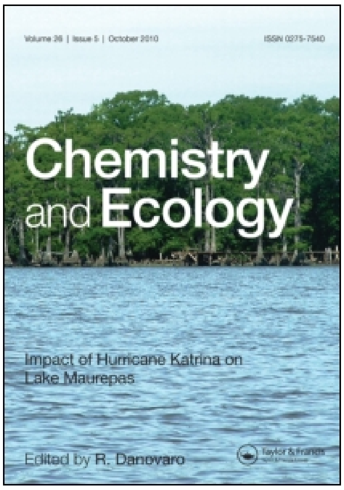

Chemistry and Ecology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713455114

Morphology, growth and carbohydrate storage of the plant *Typha angustifolia* at different water depths

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To cite this Article Sharma, P. , Asaeda, T. , Kalibbala, M. and Fujino, T.(2008) 'Morphology, growth and carbohydrate storage of the plant *Typha angustifolia* at different water depths', Chemistry and Ecology, 24: 2, 133 — 145
To link to this Article: DOI: 10.1080/02757540801919289
URL: http://dx.doi.org/10.1080/02757540801919289

Chemistry and Ecology
Vol. 24, No. 2, April 2008, 133–145

Morphology, growth and carbohydrate storage of the plant *Typha angustifolia* at different water depths

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(*Received 6 October 2007; final version received 10 January 2008*)

Morphological characteristics, growth and carbohydrate storage dynamics of *Typha angustifolia* in relation to water depth were investigated. The study was based on observations carried out in two stands, namely Akigase and Teganuma, for two growth seasons. The latter stand was about two times deeper than the former. Teganuma stands exhibited significantly higher number of thick shoots compared to those of Akigase. Conversely, the difference in shoot heights between the two stands was insignificant. The same was true for rhizome lengths. Rhizome diameters were significantly bigger for Teganuma compared to Akigase. Furthermore, both the above and belowground biomass were significantly higher for Teganuma compared to those of Akigase. Teganuma stands allocated 55% of the total biomass to the aboveground parts, while Akigase stands allocated 60%. Similarly, Teganuma exhibited significantly higher stocks of total non-structural carbohydrates (TNC) compared to Akigase. The higher number of thick shoots and the relatively bigger rhizome diameters in Teganuma are seemingly important tolerance strategies in maintaining effective aeration into the rhizosphere, by reducing internal resistance. In addition, the higher TNC stocks and biomass help not only to enhance survival under anoxia for longer durations, they also provide firm substrate anchorage in the deeper Teganuma stands.

Keywords: non-structural carbohydrates; rhizome diameter; rhizome length

1. Introduction

Hydrological regimes of wetlands such as water depth, exhibit pronounced effects on growth, production and distribution of plant species [1,2]. Different wetland plant species tolerate a wide range of water depths. The zonation of emergent macrophytes is mainly a consequence of morphological and physiological tolerance strategies to the gradation of depth-dependent factors such as soil moisture, particle size, flooding, duration of submergence, wave action, etc [3,4].

A major constraint resulting from excess water is an inadequate supply of oxygen to belowground tissues i.e. rhizomes and roots, since the diffusion of oxygen through water is 10,000 times slower than that of air [5]. In such environments where oxygen availability is a critical factor limiting plant survival, differences in oxygen transport capacity can be important in structuring communities [6].

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ISSN 0275-7540 print/ISSN 1029-0370 online

DOI: 10.1080/02757540801919289
http://www.informaworld.com

Various studies have indicated that plants with key tolerance strategies such as superior oxygen transportation [6,7], greater hypoxia tolerance [8,9], shoot elongation in order to overcome submerged environments which includes seed production timing [10], production of numerous seeds [11], and greater ability of seedlings to grow under water [12,13], can survive well in deep water habitats. The potential of plastic modification of biomass allocation [14,15], such as variable allocation of biomass between above and belowground parts, also facilitates the survival of emergent macrophytes over a wide range of water depths [2,15–19].

Thus, plants growing in deep waters exhibit various changes in their morphology in order to maintain effective aeration [9,15,16,18,20–22]. Even with a well developed system of gas pores, rhizomes may experience oxygen deficiency during winter and early growth, until the internal aeration system is fully developed. During those periods, hypoxic conditions can occur within the rhizosphere and root zones, since the substrate also becomes extremely reduced [23,24]. Hence, maintaining effective aeration and resilience towards anoxic conditions i.e. by depicting metabolic changes which ensure cell integrity and continuation of energy supply under oxygen deficiency [23], are greatly needed tolerance strategies [7,25].

