

Shoot growth in *Typha angustifolia* L. and *Typha latifolia* L. in the Kokemäenjoki River delta, western Finland

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ABSTRACT

The growth dynamics of two tall littoral helophytic plants, the narrow-leaved cattail (*Typha angustifolia* L.) and broad-leaved cattail (*Typha latifolia* L.; Typhaceae) were studied in the rapidly changing estuarine habitats in the Kokemäenjoki River delta, western Finland. The two cattails form uniform, single-species communities (monocultures) throughout the plant-covered estuary. Of the two taxa compared, the shoots were taller in *T. angustifolia* (mean 166 cm) than in *T. latifolia* (mean 120 cm). But due to the robust leaves, the relation in the average weight of individual ramets was opposite: The mean weight of *T. angustifolia* was 9.6 g (dry wt), and that of *T. latifolia* was 16.5 g. In a separate study, the leaf height was compared between the fertile (flowering) and sterile (non-flowering) ramets. In flowering ramets the average leaf length was 35 cm taller in *Typha angustifolia* than in *T. latifolia*. The differences were even more pronounced in sterile ramets, where the leaves of *Typha angustifolia* were 70 cm taller than those of *T. latifolia*. The differences were statistically highly significant. Interspecific competition between the two *Typha* species is negligible, because the microhabitats differ from each other. *T. angustifolia* grows in considerably deeper (mean depth 42 cm) waters than *T. latifolia* (mean depth 19 cm). The optimum range in the water depth is markedly stricter in *T. angustifolia* than in *T. latifolia*. The differences between the rooting depths of the two cattails were statistically highly significant. The physico-chemical characteristics of the rooting zones (rhizospheres) of the two cattails are similar, with the locally produced (autochthonous) organic matter dominating and determining the fertility of the habitats.

Keywords: Cattails; *Typha angustifolia*; *Typha latifolia*; Kokemäenjoki River delta; macrophytes; wetlands

1. INTRODUCTION

In the plant kingdom, species-specific characteristics in the habitat requirements and growth strategies are common, and even very close relatives can differ significantly from each other. In wetland ecosystems throughout the world, the cattails (*Typha* spp.) are dominant representatives especially in nutrient-rich (eutrophic) sites. In the Northern Europe, two species of cattails are common, i.e. *Typha latifolia* L. and *Typha angustifolia* L.

The basic requirements in the habitat requirements differ markedly between *T. latifolia* and *T. angustifolia*, in spite of the close relationship within the genus (Grace and Wetzel, 1982). On

the other hand, the optimal aquatic and moist habitats of these two cattails can be very similar, and yet the plants often form and maintain single-species (monotypic) communities (Olson *et al.*, 2009). The hybrid, *T. latifolia* x *T. angustifolia* (= *Typha x glauca* Godr.) is often more adaptable than the parent species, and in addition, the hybrid is more tolerant against changes and disturbances in environmental conditions. Spatially, the hybrid is often grows near the parent species, but in a Canadian follow-up study, *T. x glauca* could not displace the parent taxa (Olson *et al.*, 2009).

The high ability of cattails to accumulate water- and sediment-borne nutrients is well known, and both natural and constructed *Typha*-dominated wetlands are a valuable in preventing eutrophication and enhancing water quality (Keddy, 2010). In addition, the dense stands bind efficiently fine particles from the aqueous environment, thus clearing waters, and simultaneously, the stands cattails prevent resuspension of sediments (Horppila and Nurminen, 2001).

The present study describes biometric characteristics of the cattails growing in an exceptionally rapidly changing estuarine environment in Northern Europe. Publication of the intra- and interspecific features of the growth and production ecology is vital in the location, where both abiotic and biotic conditions change exceptionally rapidly. Basic background information is vital in understanding the present state of the nature, and such an information is needed in defining the bordering and management of conservation areas. The target of the present study, the Pihlavanlahti Bay, in the Kokemäenjoki River delta, western Finland – is one of the hotspots of biodiversity in the North, and such, the location is included in the most important international conservation networks. The data of the present study was collected and analyzed in the early 1990's, but the data has not been published previously.

