology, 46(2): 370–372.

Tsutsui, M.H., Tanaka, K., Baba, Y.G. and Miyashita, T. 2016. Spatiotemporal dynamics of generalist predators (Tetragnatha spider) in environmentally friendly paddy fields. Applied Entomology and Zoology, 51(4): 631–640.

Tsutsui, M.H., Kobayashi, K. and Miyashita, T. 2018. Temporal trends in arthropod abundances after the transition to organic farming in paddy fields. PLoS ONE 13(1): e0190946.

Uetz, G. W., Jonso, A. D. and Schemske, D. S. 1978. Web placement, web structure, and prey capture in orb-weaving spiders. Bulletin of the British Arachnological Society, 4: 141–148.

Vungsilabutr, W. 1988. The spider genus *Tetragnatha* in the paddy fields of Thailand (Araneae: Tetragnathidae). Thai Journal of Agricultural Science, 21: 63–74.