One of the crucial metabolic changes is to develop a reliable non-structural carbohydrate storage capacity [26–28]. Under anoxic conditions, greater amounts of carbohydrate reserves are required to generate sufficient energy via anaerobic fermentation in order to support cell metabolism [29,30]. Thus, the storage capacity of rhizomes also largely determines the ability of wetland plants to survive in hypoxic littoral sediments [31]. Besides, plants growing in deep waters are exposed to more mechanical stresses from wave and wind action, compared to shallow habitats [15]. Hence, increased stem strength can also be a prerequisite for survival.

Typha angustifolia is a perennial rhizomatous plant that commonly grows in nutrient-rich littoral habitats [26,31]. It is more tolerant to deep water compared to other *Typha* species [20,32]. Responses of diverse *Typha* species under variable water depths have been reported [16,18,20]. Some studies have focused particularly on changes in leaf morphology [17,18] or biomass allocation to leaf organs [16]. Not only does the allocation of biomass between the organs of emergent macrophytes change, also vivid changes in shoot height, number of shoots, stem diameter, rhizome diameter and rhizome architecture are observed [2,15,19,21,22,33,34].

Furthermore, numerous expository studies on morphological characteristics and growth dynamics of various rhizomatous plant species, in relation to water depth have been undertaken [4,15,16,21,35,36]. Also, studies on associated metabolic features (e.g. related to non-structural carbohydrate metabolism), which contribute to the understanding of the physiological background of species performance, have been done [26–28].

However, very few have been undertaken to investigate the morphological characteristics, growth dynamics and total non-structural carbohydrates (TNC) storage dynamics of *T. angustifolia*, in relation to variable water depth. In the above regard therefore, this study was conducted to give an in-depth understanding of TNC storage dynamics in the shoots and rhizomes of *T. angustifolia* in variable water depth, plus its morphology and growth dynamics.

2. Materials and methods

2.1. *Study sites*

Experiments were conducted in two different stands of *T. angustifolia*. The study sites were located in Akigase (Saitama prefecture) and Teganuma (Chiba prefecture), Japan. The former was a shallow pond (approximately 100 m long by 50 m wide, and 30 cm water depth), located within Akigase park, in the flood plains of Arakawa river (35° 51′ 10″ N, 139° 35′ 48″ E), about

Table 1. Depth, total nitrogen (TN) and total phosphorus (TP) concentrations of the two stands. The values are averages with their standard deviations in parentheses.

		Name of study site	
Parameter	SI units	Akigase	Teganuma
Water depth	cm	32 (5)	68 (7)
TN (sediment)	mg/g	3.10 (0.03)	2.34 (0.12)
TP (sediment)	mg/g	0.80 (0.04)	1.57 (0.06)
TN (water)	mg/l	2.53 (0.07)	2.8 (0.04)
TP (water)	mg/l	0.031 (0.005)	0.26 (0.008)

30 km North of Tokyo [37]. Approximately half of the pond was homogeneously covered with monospecific stands of *T. angustifolia*. The bottom sediment was dominantly soft organic mud.

The latter site was 100 m long by 30 m wide, with an average water depth of 68 cm. This monospecific stand of *T. angustifolia*, was located on the shoreline of lake Teganuma (35° 52′ 08″ N, 139° 37′ 10″ E), 30 km Northeast of Tokyo. The lake is 6.5 km^2, and its average depth is approximately 0.9 m [37]. Lake Teganuma, once the most eutrophic lake in Japan, was gradually restored by artificially diverting a nearby river called Tone, through canals. Other Physico-chemical properties of the two stands are as shown in Table 1.

The underlying sediment in Teganuma was mainly soft organic mud. Both sites depicted similar sediment texture, were largely silt free, and their *Typha* stands have been undisturbed for the last 10 years [37]. Although the stands have been established for quite some time, based on the findings of Grace and Wetzel [38], long time spans are known to exhibit virtually insignificant effects on the growth and biomass dynamics of *Typha* populations.