Typha angustifolia is newcomer in the Kokemäenjoki River delta, but the species is strongly expanding and covering wider areas than the previously dominated by *T. latifolia*. Such a trend is consistent with the data field and experimental data by Weiner (1993) that *T. angustifolia* can effectively displace *T. latifolia*. Detailed inventories and mappings of the distribution and relations between macrophytes are important in the *Natura 2000* conservation area, where the vegetation strongly influences both the flora and rich fauna. The assumption often reported that the rapid prograding of the delta towards the sea does not markedly influence the conservation values can be misleading or seriously wrong, as the variations in the macrophytic dominance can alter the vitality of fauna.

Conservation and proper management of wetlands is of paramount importance because up to 90 % of natural habitats of various wetland types have been destroyed in Europe (Čížková *et al.*, 2013).

2. MATERIALS AND METHODS

2. 1. Study Area

The production and life history ecology of *Typha angustifolia* and *T. latifolia* were studied in the Kokemäenjoki River estuary, in western Finland (Northern Europe; 61°34'N, 21°40'E) in 1990's and again in 2013 (Figure 1). The estuary, discharging into the Baltic Sea, is thoroughly covered with rich and productive macrophytic vegetation, and the stands of tall helophytic plants form distinctly separable successional zones. The variable characteristics of the estuary, the Pihlavanlahti Bay, were described in detail previously (Aulio, 1979, 2010, 2014a,b).



Figure 1. The location of the study area.

2. 2. Collection and Analyses of the Plant Materials

The plant samples of *Typha angustifolia* (Figure 2) and *T. latifolia* (Figure 3) were collected by the time of the maximum biomass of reeds (August – early September). The sampling was made randomly in the middle of uniform, monocultural stands. Samples were taken from comparable microhabitats trying to minimize the variation between different sections of the stands, typical in communities of cattails (Asaeda and Hung, 2007). The biometric measurements, as well as the frequency of the flowering ramets were determined for 200-250 randomly sampled individuals (at 12 separate stands for both species) at each of the dates throughout the growing season.

The water depth of the sites was determined by 10 measurements in each site. The sampling and measurement policies followed the international standards used in hydrobiological studies (Vollenweider, 1969). The contents of organic matter of the sediment samples were determined after dry ashing (at 475 °C, 4 h). All the results are expressed on a dry weight basis. For plant and sediment dry matter determinations, the samples were oven-dried at 105 °C for 48 h. The pH-values of the sediments was determined directly in the field by using a glass electrode (Allen, 1974).

2. 3. Statistical Analyses and Terminology



Figure 2. Monospecific stand of *Typha angustifolia* L. at the time of maximum biomass.



Figure 3. Monospecific stand of *Typha latifolia* L. at the time of maximum biomass.

The statistical analyses used follow Sokal and Rohlf (2012). The parametric (mean \pm standard deviation of the mean, one-way analysis of variance; ANOVA), and non-parametric (Kruskal–Wallis one-way analysis of variance and Mann-Whitney U-test) statistical analyses

of the numerical data were performed by using the *Analyse-it for Microsoft Excel* (version 2.12) program package (2008). The terminology of biological concepts and principles follows the latest edition of the *Oxford Dictionary of Plant Sciences* (Allaby, 2012).

3. RESULTS

3. 1. Water Depth in Cattail Habitats

The water depth amplitudes in the two cattail species growing in the Kokemäenjoki River delta were similar to the data presented by the detailed description of the ecological niche characteristics of *T. latifolia* and *T. angustifolia* by Grace and Wetzel (1982). The similar patterns in the water depth requirements are noteworthy, although the cattails grew in markedly deeper waters in the American studies than in the present study area.

In the Kokemäenjoki River delta, *Typha angustifolia* grows in considerably deeper waters than *Typha latifolia*. This pattern – as well the actual water depths in the stands – is similar to the values reported from lakes in Sweden (Andersson, 2001).

The ecological niches of the two cattail species growing in the Kokemäenjoki River delta differ markedly from each other, as far as the water depth and composition of the rhizosphere sediments are concerned. In general, the monotypic stands of broad-leaved cattail are found in shallow water littoral sites, whereas the narrow-leaved cattail grows usually in considerably deeper waters (Table 1).

