

RESEARCH ARTICLE

Open Access

Strategies in Growth of the Common Reed (*Phragmites australis*) as Related to Successional Stages in a Rapidly Varying Estuary

Kai Aulio*

Department of Biology, University of Turku, FI-20014 Turun yliopisto, Finland; Present address: Lankakatu 3 D 16, FI-20660 Littoinen, Finland.

Abstract

The common reed *Phragmites australis* (Cav.) Trin ex Steudel (= *P. communis* Trin.) is the dominant component in the Kokemäenjoki River delta, western Finland, an estuary where the changes in the vegetation are more rapid than in any other ecosystem in Northern Europe. Three phases in the successional development of *Phragmites* were characterized on the basis of decades-long follow-up. Of the biometric characteristics of the reed stands, the height, weight and density of individual shoots (ramets) were measured. In all the parameters studied, marked differences were seen between the successional stages. The growth and production of *Phragmites australis* is exceptionally high in the studied Kokemäenjoki River delta, due to the continuous supply of nutrients, and the suitable grounds in the estuary. The height and weight of the ramets were statistically significantly greater at the pioneer stage of succession than in the final, regressing phase. The average height of the shoot was 266.5 cm in the pioneer stage, 278.4 cm during the mature phase and 219.8 cm in the regressing phase. The height and weight values correlated significantly in all three successional phases. At the pioneer stage, however, the ramets were markedly more robust than in the other two phases. In the density of the monocultural stands, a clear self-thinning trend was seen in all the successional phases, i.e. the number of ramets per unit area is linearly reduced during the growing season. The average density of ramets was 151.9 individuals/m² at the pioneer stage, 176.9 ind./m² in the mature stage, and 147.1 ind./m² in the regressing stage. As a conclusion, the variations between the successional phases in a rather uniform river delta were so notable that a detailed description and characterization of the sample sites is necessary in any analysis of wetland macrophytic vegetation.

Key Words: Aquatic macrophytes, common reed, *Phragmites australis*, plant strategies, wetland succession.

(Received: 03/01/2014; Accepted: 17/01/2014; Published: 05/02/2014)

Introduction

River deltas and other coastal areas form ecosystems, where production and biological diversity support and maintain the richest communities in the world. But unfortunately, these wetlands are amongst the most vulnerable and most rapidly destroyed habitats in our planet. In Europe, 50% of wetlands have been destroyed by man during the recent century (Silva *et al.*, 2007). However, the structures and functions of coastal and deltaic wetlands are very poorly known as compared with terrestrial ecosystems (Abell, 2002).

In the river deltas, environmental conditions are changing more rapidly than in most other natural habitats (Dobson and Frid, 2009). The deposition of sediments carried by the river flow, as well as the accumulation of locally produced plant biomass makes the estuaries very diverse habitats for rich biota. As evaluated by the rapid changes of landscapes and the creation of new colonization grounds for flora and fauna, river deltas are similar to several man-made habitats (Phillips, 1978). In aquatic environments, the deltas are a natural counterpart for the sandbanks and deposition dumps of dredged sediments. