Dynamics of the reedbed at the interface of *Typha angustifolia* and *Phragmites australis patches*

Results for 2018 to 2020

Report within the framework of
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Abstract

Aim: During the last 35 years, large scale changes have been observed in the reedbed communities of Prespa National Park (PNP), especially around the area of Vromolimni. More specifically, narrowleaf cattail (*Typha angustifolia* L.) has largely encroached upon common reed [*Phragmites australis* (Cav.) Trin. ex Steud.] stands. In previous works with field research and experiments, we hypothesized that (1) the underlining cause was disturbance events and (2) in the absence of disturbance *P. australis* should outcompete *T. angustifolia*. The aim of this work is to assess if the expansion of *T. angustifolia* against *Phragmites australis* is still an ongoing process or conversely if *P. australis* is increasing its extension at the expense of *T. angustifolia.*

Methods: 10 transects, 30 m each, were established at the interface of the dominant vegetation types and were marked with metal piles. On each transect, the same 30 quadrats (0.4 X 0.4m) were sampled in 2018, 2019 and 2020. The structure of the helophyte vegetation (for each species the density of living and dead shoots, the height and basal diameter of the tallest shoot), and the species composition of vegetation (cover estimated for each taxon) were recorded in each quadrat. The topographic position was measured in 2018 as the water level in each quadrat and using DGPS in November 2020.

Analyses: The change in the number of quadrats occupied by each species between 2018, 2019 and 2020 was tested using Wilcoxon non-parametric analysis of variance. Analysis of variance for repeated measures (MANOVA) were applied to test changes between years in the parameters of the structure (density, shoot diameter and height). The effect of topography on the parameters of structure of each species was tested along with the effects of the Year and of the density and height of the other species using General Linear Models. All analyses were performed with Statistica software.

Results: 2018 and 2019 were contrasting years, the latter being characterized by low lake water level and extensive wildfires throughout most of the reedbed. 2020 was even drier than 2019, resulting in a strong drought in the reedbed. *P. australis* and *T. angustifolia* showed contrasting trends in the number of quadrats occupied. *P. australis* occupied an increasing number of quadrats in 2019 (+27) and in 2020 (+14) while *T. angustifolia* showed a contrast with a decreasing number of quadrats occupied in 2019 (–14) and in 2020 (-6).

During 2020 the density of *P. australis* decreased by 5% (after 90% increase in 2019), while its maximum height per quadrat increased by 4% (after 27% decrease in 2019). The basal diameter of *Phragmites* shoots decreased in 2020 (-14%) after the 12% decrease in 2019. For *T. angustifolia*, shoot density increased by 17% (half of 2019 lost), the height decreased by 23%, adding to the 36% decrease in 2019 and the basal diameter of shoots further decreased by 35% after 18% decrease in 2019. The comparisons between species in the hierarchy of likely causal factors suggest that *Phragmites* population was more affected by the hydrology (especially for shoot height) although a negative correlation of its density and shoot diameter was found with *Typha* density and height. In contrast, *Typha* population seems to be more affected by competition with *P. australis* whose density and height explain 94% of the variance of *Typha* density, and 57% of shoot diameter. The topographic position (closely related to hydrology) explains less than 5% of the variance of *Typha* structural parameters and between 8 (Density) and 36% (Height) of the *Phragmites* structural parameters.

Main conclusions: The observed trends in quadrat occupancy by *P. australis* and *T. angustifolia* and the changes in the population parameters of both species are consistent with our previous hypothesis of recolonization and higher competitive performance of *P. australis*. However, it is not known if the observed trends will continue in wetter conditions.

Keywords: *Phragmites australis*, common reed, *Typha angustifolia*, Prespa National Park, reedbed, ecotone, vegetation dynamics, reedbed encroachment, vegetation management

1. Introduction

The Common reed *[Phragmites australis* (Cav.) Steud.)] and the Narrow-leaf cattail *(Typha angustifolia* L.) are among the most common species in tall-helophyte wetland communities and are found in a wide range of conditions (soil, climate and nutrients). Both species tend to establish monospecific stands along lake shorelines resulting in a strong zonation pattern. This zonation results from the interplay between plant traits and various environmental factors, among which hydrology and nutrients are the most frequent drivers (review in Grillas et al. 2018). During the last 30 years, changes at the helophyte vegetation of Lake Lesser Prespa, NW Greece, have occurred, and more specifically around the area of Vromolimni (Figure 1). In this area narrow leaf cattail encroached against the common reed. During the same period the fluctuation of the water level of Lesser Prespa has been reduced after the creation of a sluice on the outlet/outflow that connects Lesser and Great Prespa while, in addition, the intensive agriculture continued resulting in a high nutrient inflow.

Physico-chemical factors are usually found as the main determinants of plant distribution in wetlands (e.g. Hutchinson 1975, Spence 1982, Duarte & Kalff 1986). Water depth has been identified as the main environmental factor selecting species on their total height, and thus access to air, and tolerance to flooding constraints (Seabloom et al. 2001, Sorrell & Hawes 2010, Sorrell, Tanner & Brix 2012). Other abiotic factors can play a role, notably wave energy and soil. However, clonal growth and high biomass favours establishment of plant communities heavily dominated by a single species (e.g. *Phragmites australis*, *Typha* spp.*, Scirpus* spp.) where competition plays an important role (Grace & Wetzel 1982, Wilson & Keddy 1985, Weisner 1993). Grazing can modify the outcome of competition and influence zonation patterns.

The conclusions of previous works investigating the potential causes of the encroachment of *T. angustifolia* in *P. australis* stands (Grillas *et al.* 2018; Sakellarakis *et al.* 2018; Sakellarakis & Grillas, 2019; Grillas & Sakellarakis, 2020a) were the following:

- The depth distribution of *P. australis* and *T. angustifolia* did not differ across the stations studied;
- Although some differences in soil chemistry were found between stations, no significant relationship could be documented between the two main dominant species;
- The nitrogen and phosphorus content of *P. australis* and *T. angustifolia* plant tissues did not differ significantly, further suggesting that nutrient status is not a key variable for explaining the dominance of species;
- The structure of the reedbed (density, height, diameter of shoots) suggests competitive interactions but did not allow identifying a competitive hierarchy;
- The floristic composition of the companion species only marginally differed between reedbed types;
- Therefore, the remaining hypothesis to explain *T. angustifolia* encroachment is a major disturbance which may have killed large areas of *P. australis.* The severe drought experienced by the lake in 1989 – 1990 could be such an event. The highest water level observed the following year could further explain *T. angustifolia* establishment: this species produces many more seeds than *P. australis* and its seedlings are more tolerant to flooding.

Once established, *T. angustifolia* can prevent the germination of *P. australis*. However, the latter is expected to be more competitive than *T. angustifolia* and should have recolonized the lost area by lateral (vegetative) growth. Frequent fires may stop and reverse this succession. This hypothesis has been supported with field experiments that showed that long flooding after wildfire events or cutting, results in strong decrease of the density of *P. australis* culms and can significantly modify all of its important structural parameters (Sakellarakis & Grillas, 2019).

- More work is needed to understand the dynamics of the reedbeds in the Vromolimni area. It will include experimental management, monitoring of the interaction between *T. angustifolia* and *P. angustifolia* by field measurement and drone survey.

In this perspective, the general objective of this work is to monitor the dynamics of the reedbed at the interface of *Typha* and *Phragmites* patches in order to identify a potential spatial trend of these two species and identify the competitive dominance at the interface of their patches.