Table 1. The water depth, contents of organic matter, and the pH-values in the habitats of *Typha angustifolia* and *Typha latifolia* in the Kokemäenjoki River delta, western Finland. Mean \pm 1 standard error of the mean (S.E.), $N = 12$ communities for both species.

	Mean water depth, cm	Sediment organic matter, % dry weight	Sediment pH
<i>Typha angustifolia</i>	42.17 \pm 3.22	10.34 \pm 1.41	5.80 \pm 0.08
<i>Typha latifolia</i>	19.08 \pm 3.88	13.30 \pm 1.45	5.73 \pm 0.05

In the Kokemäenjoki River delta, the optimal water depth for the uniform stands of *Typha angustifolia* varies between 30-50 cm. In the present study, the range of the water depth in the sampling sites was 2872 cm, with the mean depth of 42 cm. The strongest stands are bordering numerous channels of the estuary, but in sites with strong water currents the narrow-leaved cattail grows only rarely. *T. angustifolia* prefers habitats with soft and nutrient-rich sediments. The widest and most productive stands of *Typha latifolia* occupy habitats with the water depth of 5-47 cm, with the mean depth of 19 cm (Table 1). In the Kokemäenjoki River delta, the broad-leaved cattail thrives even in microhabitats above the mean water level, i.e. in late phase of macrophytic succession caused by sedimentation and deposition of autochthonous organic debris. The strongest stands of *T. latifolia* are growing bordering the channels and inside the open spaces within the stands of other helophytic macrophytes in the proximal and middle sections of the delta.

The optimal habitat characteristics for *T. angustifolia* and *T. latifolia* differ significantly from each other. In the Kokemäenjoki River delta, 12 communities were studied in detail for the two cattail species. Of the sites described, nine of the shallowest sites were occupied by *T.*

latifolia, and accordingly, four of the deepest values were measured in stands of *T. angustifolia*.

On the average, the narrow-leaved cattail grows in habitats with the water depth of more than twice of that for the stands of broad-leaved cattail. The difference in the mean water depth was statistically highly significant both in parametric t-test ($t = 4.38$, $P = 0.0002$, $df = 22$) and in non-parametric Mann-Whitney U-test ($U = 129.0$, $P = 0.0005$, $N = 24$). On the basis of the present results, the optimum for water depth is more strictly determined in *T. angustifolia* than in *T. latifolia*. The coefficient of variation in the samples of *T. angustifolia* was 26.4 %, and 70.4 % in *T. latifolia*. The growth of cattails is seriously retarded, if the habitats are left dry for long periods of time (Li *et al.*, 2004). In the Kokemäenjoki River delta, variations in the water depth are small, and thus the risks of drying of the rhizosphere are negligible in the littoral habitats occupied by *Typha* spp.

3. 2. Organic Matter of the Sediments

The primary production and accumulation/deposition of autochthonous (produced by the plants growing at the site) organic matter are effective in both *T. angustifolia* and *T. latifolia*. In the shallow-water habitats (with weak water currents) of *T. latifolia*, the mean contents of organic matter in the rhizosphere was 13 % (dry weight), with range of 4.5–24.6 %. In habitats of *T. angustifolia* (with deeper water depth and stronger currents) the mean organic matter content was 10 % (range 3.9–21.9 %) (Table 1).

In the comparisons of the sediment organic matter contents, the two cattails did not differ significantly from each other. The value in the parametric test was $t = 1.41$, $P = 0.1733$, $df = 22$, and accordingly, in the non-parametric test $U = 46.0$, $P = 0.1432$, $N = 24$. Variations between the stands were great in both species. In the results for *T. angustifolia* $CV = 46.7$ %, and for *T. latifolia* $CV = 37.8$ %.

The high concentrations of organic matter in the rhizosphere are often a risk in littoral habitats because the decomposition of biomass often causes oxygen depletion. However, in *Typha*-dominated stands, the risk of anaerobic conditions is minor because the cattails effectively transport oxygen from the atmosphere into the rooting zone (Sharma *et al.*, 2008).