For each sampling day, both overlying water and sediment samples were collected from the sites. They were then taken to the laboratory for further analysis, in order to determine the total nitrogen (TN) and total phosphorous (TP) concentrations as stipulated by APHA et al. [39]. As depicted in Table 1 (i.e. the relatively low standard deviations in parentheses), the seasonal variation of the nutrient concentrations of each site was not significant. The study was conducted from April 2002 to December 2003 (Akigase), and April 2003 to December 2004 (Teganuma).

2.2. *Sampling and measurements*

Sampling expeditions were carried out once, on a monthly basis per site, with Teganuma sampling being conducted mid-monthly, while that of Akigase was conducted at the end of the month. Each time, three replicate plant samples (50 cm by 50 cm) were taken randomly in areas, at least 2 metres from the periphery and/or previously sampled areas. Thereafter, the depth of the holes from which the plant replicates were taken was measured and recorded. For Akigase and Teganuma, the replicates were taken at average water depths of 32 cm and 68 cm, respectively (Table 1). Throughout the entire study period, the water depths of both sites were quite stable. This is probably attributed to the slow and adequate flushing available at their effluent zones [37].

All the above and belowground biomass, including dead organs in the subsequent hole was carefully collected, together with the loose soil substrate (up to a soil depth of about 20 cm). The samples were partly washed out in the field. Later on, final washing with the aid of pressurised tap water, was also carried out in the laboratory using clean polyethylene bags. The plants were then sorted into aboveground and belowground parts. After separation in the laboratory, the number of shoots per square meter (shoot density) was recorded, while for each individual shoot, shoot height and shoot diameter were measured and recorded.

Belowground parts were further sorted into vertical rhizomes, horizontal rhizomes and roots. The length and diameter of the horizontal rhizomes were also measured in the laboratory. Thereafter, all the sorted material was dried in the oven for more than 72 h at 85 °C until constant mass was obtained. The dry weight (DW) was then measured and recorded.

2.3. *Measurement of total non-structural carbohydrates (TNC)*

To analyse TNC, oven dried plant samples (from each replicate) for rhizome and shoot organs were selected and ground to pass through a 0.425 mm mesh, with the aid of a Wiley-mill grinder. Starch and water soluble carbohydrates were analyzed. Starch was analyzed following the Perchloric acid method [39,40], while water soluble Carbohydrates (WSC) were analyzed by extracting with hot water [39,41]. Thereafter, concentrations were determined using a phenol-sulfuric acid mixture [42]. TNC was obtained by summing up the starch and WSC concentrations. Finally, the TNC stock was calculated by multiplying the TNC concentration with the biomass of the respective plant organs.

2.4. *Total nitrogen (TN) and total phosphorous (TP) concentrations*

Total nitrogen (TN) and total phosphorous (TP) in overlying water were determined using spectrophotometry, by the Koroleff colorimetric method (Nitrogen Spectroquant Method 00613-Merck, Darmstadt, Germany), and by the molybdenum blue colorimetric method [43] after digesting with $K_2S_2O_8$ in an autoclave (120 °C) for 30 min [26], respectively. Concerning sampled sediment for the two stands, TN and TP concentrations were measured by using a CHN-analyzer (Yanaco CHN Corder, MT-5, Japan) and by the ammonium–molybdate colorimetric method [43].

2.5. *Data analyses*

All statistical analyses, particularly unpaired t-tests and one-way analysis of variance (ANOVA), were performed by using SPSS version 12.0 for Microsoft Windows (dated September 2003, SPSS Inc., 1989–2003), so as to compare the seasonal variations of TNC, biomass, differences in sampling times, etc., between the two sites. The obtained values from the replicates were averaged, prior to further statistical analysis. Thereafter, a statistical comparison of those population averages was done.

The Akigase *Typha* stands have been subjected to almost similar meteorological conditions over the last 8 years (all $p > 0.05$ for annual temperature, solar radiation and precipitation, Kruskal–Wallis test), without being damaged by catastrophic floods, insects or disease for at least 10 years [37]. Due to relatively close proximity and similar geographical features, Teganuma *Typha* stands have undergone more or less similar climatic conditions (ANOVA, all $p > 0.05$ for annual temperature, solar radiation and precipitation). The climatic conditions affecting the growth of *T. angustifolia* were similar at both observation sites over the study years. Therefore, the difference in specific annual timing of growth between the sites had no significant effect on the outcome of our findings.

3. Results and discussion

3.1. *Variation of aboveground and belowground biomass*

The peak average aboveground biomasses for Teganuma stands were found to be about two times higher than those of Akigase (Figure 1). Also, belowground biomass was found to be

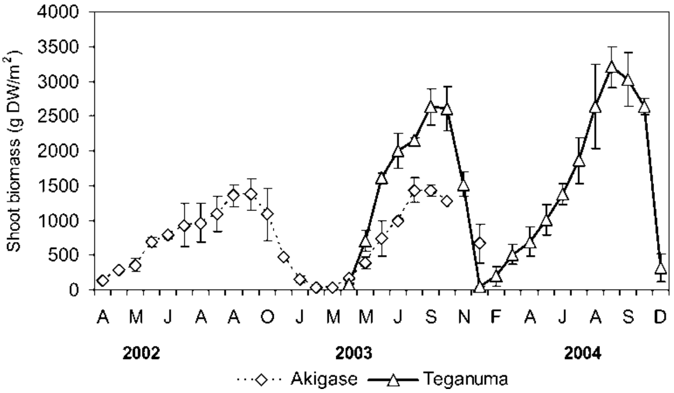

Figure 1. Seasonal variations of the average shoot biomass for *T. angustifolia* in Teganuma and Akigase. Each value is the average of three sampled quadrates. The bars indicate standard deviations.

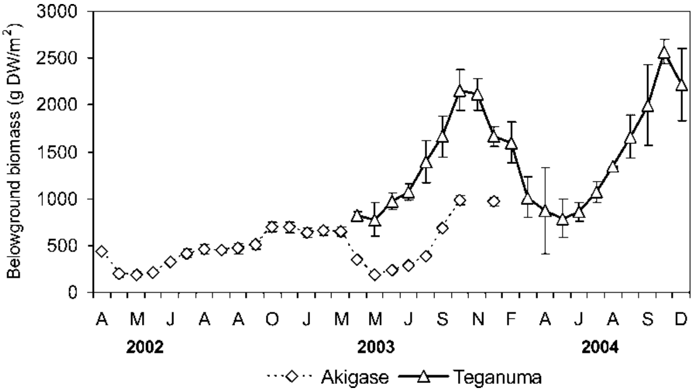

Figure 2. Seasonal variations of average belowground biomass for *T. angustifolia* in Teganuma and Akigase. Each value is the average of three sampled quadrates. The bars indicate standard deviations.

three times higher in Teganuma compared to Akigase (Figure 2). Although the seasonal trend of both above and belowground biomasses was similar in the stands, both (the former and the latter) were found to be significantly higher for Teganuma. (t-test, $^{*}p < 0.05$). Similarly, the biomass of all the belowground parts i.e. vertical rhizome (stem base), horizontal rhizome, plus roots were also found to be significantly higher for Teganuma compared to Akigase (for all, t-test, $^{*}p < 0.05$). The annual seasonal changes in biomass for both stands were similar to those reported elsewhere [44–46].

For the belowground biomass in Teganuma, the vertical rhizomes (stem base) were found to constitute a bigger proportion of the total belowground biomass compared to horizontal rhizomes (Figure 3), while the opposite was found for Akigase. One of the reasons for this relatively high proportion of vertical rhizomes in the deeper stand could be due to the translocation of reserved resources to shoots more rapidly during the early growing period, when shoots need to grow fast, plus their location in the rhizome hierarchy.

Besides, being subjected to strong winds blowing against the stands embedded in extremely soft substrate composed of accumulated organic sediments, the stands in Teganuma require stable, reliable anchorage to sustain the relatively long and bigger shoots, compared to Akigase. *Typha* in Teganuma most likely developed bigger vertical rhizomes to sustain the plant body, just in case disturbance occurs [35]. On the other hand, the root organs occupied the lowest portion for both sites (Figure 3).

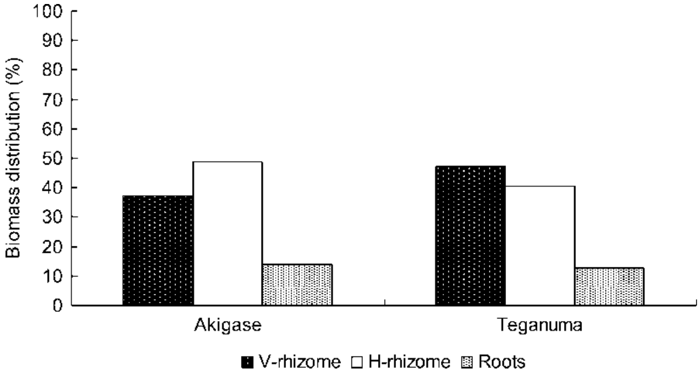

Figure 3. The belowground biomass distribution (%) for vertical rhizomes (V-Rhi), horizontal rhizomes (H-Rhi) and roots of *T. angustifolia* for both Akigase (A) and Teganuma (T).