The specific objectives were to answer the following questions / hypotheses:

- In absence of disturbance is *Phragmites* encroaching on *Typha* dominated stands?
- Is the structure of *Typha* population showing a declining trend (decreased density, height and diameter of shoots) possibly resulting from competitive dominance of *Phragmites?*

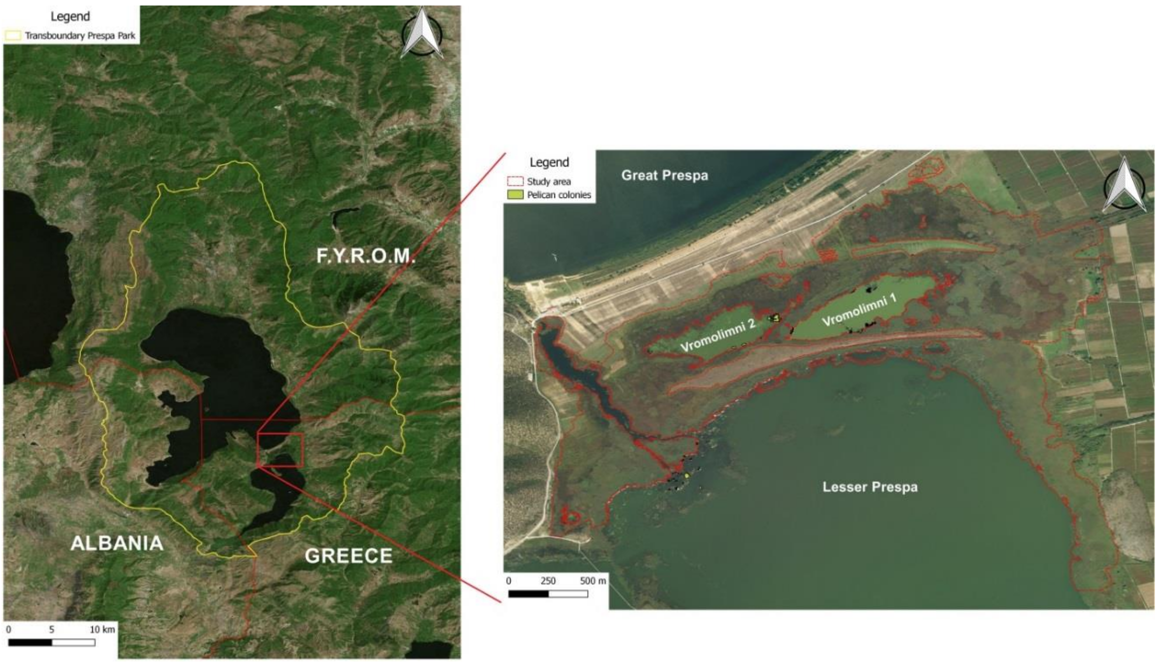

Figure 1. Study area.

2. Methods

2.1. Site selection

Twelve transects, in blocks of three, were randomly selected at the interface of *Phragmites australis* and *Typha angustifolia* dominated patches. As a result of large scale wildfires in 2019 two transects (T5 and T8) were lost, then only 10 transects were monitored in 2019 and 2020 (Figure 2). On each station a 30m permanent transect was established in 2018 and was oriented in a way to include approximatively 3 different zones, (1) a pure stand of *P. australis*, (2) a pure stand of *T. angustifolia* and (3) a mixed zone at their interface.

On every sampling station, the start and the end of each transect was marked with an iron bar and their coordinates taken using a handheld GPS (Garmin 64 Map). DGPS points were collected from each transect in October 2020 in order to have accurate elevation data. In every transect 7 points were marked, starting from the beginning of the transect and following a 5-meter interval.

2.2. Vegetation measurements

On each transect the structure of the reedbed was measured each year in July on 30 quadrats (0.4 X 0.4m) placed every meter. In these quadrats the number of living and of dead shoots of *Phragmites australis* and *Typha angustifolia* were measured, and for each of these species the total height and the basal diameter (measured about 10cm above soil surface) of the tallest shoot. In addition, every plant taxon was recorded and its cover in the quadrat was estimated according to a modified Braun Banquet scale (Braun Banquet 1964; see Grillas et al. 2018). When present, water depth was measured on every quadrat.

2.3. Environmental conditions

- The study period was characterized by major events. During winter 2018 (November) an extreme event of snowfall was recorded which resulted in heavy damages across the whole reedbed vegetation of Lesser Prespa. This event had an effect on all sampling stations, broke the standing stems of *Phragmites*) and additionally transformed the *Typha* stands with the creation of a closed and compact layer of dead biomass.
- 2018 was a wet year and the water level of lake was above the mean from the second trimester until the end of the year (Figure 3). For more information on Prespa climate see Grillas and Sakellarakis 2020).
- Conversely 2019 was a dry year and 2020 an extremely dry year (mean water level of 2020: 853.57, mean since 1969: 853.87) with the water level of Lesser Prespa reaching very low values especially during the period mid-March until the end of July (Figure 3), a critical period for the growth of the characteristic helophyte species that compose the reedbeds of Prespa.
- Large scale wildfires occurred during winter-spring 2019 burning 300 ha of reedbeds of Lesser Prespa (Photo 2) (Figure 4; Willm et al., 2020). All sites, except transect 10, 11 and 12 were affected by these wildfires, even though not in the same degree. Transect 9 was partially burnt. During 2020, three large scale wildfire events were recorded and mapped in Prespa resulting in about 54 hectares of burnt reedbeds, including 37.5 ha which had been already burnt in 2019 (Figure 4). None of these events affected the permanent transects in 2020.

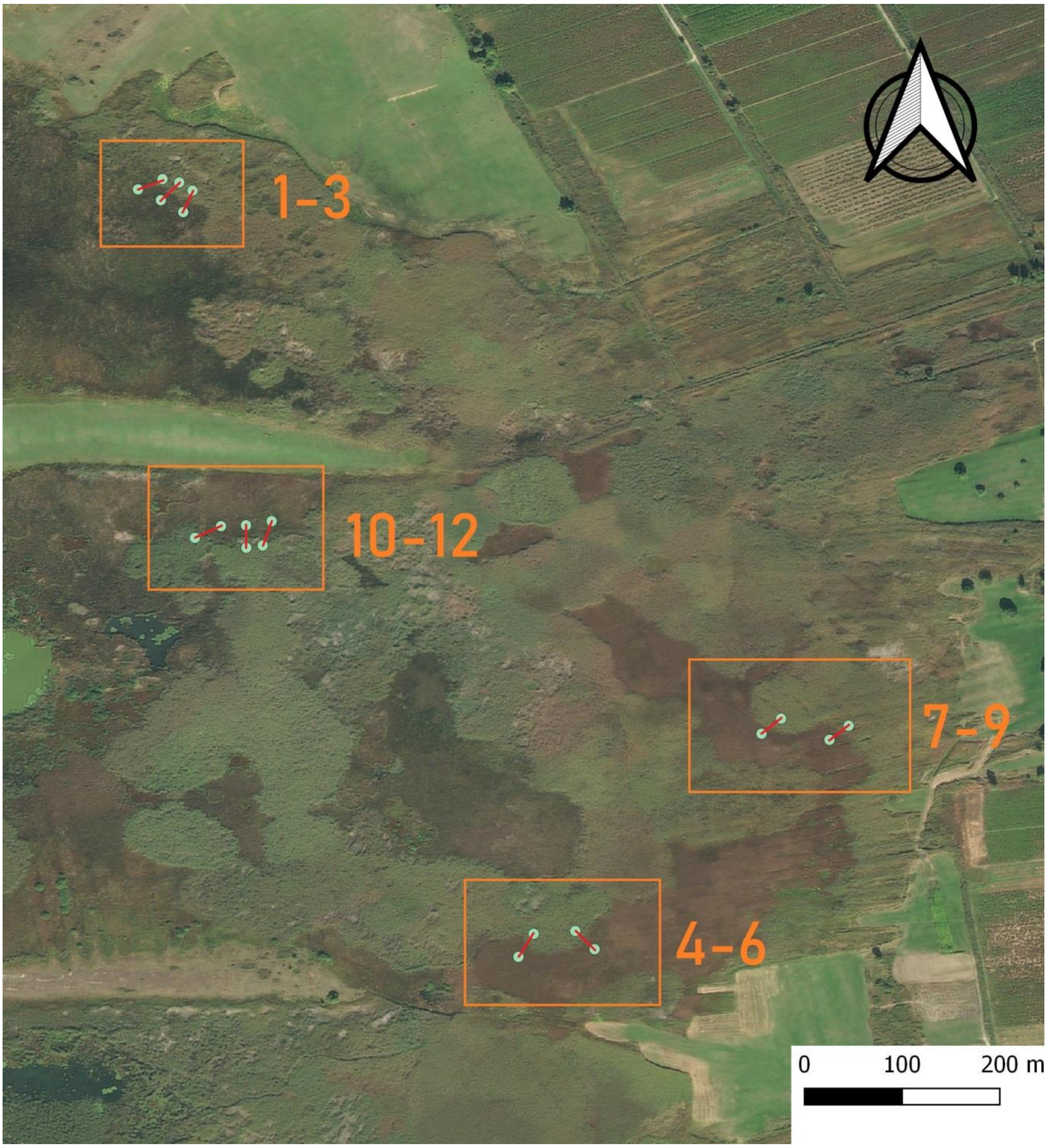

Figure 2: Location of transects.