3. 3. pH of the Sediments

The pH-values in the rhizospheres of the cattail stands were rather uniform, with no interspecific differences. In both species studied, the pH of the sediment layer was slightly acidic: 5.7 in *Typha latifolia* and 5.8 in *T. angustifolia* (Table 1).

The deposition of organic matter in the shallow-water habitats of *T. latifolia* (with weaker water currents) was slightly larger than the deposition of organic matter in habitats of *T. angustifolia* with deeper water and stronger water flow.

The organic matter content of the sediments in cattail habitats can affect significantly on competitive relations between plant taxa. In cattails, especially the hybrid *T. x glauca* gains advantage of the accumulation of organic matter (Vaccaro *et al.*, 2009).

3. 4. Temperatures of Water and Sediments

Variations in temperatures of the water and bottom deposits in the shallow estuarine environment were rather slight throughout the growing season (from late May to mid-September) (Figure 2). Two rather regular trends can be seen in the present material from the cattail-dominated communities.

- (i) The ambient water in the cattail stands was some two degrees ($^{\circ}\text{C}$) higher than the temperature prevailing in the rhizosphere (upper sediment layer) of the same sites.
- (ii) In the stands of *Typha angustifolia*, both water and sediment temperatures were 1–3 degrees ($^{\circ}\text{C}$) higher than those prevailing in *T. latifolia* stands (Figure 4). The main reason for these differences lays the most probably in shadowing effect in the more dense stands of the broad-leaved cattail.

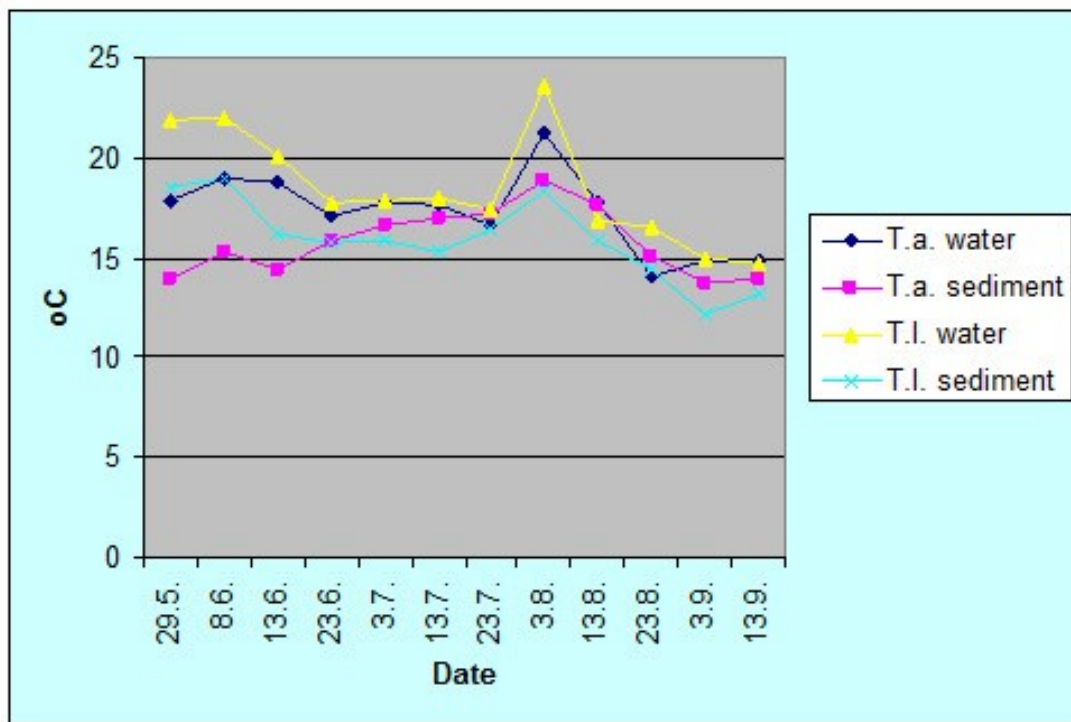


Figure 4. The temperature trends of ambient water and rhizosphere sediments in the stands of *Typha angustifolia* (T.a.) and *Typha latifolia* (T.l.) in the Kokemäenjoki River delta, western Finland.