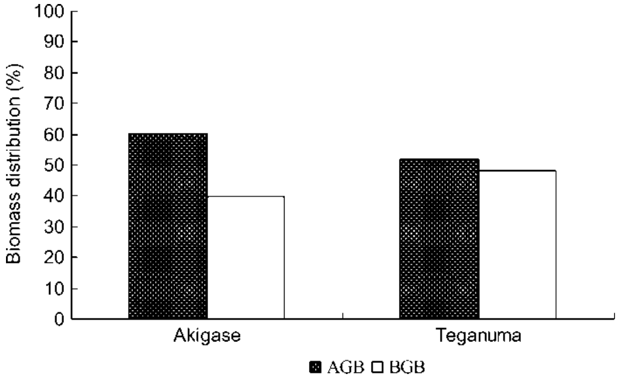

Figure 4. The total biomass distribution (%) for aboveground organs (AGB) and belowground organs (BGB) of *T. angustifolia* for both Akigase (A) and Teganuma (T).

The biomass distribution between aboveground and belowground biomass showed that Teganuma stands allocated 55% of the total biomass to the aboveground parts, while the Akigase stands allocated 60% of their total biomass to the same (Figure 4). Several studies have shown that plants growing in deeper waters allocate higher fractions of biomass to the aboveground parts in order to maintain a positive carbon balance [47]. In our study also, it was observed that both stands allocated more than 50% of their total biomass to the shoot organs. Grace and Wetzel [17] stated that the rhizome fraction versus total biomass is smaller in deeper populations mainly because of the need to ventilate the rhizosphere [4,36,48]. However, an opposite trend was observed in our study.

Clevering and Hundschneid [14] and Grace [1] reported higher allocation to the shoots, only for the species that grow in ‘intermediate water-depth zones’, but not for those growing in ‘deep-water zones’. Conversely, Grace [1] reported that deep water species such as *T. domingensis*, increase allocation particularly to the rhizome, as the depth increases. A similar observation was reported for the *E. sphacelata* species, which mainly proliferates in organic dominated soil substrates [4].

In addition, other studies have indicated that water depth reduces plant anchorage capacity by decreasing biomass allocation to the rhizomes [15,17]. This was also not observed in our study. Grace [1], on the other hand reported that *T. domingensis* adopted a deep water survival strategy through changes in shoot and ramet morphology, but not through biomass allocation patterns.

3.2. *Shoot morphology*

Figure 5 shows the seasonal variation of shoot heights for the two stands. Although, the maximal average shoot height for Teganuma was higher than that of Akigase, the difference was not significant between them (t-test, $^*p > 0.05$). Shoot elongation is the usual and well documented plant response to flooding [1,10,15,33,49]. However, some authors have suggested no response to shoot lengths in the aftermath of floods [50], while others have even suggested negative growth responses [51].

However, the plants in the Teganuma stands, compared to Akigase, depicted faster growth rate during early growth season (Figure 5). This early rapid response is one of the most important tolerance strategies for plants growing in deep water, and has been reported in some plants, because their survival under water will probably not be longer than two months [27,28,52]. Therefore, for them to survive and grow well, they ought to depict a rapid response in maintaining sufficient shoot area above the water surface during early growth, where they can get more access to light, oxygen and carbon dioxide, for adequate gaseous exchange [9,53].