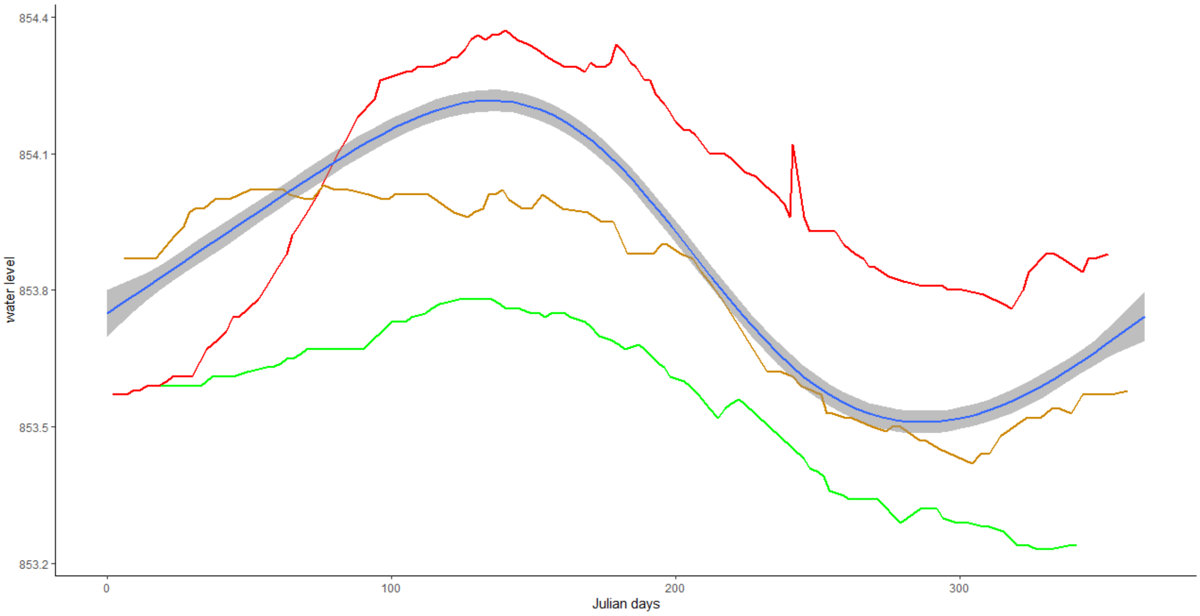

Figure 3. Water level (m) of Lesser Prespa during 2018 (red), 2019 (dark ochre), and 2020 (green); Julian day 0 is the 1st of January. Water level fluctuations from 1969 till 2020 are depicted with the blue line corresponding to the mean and grey to the intervals of the standard error.

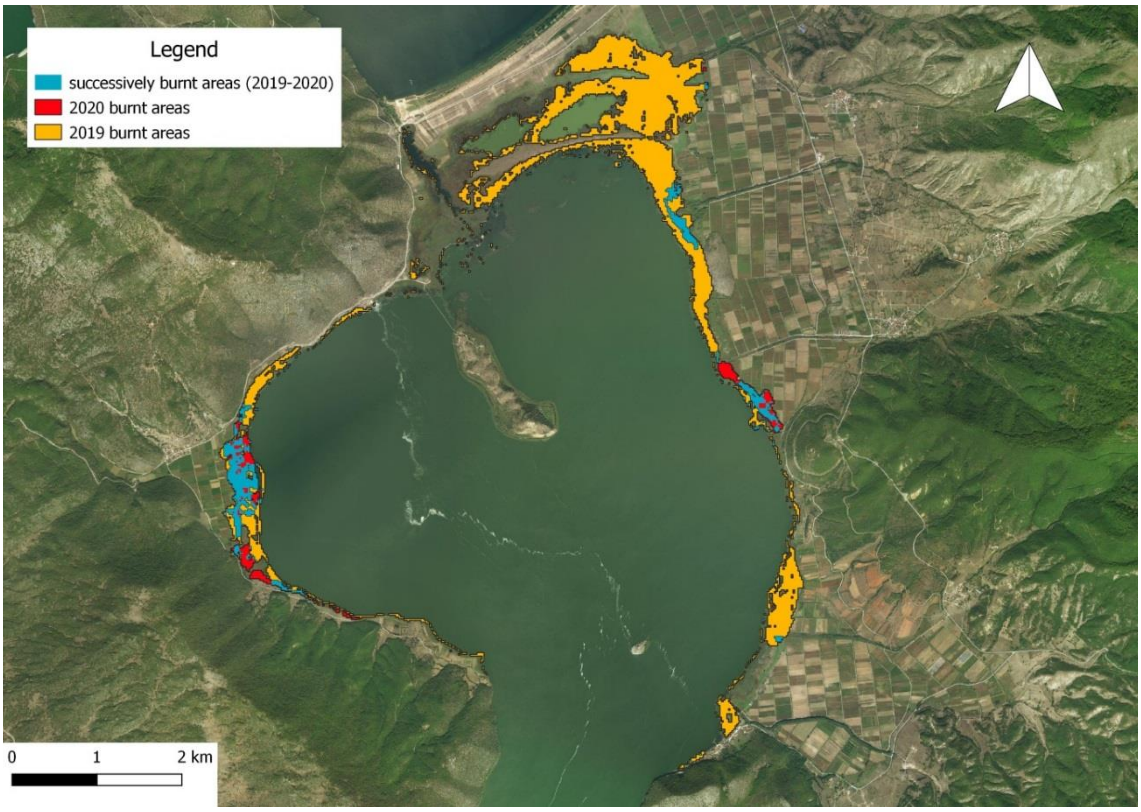

Figure 4. Areas burnt in 2019 and in 2020 as well as areas burnt successively (2019 & 2020) in the reedbeds of Lesser Prespa. (from Willm et al. 2020).

2.4. Data analysis

2.4.1. Physical expansion of the *Phragmites* and *Typha* along permanent transects.

For each species (*Phragmites australis* and *Typha angustifolia*) the number of quadrats occupied in 2018, 2019 and 2020 were compared. The presence / absence of *P. angustifolia*. on each quadrat was compared between successive years and value +1, 0 or -1 was attributed respectively when a quadrat was newly occupied, remained unchanged (remained empty or remained present both years) or when the species disappeared from that quadrat. The same procedure was applied to *T. angustifolia*. The sum of the values per quadrat was calculated in 2019 and 2020 as the net annual budget of increases and decreases. A Wilcoxon non-parametric analysis of variance for paired samples was used to compare the trends of *Phragmites australis* and *Typha angustifolia* over the 10 transects. The relation between the variation between years of the number of quadrats occupied by *T. angustifolia* and by *P. australis* was tested using Spearman rank correlation.

2.4.2. Annual dynamics of the structure of the reedbed between 2018 and 2020

The parameters of the structure studied were for each species the density of living shoots and the height and shoot diameter of the dominant (tallest) living shoot per quadrat. Previous work in Prespa reedbeds showed that these parameters are strongly correlated between them for each species and are good descriptors of the structure of the reedbed for both species (Grillas et al. 2018). The shoot density values per quadrat were transformed (√ density) for variance analyses in order to meet the distribution assumptions, while no transformation were needed for the height and the basal diameter of shoots.

The variations between 2018, 2019 and 2020 of the parameters of the structure for *Phragmites australis* and *Typha angustifolia* were studied using analysis of variance for repeated measures (MANOVA) where quadrats were considered as samples within transects. Only quadrats where the species was present in at least one year were used in order to reduce the number of zero values and prevent bias in mean values. In these MANOVA the effects tested were the Year, Transect and their interaction. When significant differences were found, a post hoc test (LSD Fisher) was performed for pair comparisons.

2.4.3. Effects of environmental variables and competition on *P. australis* and *T. angustifolia*

For each of the two dominant species (*P. australis* and *T. angustifolia*) the effect of the year, of the topographic location (elevation) of the transects (a substitute to hydrological conditions), and the density and height per quadrat of the other dominant species were tested. We used General linear models to assess the effect of each variable on the density, the height and the basal diameter of shoots of *P. australis* and *T. angustifolia*.

3. Results

3.1. Physical expansion of *Phragmites* / *Typha* along permanent transects

Phragmites australis and *Typha angustifolia* showed contrasting trends between 2018 and 2020 (Figure 5, Table 1a,b). *P. australis* was present on 188 quadrats in 2018, 215 quadrats in 2019 (+27 quadrats,) and 229 in 2020 (+14 quadrats; +41 quadrats in 2 years). Out of 10 transects, the number of quadrats occupied by *P. australis* was higher in 8 transects in 2019 and 5 transects in 2020. Over the two years all transects showed an increase in the number of quadrats where *Phragmites australis* was present; the increase ranged between 1 (T1) and 9 quadrats (T5 and T10) (mean= 4 quadrats). Conversely, *T. angustifolia* showed a declining trend (Figure X, Table 1a,b); the species. The number of quadrats occupied by *T. angustifolia* had decreased on 7 transects in 2019 and 5 transects in 2020. Over the two years, the number of quadrats occupied by *T. angustifolia* has decreased on 5 transects (T1, T5, T7, T9 & T10), remained stable on 3 (T3, T11 & T12) and had increased on 2 transects (T2 & T4).

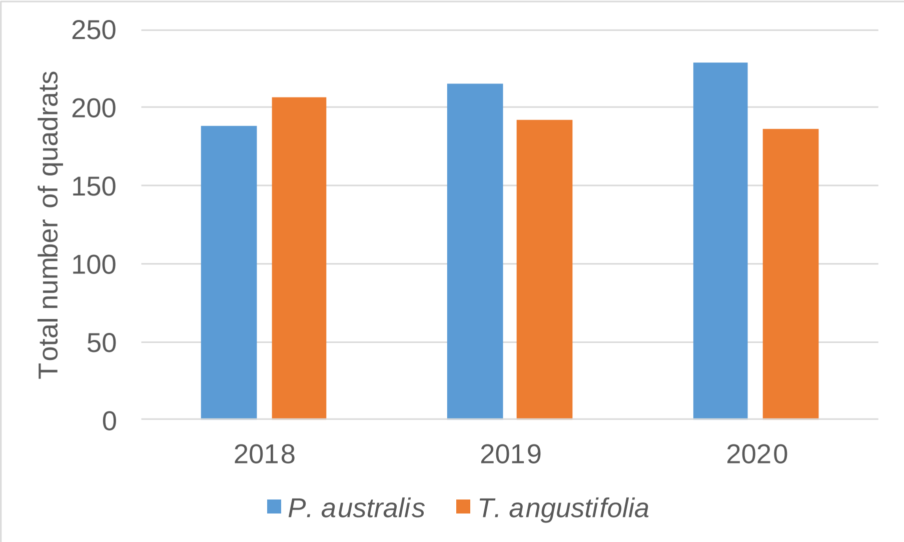

Figure 5. Cumulated number of quadrats occupied per year by *P. australis* and *T. angustifolia* on the 10 monitored transects.

Table 1. Variation between 2018 and 2019 in the number of quadrats occupied by *Phragmites australis* (PA) and *Typha angustifolia* (Ty) in each transect and the cumulated sum of these changes; a) Change in occupancy between years (18= 2018, 19= 2019, 20= 2020).; b) Results of Wilcoxon test for paired samples (significant p-values are in red).

a) Change in quadrat occupancy

	Phragmites australis			*Typha angustifolia*		
Transects	19-18	20-19	20-18	19-18	20-19	20-18
T1	0	1	1	-7	-2	-9
T2	-1	3	2	1	1	2
T3	3	-1	2	-1	1	0
T4	2	1	3	3	-1	2
T5	9	0	9	-2	-4	-6
T7	3	0	3	0	-5	-5
T9	2	4	6	-3	2	-1
T10	5	4	9	-2	-2	-4
T11	2	2	4	-1	1	0
T12	2	0	2	-3	3	0
Total	**27**	**14**	**41**	**-15**	**-6**	**-21**

b) Results of Wilcoxon test for paired samples (significant differences p<0.05 are shown in red).

Wilcoxon test for paired samples				
Comparisons	N	T	Z	p value
PA 19-18 & Ty 19-18	10	3.000	2.497	0.012516
PA 20-19 & Ty 20-19	10	10.000	1.784	0.074463
PA 20-18 & Ty 20-18	9	0.000	2.666	0.007686
PA 19-18 & PA 20-19	9	14.000	1.007	0.313939
Ty 19-18 & Ty 20-19	8	12.000	0.840	0.400815

The trend in the number of quadrats occupied between 2018 and 2019 and between 2018 and 2020 differs significantly between *P. australis* and *T. angustifolia* (Wilcoxon for paired samples, Table 2b). However, no correlation was found between the changes in the number of quadrats occupied by both species between 2018 and 2020 (Spearman R= -0.2038; p > 0.05).
No correlation with water depth was found with the changes in the number of quadrats occupied by *P. australis* (Land elevation: F= 0.0529, p= 0.824) or *T. angustifolia* (water level: F= 0.0700, p= 0.798).

3.2. Structure of the reedbed

Phragmites australis

The density of living shoots of *Phragmites australis* was significantly higher in 2019 and 2020 than in 2018 with a significant effect of the Transect and of the interaction Transect X Year (Table 2a, Figure 6a). Most of the variance results from the large differences between quadrats within transect which is explained by the heterogeneity of the transects and the small size of the quadrat. The remaining variance is explained by differences between years (79%) while differences between transects and the interaction between transects and year explain respectively 11% and 10%.

The mean density of living shoots had doubled in 2019 (from 4.1 to 8.4 shoots/quadrat) with large differences between transects. The increase was the largest in transects 3- 2- 1 (respectively +296%, +271%, +158%, $p < 10^{-7}$). The increase of density between 2019 and 2018 were smaller but significant for T6 (p= 0.000036) and T12 (p= 0.000081) (pair comparisons, post hoc LSD test Fisher) and not significant for other transects (T4, T7, T9 and T10) (Table in Figure 5). In 2020, the density of shoots decreased slightly from values in 2019 but remained much higher than in 2018. In 2020, the density of shoots decreased slightly from values in 2019 but remained much higher than in 2018. The density in 2020 was intermediate between 2018 and 2019 on Transects T1, T2 and T3 and was higher than in 2018 and 2019 on transects T9, T10 and T11.

Table 2. Results of the MANOVAs testing for the effects of Year, Transect and their interaction on the variation between 2018 and 2019 of a) shoot density, b) Height and c) basal diameter of shoots of *Phragmites australis*.

a) Density	SC	Degree of freedom	F	p
ord. Origin	3344.25	1	3737.04	0.000000
transect	68.74	9	8.53	0.000000
Error	154.82	173		
YEAR	54.02	2	60.87	0.000000
YEAR*transect	60.60	18	7.59	0.000000
Error	153.54	346		

c) Height	SC	Degree of freedom	F	p
ord. Origin	6097.144	1	18208.32	0.000000
transect	140.862	9	46.74	0.000000
Error	57.930	173		
YEAR	132.547	2	347.87	0.000000
YEAR*transect	18.069	18	5.27	0.000000
Error	65.917	346		

b) Diameter	SC	Degree of freedom	F	p
ord. Origin	44702.22	1	11541.39	0.000000
transect	1345.60	9	38.60	0.000000
Error	670.07	173		
YEAR	546.74	2	89.10	0.000000
YEAR*transect	175.48	18	3.18	0.000017
Error	1061.56	346		

Table 3. Pair comparisons for differences between years (18 ; 19 ; 20) for each transect for the density of shoots and the height and basal diameter of the tallest shoot of *P. australis* per quadrat ; for each transect and parameter, years with the same letter (a, b or c) are not statistically different(p<0.05).