3. 5. Shoot Height in *Typha* Spp.

In the Kokemäenjoki River delta, both *Typha angustifolia* and *T. latifolia* form practically monospecific communities, and hence the interspecific competition between the two cattails is negligible. On the other hand, the pure monocultures manifest the vitality and competitiveness against other plants, also the helophytes growing taller than cattails in the study area. The main competitor with cattails in the study area is the common reed *Phragmites australis*. On the other hand, there are open spaces inside the wide stands of cattails, and in these gaps floating-leaved and submerges aquatic plants can form dense communities.

Due to rapid propagation of the delta towards the sea, and the succession of macrophytic vegetation, clearly defined, both spatially and temporally variable developmental classes can be separated and described in some species, such as the dominant helophyte *Phragmites australis* (Aulio, 2014). In the two cattails, the majority of rather small-area communities represent the same developmental stage – i.e. the pioneer phase of vegetation succession. Both intraspecific and interspecific variations can be found in the temporal growth characteristics of the two *Typha* species.

In the interspecific competition, *T. angustifolia* is stronger than the dominant helophytes *Phragmites australis* and *Schoenoplectus lacustris* in habitats, where the water depth is tens of centimeters. But when the sedimentation and especially the deposition of autochthonous plant materials have reduced the water depth near the mean surface level, *Phragmites australis* is capable of displacing the narrow-leaved cattail. *Typha angustifolia* is one of the most successful macrophytes in the Kokemäenjoki River delta during the latest century, i.e. the period with reliable vegetation inventory and follow-up in the area. The narrow-leaved cattail was mentioned as rare and solitary stands in a few bays as early as in the beginning of the 20th century (Häyrén, 1909). In the mapping of the whole estuary's vegetation, Sääntti (1954) describes small-scale communities, mixed in the wider communities of *Phragmites australis* and *Scirpus lacustris* (= *Schoenoplectus lacustris*). More recently, Suominen (2013) showed that the narrow-leaved cattail has become markedly more common, and nowadays *T. angustifolia* is one of the dominant helophytes in the estuary.

3. 5. 1. Dynamics of Shoot Height

The patterns in the growth – both length and weight – in *Typha angustifolia* and *T. latifolia* growing in the Kokemäenjoki River delta follow similar patterns. The growth commenced in both species in the first week of August. The date reflects directly the trend in the temperature of water and rhizosphere sediments in the plants' ambient habitats.

In the interspecific comparison, *T. angustifolia* produced markedly taller ramets than *T. latifolia* (Figure 5). The average height of *T. angustifolia* reached 166.2 ± 13.0 cm, whereas mean height of the ramets of *T. latifolia* was 120.1 ± 8.25 cm. In the follow-up study covering the whole growing season, the ramets of the narrow-leaved cattail were statistically significantly taller than the shoots of the broad-leaved cattail. In the parametric t-test the value of $t = 2.99$, $P = 0.0067$, $df = 22$, and in the non-parametric Mann-Whitney U-test the value of $U = 25.0$, $P = 0.0056$, $N = 24$.