The difference in shoot basal diameter was insignificant during the early growth stage, but later depicted a remarkable increase in Teganuma (Figure 6), consequently giving a significant difference (t-test, $^*p < 0.05$). Several studies have shown that the deep water strain results into

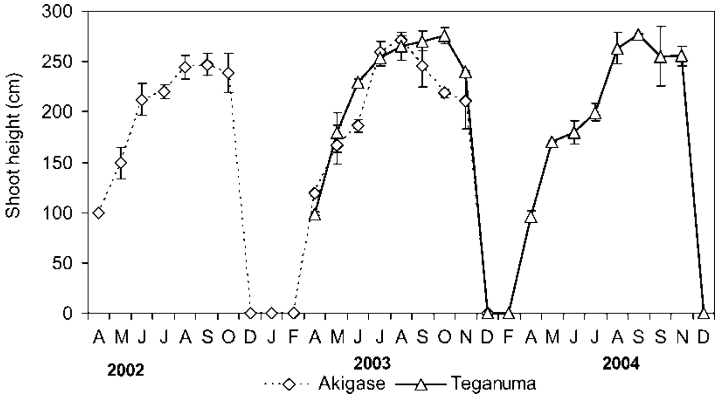

Figure 5. Seasonal variations of average shoot heights for *T. angustifolia* in Teganuma and Akigase. Each value is the average of three sampled quadrates. The bars indicate standard deviations.

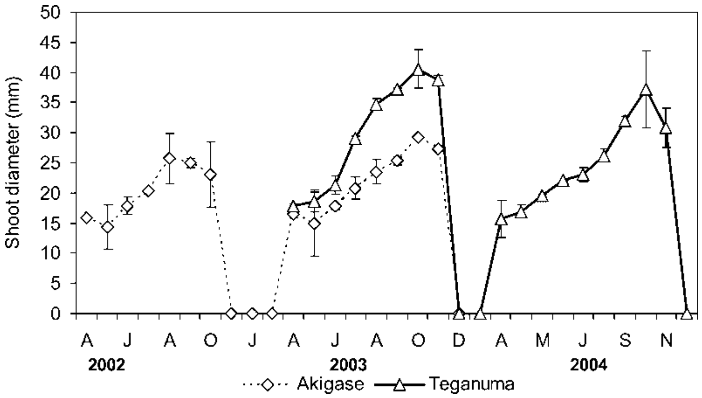

Figure 6. Seasonal variations of average basal shoot diameters for *T. angustifolia* in Teganuma and Akigase. Each value is the average of three sampled quadrates. The bars indicate standard deviations.

low internal resistance in the basal parts of the stem of emergent macrophytes [54–56]. Under such conditions, the stem swells at the base, which helps the plants to enhance aeration by increasing the porosity of the stem base [8,9,20,21].

Thus, the bigger shoot basal diameter in Teganuma was likely to increase ventilation capacity by facilitating flow of oxygen to the rhizosphere and roots, and reducing resistance to gas flow [4,6,36,54–56]. Although, bigger basal diameters effectively reduce gas flow resistance as discussed above, the same changes may also be seen as structural responses to mechanical bending stress in deeper habitats, rather than oxygen stress alone. In our study, we did not measure mechanical stresses, neither did we lay emphasis on it, since it wasn't the main focus.

Further to the above, higher shoot density was found in Teganuma compared to Akigase (Figure 7). Although, some studies have reported that shoot density decreases with increasing water depth [1,4], in this study there was no trend to that effect. Probably other factors like substrate type, nutrient availability [2,4,28] also affected shoot density. In our study we performed a scanty analysis of the effect of nutrients on growth dynamics. Therefore, discussions on the same have been limited. Conversely, Grace and Wetzel [38] reported a general increase in shoot density with increasing depth for monoculture and mixed stands of *T. angustifolia*.

3.3. *Rhizome morphology*

Figure 8 shows the average monthly rhizome lengths for the two stands. Although the average monthly length of rhizomes in Akigase was 3 cm longer than that of Teganuma, the difference between them was insignificant (t-test, $^{*}p > 0.05$). Some studies showed that plants that grow in deep water produce shorter rhizomes in order to reduce the oxygen transportation distance [19]. However, White and Ganf [25] reported that *T. domingensis* produced significantly longer rhizomes as water depth increased. Unfortunately, we did not collect dissolved oxygen data in order to analyze the degree of anoxicity in both habitats. This is one of the shortcomings of our study. The rhizome length is also important for foraging capacity [9,21] and anchorage [36].

In addition, the Teganuma rhizomes were thicker than those of Akigase (Figure 9), and the difference between the two sites was significant (t-test, $^{*}p < 0.05$). Some studies have reported that plants growing in deep water habitats produce short but thicker rhizomes [16,19]. This necessitates these plants to put a high demand on oxygen consumption, in order to maintain a constant internal oxygen concentration, thus bracing themselves against anoxic conditions [55].