(a) *Phragmites australis*			
Transect	**Density**	**Height**	**Diameter**
T1	18^{a} 19^{b} 20^{c}	18^{a} 19^{b} 20^{c}	18^{a} 19^{b} 20^{b}
T2	18^{a} 19^{b} 20^{c}	18^{a} 19^{a} 20^{c}	18^{a} 19^{a} 20^{b}
T3	18^{a} 19^{b} 20^{c}	18^{a} 19^{b} 20^{b}	18^{a} 19^{b} 20^{b}
T4	18^{a} 19^{ab} 20^{b}	18^{a} 19^{b} 20^{b}	18^{a} 19^{b} 20^{c}
T6	18^{a} 19^{b} 20^{ab}	18^{a} 19^{b} 20^{c}	18^{a} 19^{a} 20^{b}
T7	18^{a} 19^{a} 20^{a}	18^{a} 19^{b} 20^{b}	18^{a} 19^{b} 20^{c}
T9	18^{a} 19^{ab} 20^{b}	18^{a} 19^{b} 20^{c}	18^{a} 19^{b} 20^{b}
T10	18^{a} 19^{a} 20^{b}	18^{a} 19^{b} 20^{b}	18^{a} 19^{a} 20^{b}
T11	18^{a} 19^{ab} 20^{c}	18^{a} 19^{b} 20^{c}	18^{a} 19^{b} 20^{b}
T12	18^{a} 19^{b} 20^{b}	18^{a} 19^{b} 20^{b}	18^{a} 19^{a} 20^{b}

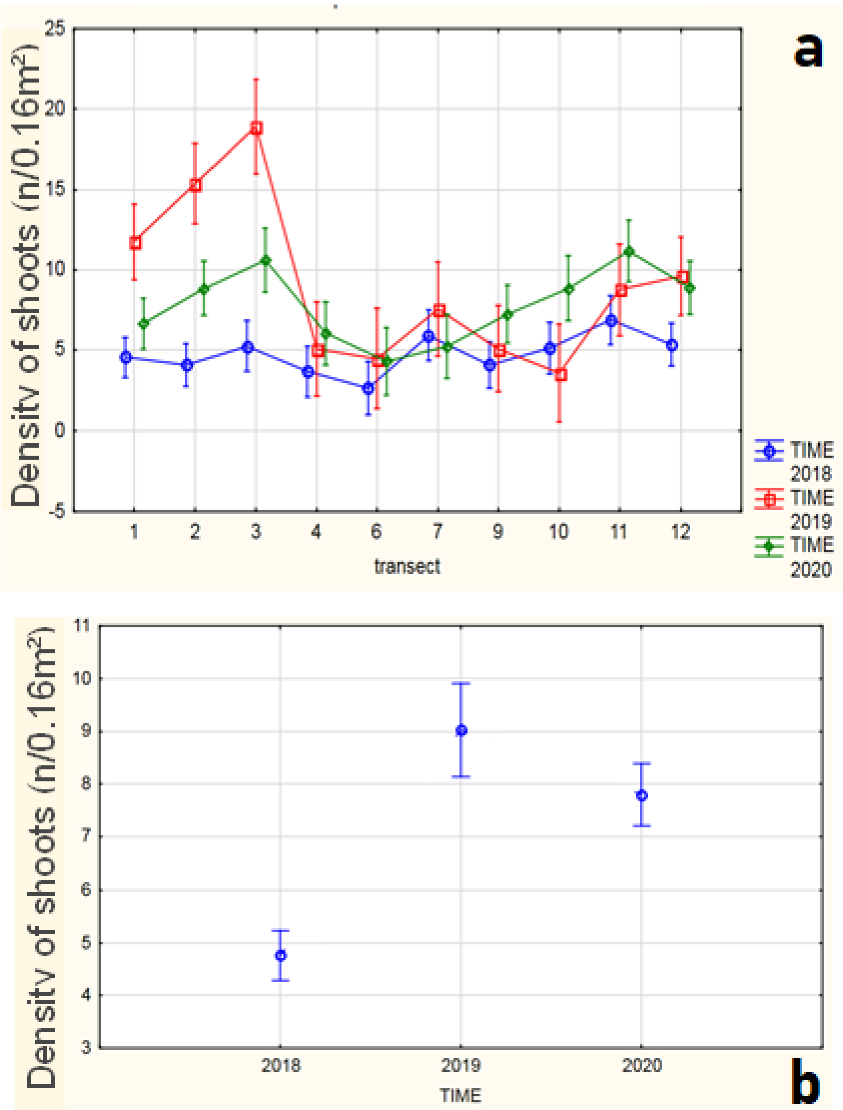

Figure 6. Mean values and confidence limits (95%) for the density of shoots of *Phragmites australis* in 2018, 2019 and 2020 on the permanent transects a) per transect and year b) mean values per year; significant differences between years and transect are indicated on Table 3.

The height of shoots of *P. australis* was significantly smaller in 2019 (mean= 3.0m) than in 2018 (mean: 4.1m) with a significant effect of the Transect and of the interaction Transect X Year (Table 2c, Figure 7b). In 2020, when compared with 2019, the maximum height of *P. australis* increased slightly (+0.1m) but remained 1m below the 2018 value (Figure 7b). This increase was significant only for transects T1, T2, and T9 and T11, while in T6 there was a significant decrease (Table 3). In contrast, the maximum height in 2020 was smaller than in 2019 only on transect T6.

Most of the variance results from the large differences between quadrats within transects which is explained by the heterogeneity of the transects and the small size of the quadrats. The remaining variance is explained by differences between years (87%) while differences between transects and the interaction between transects and year explain respectively 12% and 1% (although highly significant).

There was no significant relationship between the height changes between years per station with the topographic level.

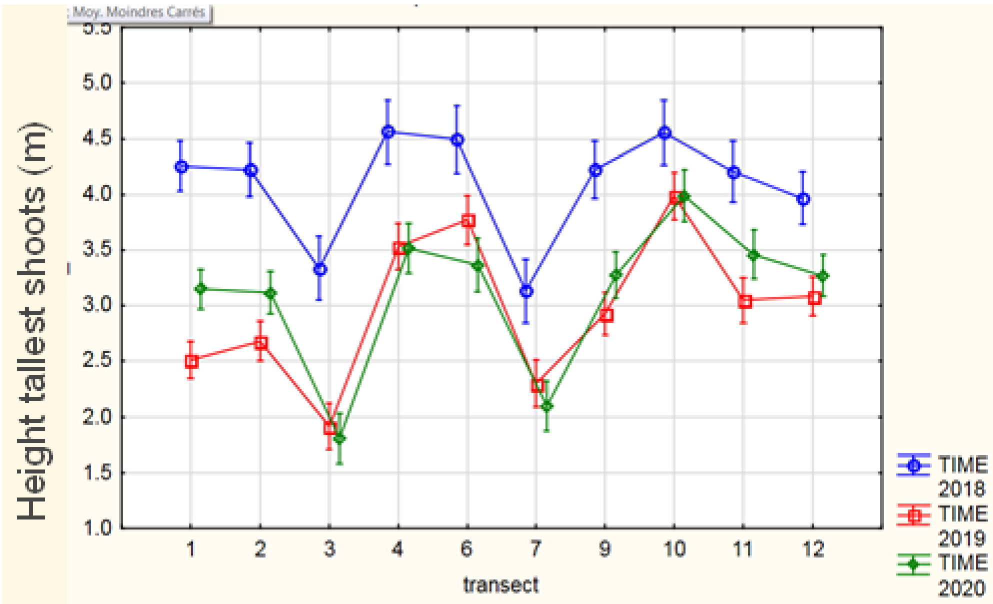

Figure 7a. Mean values and confidence limits (95%) per transect and per year (2018 to 2020) for the height of the tallest shoot per quadrat of *Phragmites australis*; significant differences between years and transect are indicated on.