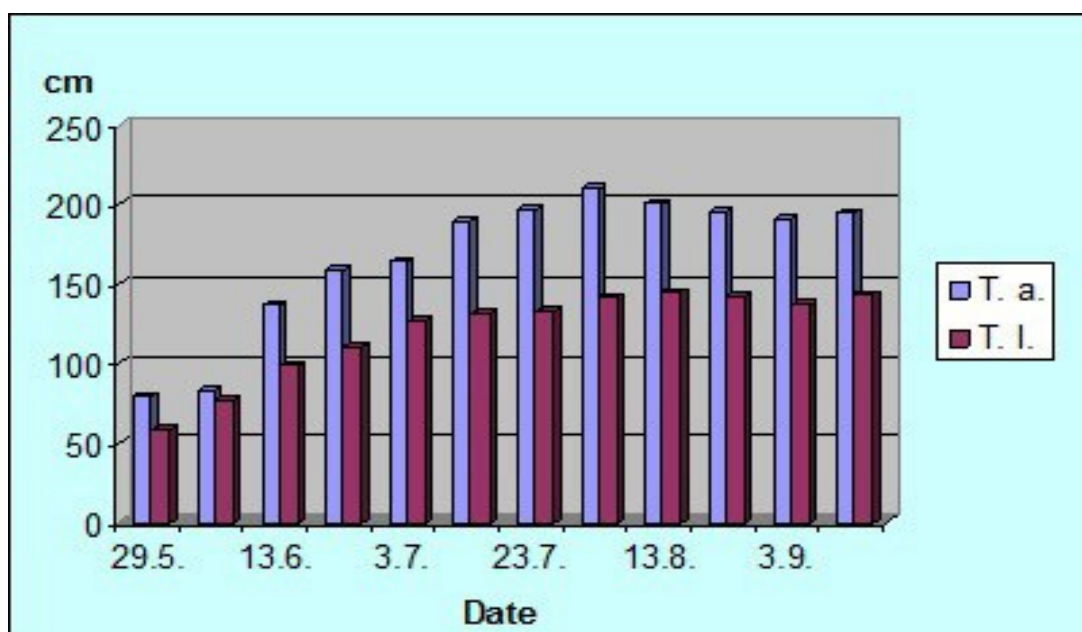


Figure 5. The trends in the growth of shoot (ramet) height in *Typha angustifolia* (T.a.) and *Typha latifolia* (T.l.) in the Kokemäenjoki River delta throughout one growing season. $N = 12$ stands for both species.

In eutrophic conditions, the optimal nutrient availability permits the maximal height of the leaf growth, and in such conditions *T. angustifolia* is superior to *T. latifolia* in interspecific competition – especially in the radiation conditions of the high latitudes – such as in the Kokemäenjoki River delta (Tanaka *et al.*, 2004).

3. 5. 2. Comparison of Shoot Height between Fertile and Sterile Ramets

The difference in the shoot height between the two cattails growing in the Kokemäenjoki River delta follows the pattern reported from other sites throughout the world. But there is another – and often neglected – difference on the pattern of height of ramets. Intraspecific differences (variations within one species) are mostly neglected in determinations and reports of cattails' shoot dimensions. In the separate study, the height of the leaves by the time of the maximum biomass (mid-August) were determined and compared between the fertile (= flowering) and sterile (= non-flowering) ramets of *Typha angustifolia* and *T. latifolia* (Table 2).

Table 2. The length of leaves of *Typha angustifolia* and *Typha latifolia* in fertile and sterile ramets in the Kokemäenjoki River delta, western Finland.

	Typha angustifolia	
	Fertile (Flowering)	Sterile (Non-flowering)
Mean height (± 1 S.E.), cm	166.09 \pm 4.12 ^a	200.73 \pm 3.04 ^b
Coefficient of variation, %	8.22	7.73
	Typha latifolia	
	Fertile (Flowering)	Sterile (Non-flowering)
Mean height (± 1 S.E.), cm	131.94 \pm 4.84 ^c	131.24 \pm 3.23 ^c
Coefficient of variation, %	10.38	11.03

Arithmetic mean \pm standard error of the mean (S.E.). N = 150–250 in both species. Statistical differences: In ANOVA, the different superscript letters in vertical columns and horizontal rows indicate highly significant difference ($P < 0.001$).

The interspecific difference in the sterile ramets – 43 cm taller ramets in *T. angustifolia* than in *T. latifolia* – was statistically highly significant both in parametric analysis of variance (ANOVA), $F_{1,35} = 41.21$, $P < 0.0001$; and in non-parametric Kruskal-Wallis one-way analysis of variance, $\chi^2 = 18.95$, $P < 0.001$, $df = 1$.

In *Typha latifolia*, the lengths of the leaves were identical in the flowering and non-flowering ramets – 131 cm in both types (Table 2).

The leaf dimensions were rather stable – as evaluated by the coefficient of variation – in each of the four categories studied. In *Typha latifolia*, the variations were slightly wider than in *T. angustifolia*.