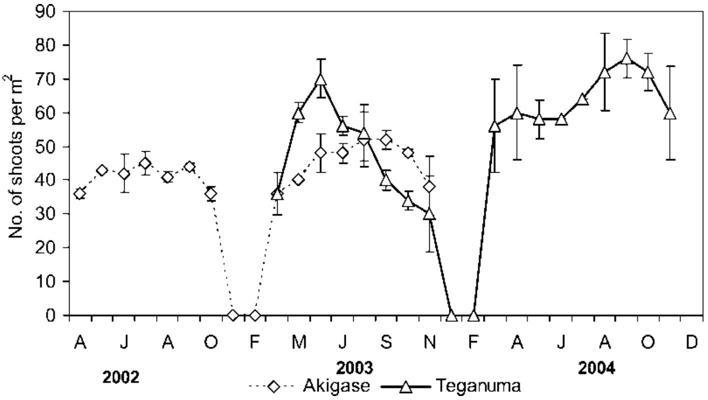

Figure 7. Seasonal variations of average shoot densities for *T. angustifolia* in Teganuma and Akigase. Each value is the average of three sampled quadrates. The bars indicate standard deviations.

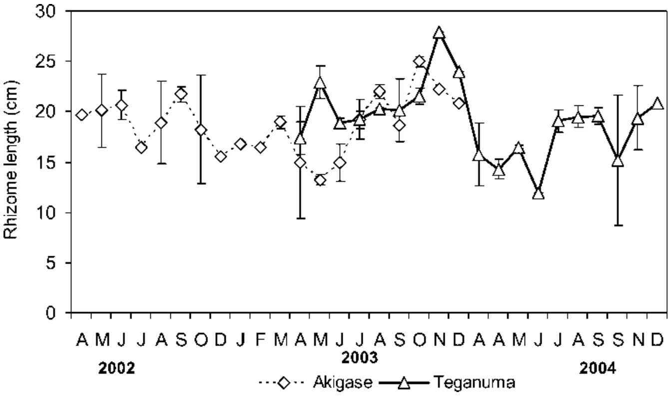

Figure 8. Seasonal variations of average monthly rhizome lengths for *T. angustifolia* in Teganuma and Akigase. Each value is the average of three sampled quadrates. The bars indicate standard deviations.

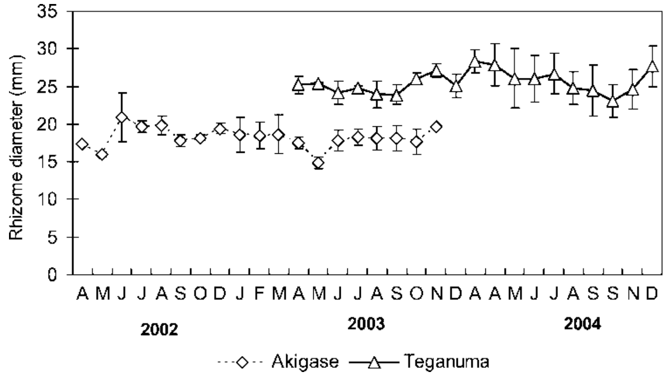

Figure 9. Seasonal variations in the average rhizome diameter for *T. angustifolia* in Teganuma and Akigase. Each value is the average of three sampled quadrates. The bars indicate standard deviations.

The relatively thicker rhizomes in Teganuma help maintain high tissue porosity required for internal gaseous transport, therefore efficient oxygen transport to the rhizosphere can be easily achieved [7,55–58]. Sorrell and Tanner [36] also reported thick rhizomes for *E. sphacelata* plant species growing in deeper water. Brändle and Crawford [31] reported that plants with thicker rhizomes were able to survive for longer periods of time compared to those with smaller rhizomes, when they are subjected to anoxic conditions.

3.4. *Total non-structural carbohydrates (TNC) storage dynamics*

The TNC stocks for shoots and rhizomes are as depicted in Figures 10 and 11, respectively. The *Typha* population in Teganuma, compared to that of Akigase, had significantly higher TNC stocks per unit area (t-test, $^{*}p < 0.05$). Since Teganuma was two times deeper than Akigase, the Teganuma *Typha* population is likely to experience more oxygen stress [2,4,5], especially during the early growth period, or after occurrence of senescence, compared to the Akigase population [27,28,31].