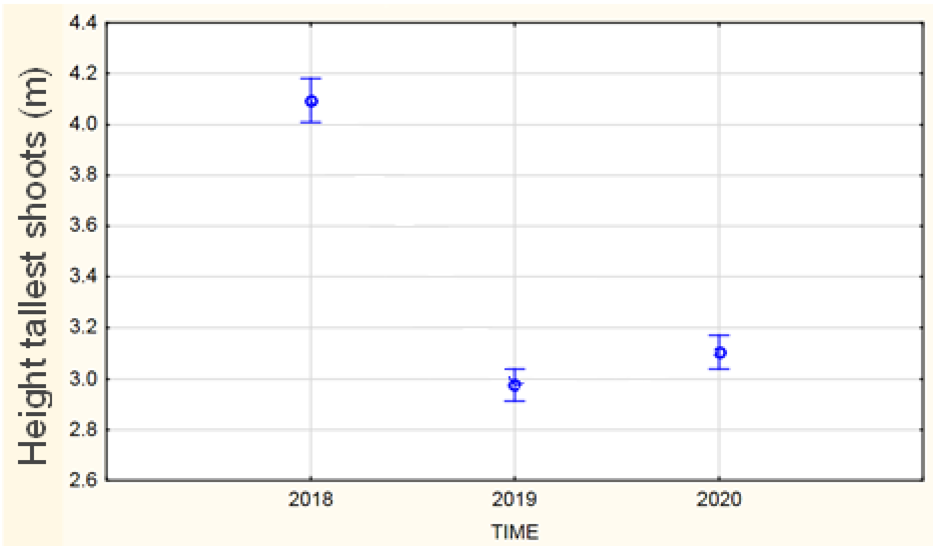

Figure 7b. Mean values and confidence limits (95%) per year (2018 to 2020) for the height of the tallest shoot per quadrat of *Phragmites australis*; significant differences between years and transect are indicated on Table 3

The basal diameter of shoots was significantly smaller in 2020 (8.0mm) than in 2019 (mean: 9.1mm) and 2018 (10.5mm). Most of the variance results from the large differences between quadrats within transects which is explained by the heterogeneity of the transects and the small size of the quadrats. The remaining variance is explained by differences between years (68%) while differences between transects and the interaction between transects and year explain respectively 29% and 2% (although highly significant) (Table 2b, Figure 8a,b). After the strong decline in shoot diameter in 2019, the decreased continued in 2020 and were the strongest on transects T4 and T6.

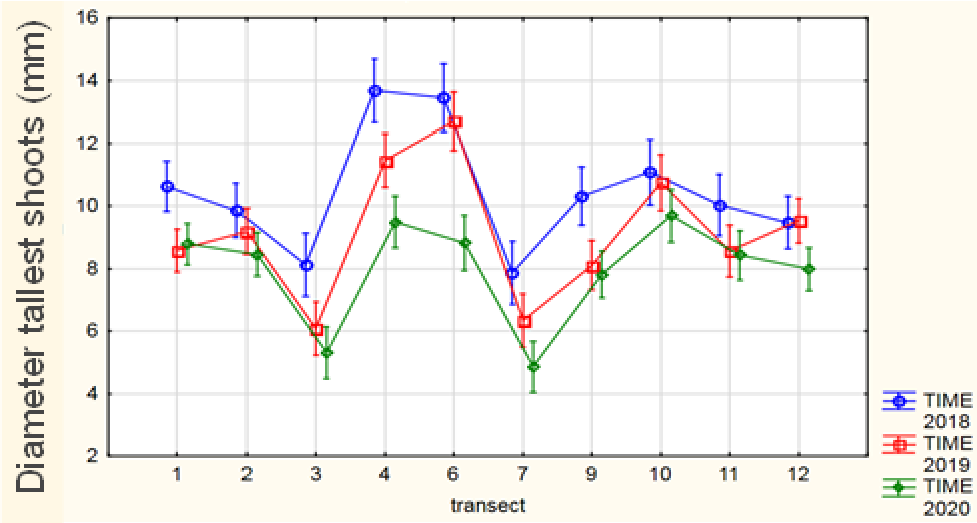

Figure 8a. Mean values and confidence limits (95%) per transect and per year (2018 to 2020) for the basal diameter of the tallest shoot per quadrat of *Phragmites australis*; significant differences between years and transect are indicated on Table 3

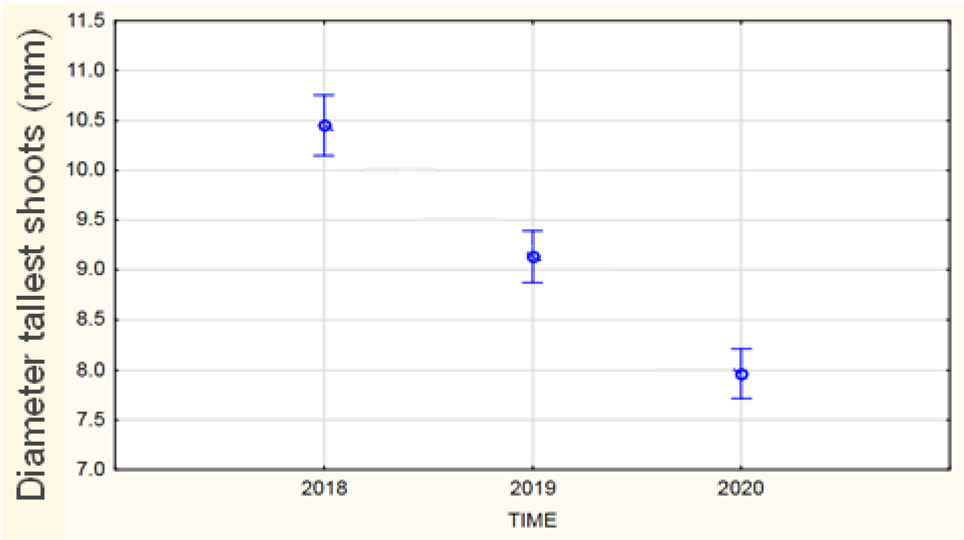

Figure 8b. Mean values and confidence limits (95%) per year (2018 to 2020) for the basal diameter of the tallest shoot per quadrat of *Phragmites australis*; significant differences between years and transect are indicated on Table 3

Typha angustifolia

Shoot density

Between 2018 and 2020 the density of *Typha angustifolia* per quadrat differed significantly with a significant effect of the year, of the transects and their interactions (Figure 9a, Table 4). Most of the variance results from the large differences between quadrats within transects which is explained by the heterogeneity of the transects and the small size of the quadrats. The remaining variance is explained by differences between years (81%) while differences between transects and the interaction between transects and year explain respectively 7% and 12%.

After a 33% decline in 2019 (from 7.5 to 5 shoots per quadrat) the density of living shoots of *Typha angustifolia* increased by 12% in 2020 but was significantly smaller in 2019 than in 2018 (from 4.6 shoots /quadrat to 2.9 shoots / quadrat) (Figure 9). The pattern of change in the density differed between blocks of transects. On transects 1-3 differences between years were the largest and significant for each transect. In contrast, on transects 10-12 differences between years were not significant (Figure 9, Table 5). Other transects show intermediate situations except T6 where the density of *Typha* was the smallest in 2018 (2.0 shoots/quadrat) and further declined in 2019 and 2020 (below 1.5 shoot/quadrat).

Table 4. Results of the MANOVA testing for the effects of Year, Transect and their interaction on the variation between 2018 and 2019 of a) shoot density, b) basal diameter of the tallest shoot per quadrat and c) Height of the tallest shoot per quadrat of T*ypha angustifolia*.

a) Density	Sum squares	Degr. of freedom	F	p
ord. origine	2636.193	1	3475.84	0.000000
transect	25.011	9	3.66	0.000354
Error	116.799	154		
YEAR	19.871	2	42.80	0.000000
YEAR*transect	26.255	18	6.28	0.000000
Erreur	71.504	308		

b) Diameter	Sum squares	Degr. of freedom	F	p
ord. origine	98890.58	1	4512.97	0.000000
transect	1522.05	9	7.72	0.000000
Erreur	3374.53	154		
YEAR	5825.90	2	237.85	0.000000
YEAR*transect	2758.98	18	12.52	0.000000
Error	3772.12	308		

c) Height	Sum squares	Degr. of freedom	F	p
ord. origine	2194.817	1	23500.84	0.00
transect	33.775	9	40.18	0.00
Erreur	14.383	154		
YEAR	193.916	2	1326.93	0.00
YEAR*transect	43.835	18	33.33	0.00
Erreur	22.505	308		

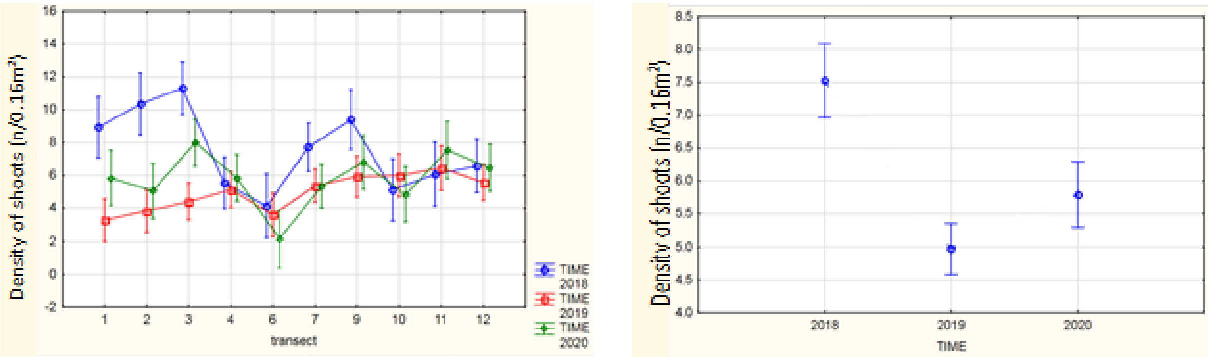

Figure 9. Mean values and confidence limits (95%) for the density of shoots per quadrat of *Typha angustifolia* ; a) mean density per transect and per year (2018 to 2020); b) mean density per year; significant differences are shown on Table 5.