In the interspecific comparisons, the leaves in *Typha angustifolia* were markedly taller than in *T. latifolia*. In flowering ramets – with the conspicuous spadix-inflorescences – the average leaf length was 35 cm taller in *Typha angustifolia* than in *T. latifolia*. The differences

were statistically highly significant both in parametric analysis of variance ($F_{1,19} = 28.91$; $P < 0.0001$) and in nonparametric Kruskal-Wallis one-way analysis of variance ($\chi^2 = 12.03$; $P = 0.0005$; $df = 1$).

The differences between the two cattails were even more pronounced in non-flowering (sterile) ramets, where the leaves of *Typha angustifolia* were, on average, 70 cm taller than those of *T. latifolia*. Statistically, the differences were highly significant in the analysis of variance with $F_{1,44} = 240.34$; $P < 0.0001$), and in non-parametric test with $\chi^2 = 33.20$; $P = 0.0001$, $df = 1$).

3. 6. Weight Increment of the Flowering Ramets

The increment of shoot (ramet) weight increases a couple of weeks later towards the autumn than the growth in leaf height (Figure 6). The deviating patterns are due to the development of the inflorescences, where the development of seed is the main component. The growth dynamics is similar in the two cattails, but the interspecific difference is marked. The average weight of the fertile ramets determined as the average phytomass across the whole growing season (late May to mid-September) was 9.6 ± 1.04 grams (dry weight) in *Typha angustifolia*, and 16.5 ± 2.24 g in *T. latifolia*.