Therefore, they require greater amounts of glucose to produce sufficient adenosine triphosphate (ATP) for the continuation of cell metabolism [29,30,62]. The comparatively high reserves of TNC in Teganuma seem to be one of the important tolerance strategies to overcome stress caused by

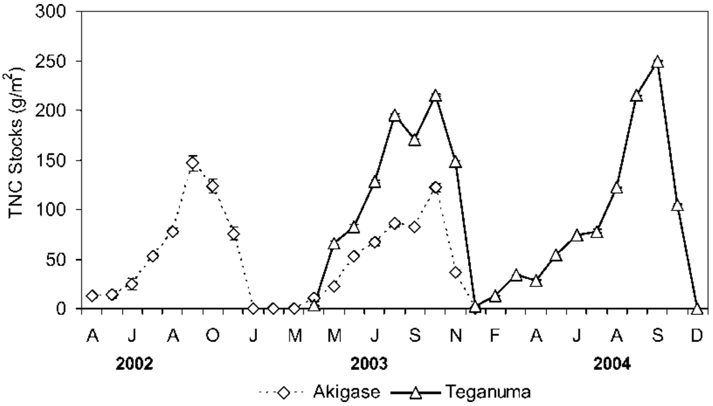

Figure 10. Seasonal variations of shoot TNC stocks for *T. angustifolia* in Teganuma and Akigase. Each value is the average of three sampled quadrates. The bars indicate standard deviations.

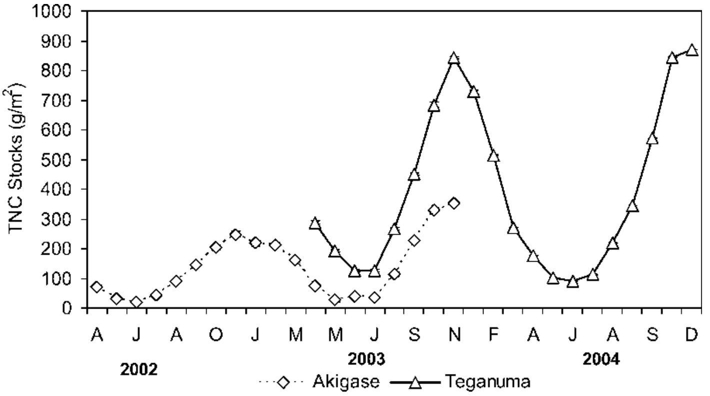

Figure 11. Seasonal variations of rhizome TNC stocks for *T. angustifolia* in Teganuma and Akigase. Each value is the average of three sampled quadrates. The bars indicate standard deviations.

anoxia, and to endure longer periods of anoxia [26–28]. In addition, plants in Teganuma require more energy stocks to support the rapid shoot extension above the water surface, especially during early growth [9,53].

Since stem growth is rapid in order to break forth above water, the plants then come into contact with oxygen and carbon dioxide, before the TNC winter reserves are exhausted [53,59,63]. For the plants that are growing in deep habitats, balanced carbohydrate storage and use may be of more importance as they require more reserve material not only to support rapid shoot growth [28,52], but also for the survival of new shoots during subsequent growth periods, failure to do so may cause them to be vulnerable to environmental stress [31,55,63].

4. Conclusion

Finally, from this study, it can be inferred that *T. angustifolia* responds to changes in water depth by producing thick and strong shoots, thicker rhizomes and TNC storage, in order to address the challenges that inevitably arise from water depth increase. One of the challenges is to build resilience towards anoxic conditions for longer periods of time, especially during early spring.

However, the decrease in number of shoots and the allocation of lower biomass to the rhizome with increasing water depth was not observed in this study, as reported by other researchers. This is most probably due to the fact that, water depth can't solely and exhaustively describe shoot density or biomass allocation patterns in plants. For instance, in our study we performed a scanty analysis of the effect of nutrients on the growth dynamics. Therefore, other factors like *in-situ* nutrient availability, sediment composition and sediment chemistry, also probably play their roles [60,61]. Further in-depth research, in the two stands is needed to further investigate to what extent these factors affect the morphology, growth and carbohydrate storage dynamics of *T. angustifolia*.

Acknowledgements

The authors are greatly indebted to colleagues at the Ecological Engineering Laboratory, Saitama University (Japan), who offered their technical support, especially during field work and data collection.

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