Table 5. Pair comparisons for differences between years for each transect for the density of shoots and the height and basal diameter of the tallest shoot of *T. angustifolia* per quadrat. For each transect and parameter, years with the same letter (a, b or c) are not statistically different (p<0.05).

	Typha angustifolia		
Transect	Density	Height	Diameter
T1	18^a 19^b 20^c	18^a 19^b 20^b	18^a 19^b 20^c
T2	18^a 19^b 20^b	18^a 19^b 20^b	18^a 19^b 20^b
T3	18^a 19^b 20^c	18^a 19^b 20^b	18^a 19^b 20^b
T4	18^a 19^a 20^a	18^a 19^b 20^c	18^a 19^a 20^b
T6	18^a 19^a 20^b	18^a 19^b 20^c	18^a 19^b 20^c
T7	18^a 19^b 20^b	18^a 19^b 20^c	18^a 19^b 20^c
T9	18^a 19^b 20^b	18^a 19^b 20^c	18^a 19^a 20^b
T10	18^a 19^a 20^a	18^a 19^b 20^c	18^a 19^b 20^c
T11	18^a 19^a 20^a	18^a 19^b 20^c	18^a 19^a 20^b
T12	18^a 19^a 20^a	18^a 19^b 20^c	18^a 19^b 20^c

Between 2018 and 2020 the height of the tallest shoot per quadrat for *Typha angustifolia* differed significantly, with a significant effect of year, of transects and their interactions (Figure 10a, Table 4). Most of the variance results from the large differences between quadrats within transects which is explained by the heterogeneity of the transects and the small size of the quadrats. The remaining variance is mainly explained by differences between years (95%), while differences between transects and the interaction between transects and year explain respectively 3% and 2% of the variance.

Height of the tallest shoot

The height of shoots of *T. angustifolia* experienced a sharp decline between 2018 and 2019 (-2.1m, i.e. 35% reduction). In 2020, the height of *Typha* shoots further declined to reach 1.5m (50% of 2018 value). The trend between years and the mean height per transect showed different patterns. In 2018, the mean height per transect was fluctuating around 3.0 m (min= 2.84: T3, max 3.22: T3). In 2019, *Typha* height decreased by more than 1.5m in transects T1-T3. In contrast, the height decreased by less than 0.5m in transects T4, T10 and T11, other transects showing intermediate values. In 2020, the mean height of *Typha* decreased by 0.36m, ranging from a small decrease in T1 (-0.10m) and T2 (-0.16m) and even a small increase in T3 (+0.18m) to -1.13m (T10). Therefore, the difference in height between transects decreased in 2020 compared to 2019 values. The decline of the height of *Typha* was enhanced and was more homogeneous in 2020.

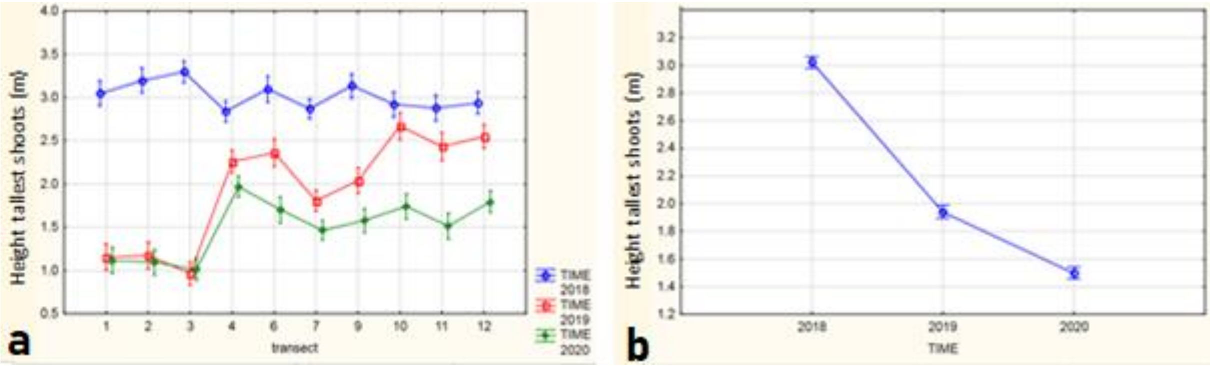

Figure 10. Mean values and confidence limits (95%) for the height of the tallest shoot per quadrat of *Typha angustifolia* ; a) mean height per transect and per year (2018 to 2020); b) mean height per year; significant differences are shown on Table 5.

Basal diameter of shoots

Between 2018 and 2020 the basal diameter of the tallest shoot per quadrat of *Typha angustifolia* differed significantly with a significant effect of the year, of the transects and their interactions (Figure 11a, Table 4). Most of the variance results from the large differences between quadrats within transects which is explained by the heterogeneity of the transects and the small size of the quadrats. The remaining variance is mainly explained by differences between years (89%) while differences between transects and the interaction between transects and year explain 5% of the variance each.

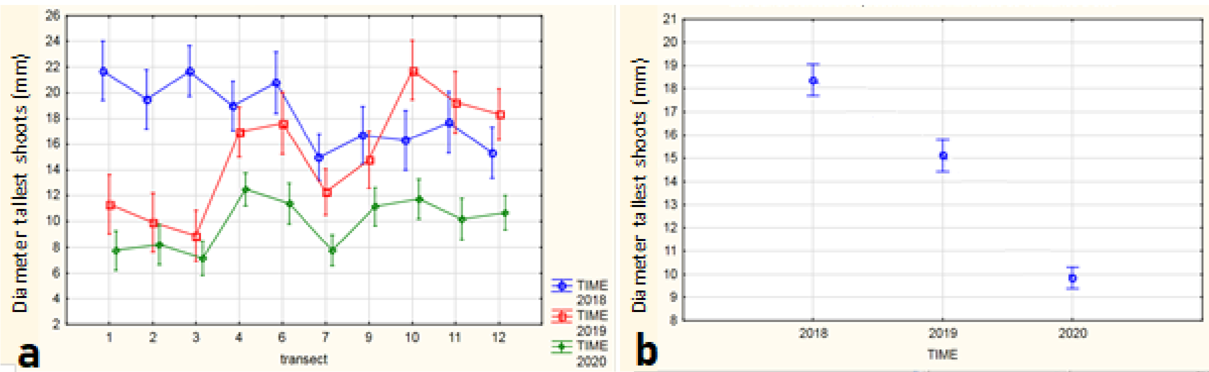

Figure 11. Mean values and confidence limits (95%) for the basal diameter of the tallest shoot per quadrat of *Typha angustifolia* ; a) mean diameter per transect and per year (2018 to 2020); b) mean diameter per year; significant differences are shown on Table 5

Between 2018 and 2019, the basal diameter of shoots of *T. angustifolia* decreased significantly (mean: -3.2mm) with contrasting trends, ranging from +38% (T10) to -59% (T3) (Figure 11). In 2020, the decrease of the basal diameter was stronger (-5.0mm) and common to all transects (range: -1.3 - -10.6mm), resulting in more homogeneous values between transects

3.3. Effects of environmental variables and competition on *P. australis* and *T. angustifolia*

The density, the height and the basal diameter of the tallest shoot per quadrat of *P. australis* were significantly correlated with all variables tested (except the "Year" for the basal diameter of shoots (Table 6). The topographic position ("Water level") explains 36% of the total variance (calculated as the F ratio) of the Height and 21% of the diameter of the tallest shoot of *Phragmites* and only 8% of the variance of its density (positive correlation with Water level). The Height of *Typha angustifolia* (negative correlation) explains 38% of the variance of Diameter and 24% of the Height of the tallest shoot of *Phragmites* and 31% of its density. Similarly, *Typha* density (negative correlation) explains 33% of the variance of Diameter and 17% of the Height of the tallest shoot of *Phragmites* and 14% of its density. The Year explains 23% of the variance of the density and 12% of the variance of the Height; the effect is minor and not significant on the Diameter.