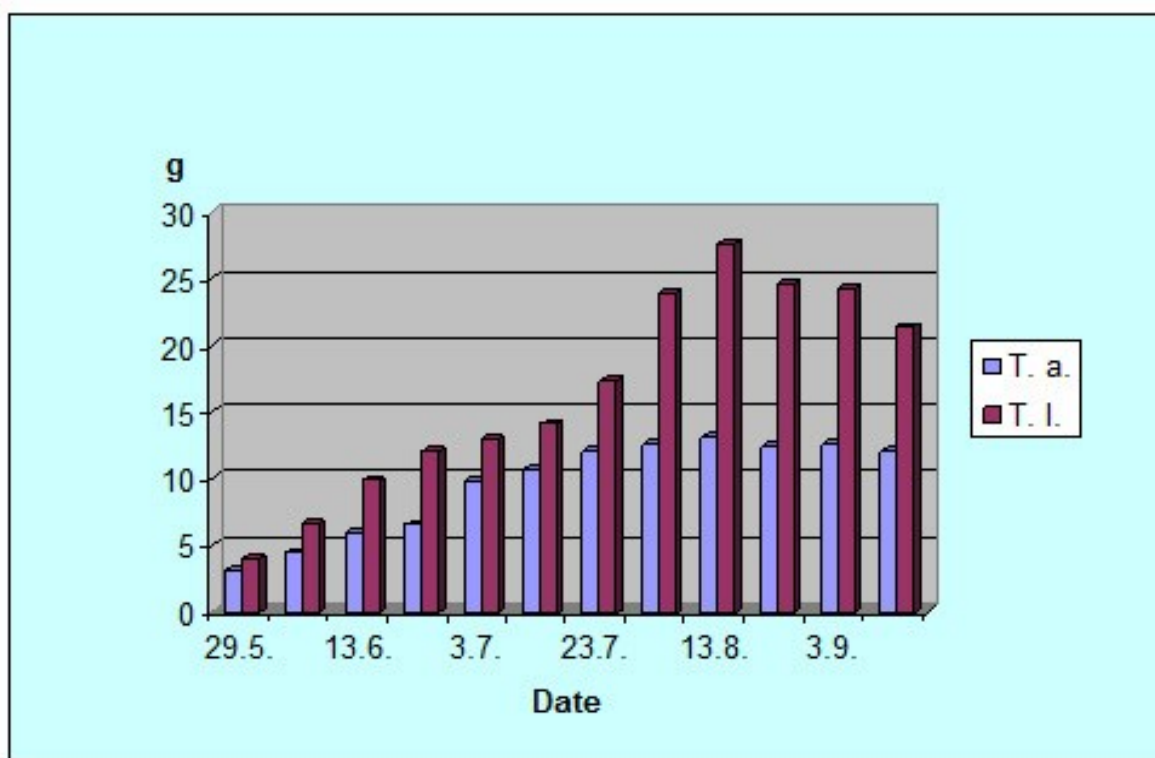


Figure 6. The trends in the weight increment in the fertile ramets of *Typha angustifolia* (T.a.) and *Typha latifolia* (T.l.) in the Kokemäenjoki River delta, western Finland throughout a growing season. $N = 12$ stands for both species.

Statistically the difference between the species is highly significant: In the parametric t-test, $t = 2.82$, $P = 0.0209$, $df = 22$, and in the non-parametric Mann-Whitney U-test, $U = 112.0$, $P = 0.0205$, $N = 24$.

4. DISCUSSION AND CONCLUSIONS

The Kokemäenjoki River delta is eutrophic, and heavily affected by anthropogenic nutrient discharges, and thus the nutrient availability for the macrophytic primary producers is excellent. In general, the availability of sufficient and/or excess resources of the major nutrients is reflected in the biometric dimensions of macrophytes. In very eutrophic environments, the share of total biomass produced is allocated to the aboveground shoots (i.e. ramets in clonal taxa), as compared to the allocation patterns in the same plant species growing at some less fertile habitats (Neely and Davis, 1985). Such an allocation strategy is a logical explanation for the tall and heavy ramets in both *Typha angustifolia* and *T. latifolia*, seen in the present study. The enhanced availability of nutrients can change the competition relations between macrophytes. The eutrophication caused principally by nitrogen nutrients gains advantage to cattails (*Typha* spp.). In nitrogen-rich habitats, cattails can displace other tall helophytes, such as *Phragmites australis* and bulrushes (*Schoenoplectus* spp.). As a consequence, the dominance of *Typha* spp. can change the previously stable zonation of littoral vegetation (Escutia-Lara *et al.*, 2009).

Eutrophication – together with the rapid sedimentation and consequent water level shallowing – seems to be the principal motor in the determining the development vegetation in the Kokemäenjoki River delta, where the cattails are very prominently increased in recent decades. On the basis of tissue analyses and availability of the major nutrients, the levels of nitrogen and phosphorus are sufficient to support maximal growth and production potential for helophytic plants (Aulio, 2014b). *Typha latifolia* is known to tolerate wide variations in the hydrological conditions of habitats. In the comparison between 17 wetland macrophytes, the broad-leaved cattail was classified as an aggressively colonizing plant tolerating fluctuations in the water depth – from flooding to long-time drying of the sites (Kercher and Zedler, 2004). The competitive abilities realize, however, only in eutrophic habitats, and this requirement is met in the Kokemäenjoki River delta. Here the interspecific competition – especially with *Typha angustifolia* and *Phragmites australis* – are more important factors than abiotic environmental conditions. When the nutrient availability is very high – in hypereutrophic conditions – the growth and physiological condition of the nutrient-demanding plants, such as *Typha angustifolia* can weaken (Steinbachova-Vojtiskova *et al.*, 2006). At present, *T. angustifolia* is very common and forms large monocultures in the Kokemäenjoki River delta (Suominen, 2013). This kind of successional development delta confirms earlier observations that *T. angustifolia* is capable of displacing *T. latifolia* in most littoral conditions where the two cattails co-occur (Weiner, 1993).

In the interspecific competition, *Phragmites australis* displaces the cattails, due to greater morphological flexibility (Bellavance and Brisson, 2010). Competition can, however, affect both winners and losers. In the Canadian study, in a mixed stands of helophytes, biomass production was reduced both in the strongest competitor *Phragmites australis* and the suffering parties *Typha latifolia* and *T. angustifolia* (Bellavance and Brisson, 2010). The elevated concentration of atmospheric CO₂ is one of the factors behind the recent success of *Typha angustifolia* over the near relatives (Sullivan *et al.*, 2010).

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