The density of *Typha angustifolia* shoots was only significantly correlated with the Density and the Height of *Phragmites* shoots which explain respectively 72% and 22% of the total variance (Table 7). The Height of *Typha* shoots was explained by *Phragmites* density (32% of variance) and Height (17% of variance) while the Water level and the Year explained respectively 24% and 3% of the variance. The basal Diameter of *Typha* shoots was mostly explained by *Phragmites* Density, (57% of variance) and the Year (22% of variance). Overall, the Water level was only weakly correlated with the structure parameters of *Typha angustifolia* stands.

Table 6. Results of the GLMs testing for the effects of Year, Water level, Typha Density (typh-liv) and Typha Height (t_max_h) on a) shoot density, b) basal diameter of the tallest shoot per quadrat and c) Height of the tallest shoot per quadrat of *P. australis*.

a) Density	Sum squares	Degr. of freedom	F	p
Ord.Orig.	392.157	1	24.37768	0.000001
year	390.575	1	24.27933	0.000001
water_level	132.754	1	8.25239	0.004343
typh_liv	226.859	1	14.10225	0.000206
t_max_h	525.231	1	32.64994	0.000000
Error	5115.578	318		

b) Diameter	Sum squares	Degr. of freedom	F	p
Ord.Orig.	9.903	1	1.86950	0.172504
year	10.075	1	1.90195	0.168836
water_level	48.877	1	9.22727	0.002583
typh_liv	77.247	1	14.58306	0.000161
t_max_h	91.029	1	17.18488	0.000044
Error	1673.862	316		

c) Height	Sum squares	Degr. of freedom	F	p
Ord.Orig.	7.8557	1	18.92347	0.000018
year	7.9063	1	19.04523	0.000017
water_level	23.3148	1	56.16259	0.000000
typh_liv	10.9579	1	26.39628	0.000000
t_max_h	15.4581	1	37.23672	0.000000
Error	131.5964	317		

Table 7. Results of the GLMs testing for the effects of Year, Water level, *Phragmites* Density (phra-liv) and Height (p_max_h) on a) shoot density, b) basal diameter of the tallest shoot per quadrat and c) Height of the tallest shoot per quadrat of *T. angustifolia*.

a) Density	Sum squares	Degr. of freedom	F	p
Ord.Orig.	6.027	1	0.74211	0.389639
year	5.904	1	0.72692	0.394530
water_level	5.044	1	0.62104	0.431252
phra_liv	218.009	1	26.84378	0.000000
p_max_h	66.652	1	8.20702	0.004452
Errorr	2566.363	316		

b) Diameter	Sum squares	Degr. of freedom	F	p
Ord.Orig.	376.296	1	18.51565	0.000022
year	374.434	1	18.42403	0.000024
water_level	1.107	1	0.05446	0.815621
phra_liv	982.930	1	48.36506	0.000000
p_max_h	1.152	1	0.05671	0.811933
Error	6422.113	316		

c) Height	Sum squares	Degr. of freedom	F	p
Ord.Orig.	10.58748	1	47.24378	0.000000
year	10.55437	1	47.09601	0.000000
water_level	1.18168	1	5.27295	0.022313
phra_liv	13.78628	1	61.51756	0.000000
p_max_h	7.40245	1	33.03143	0.000000
Error	70.81660	316		

4. Discussion and preliminary conclusions

In the reedbeds of the Lake Lesser Prespa, a replacement of *Phragmites australis* by *Typha angustifolia* has been noticed in the past. Although no strong evidence of the reason for *Typha* increase has been found, previous analyses suggested the following hypotheses (1) the cause was a large disturbance event, possibly a severe drought followed immediately by the highest water level ever recorded on the lake and (2) *P. australis* is more competitive for light (taller) than *T. angustifolia.* The objective of the monitoring of the transects at the interface between *Phragmites*- and *Typha*-dominated reedbeds had been to identify the current spatial dynamics of both populations.

After three years of monitoring, there is growing evidence that *Phragmites* is slowly increasing its occurrence along the transects (+20% of quadrats occupied between 2018 and 2020) while *T. angustifolia* showed a 10% decline. The process was relatively slow but similar during 2019 and 2020. These changes occurred mostly at the edges of their populations suggesting spatial expansion/colonization rather than increased density within patches.

A second clue for *Phragmites* competitive dominance is the taller size of its shoots compared to Typha (Figure 12, left). The size of both species declined during the dry years 2019 and 2020 but *Phragmites* shoots mean size remained at least 1 m taller those of *Typha*.

The density of *Phragmites* shoots increased during the study period while *Typha* showed a decreased density (Fig 12, right).

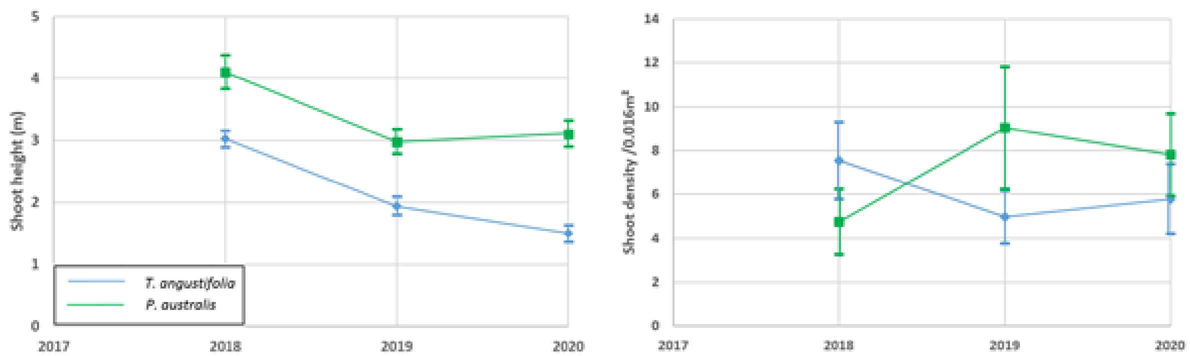

Figure 12. Comparisons between *P. australis* and *T. angustifolia* for (left) the height of the tallest shoot per quadrat and (right) shoot density per quadrat; error bars correspond to 95% probability intervals.

Plant size and density are commonly used traits for assessing competitive interactions (e.g. Weiner 1993, DeMalach et al. 2016). Size alone -or density- is not sufficient to demonstrate competitive output and more sophisticated field measures and calculation than we could afford in the framework of this project would be needed. However, the high nutrient level in soil within the reedbed and the tall size of helophytes suggest that competition for light is probably decisive. In that perspective, the higher stature of *Phragmites* forming a canopy above *Typha* should give a competitive advantage. Similarly, the standing biomass has been increasing for *Phragmites* while it decreased for *Typha*.

The General Linear Models highlighted that for each species, a significant negative impact of the density and the height of the other species had a negative effect on its structural parameters (density, height and shoot diameter). However, this effect appeared asymmetric with a stronger effect of *Phragmites* on *Typha* density and height than the opposite. Conversely, the effect of *Typha* on *Phragmites* was stronger than the opposite.

Conclusions

These changes occurred during two successive dry years. It is not possible at this stage to conclude for a long term competitive exclusion of *Typha angustifolia* by *Phragmites australis*. More data will be needed, especially during "normal" or "wet" years in order to assess whether the observed trends in 2019 and 2020 are constant. However, climate change will most probably have an increasingly important long-term effect on the water levels of Lesser and Great Prespa lakes (van der Schriek & Giannakopoulos, 2017, van der Schriek et al. 2020) and thus on the ecology of their riparian and lakeshore vegetation.

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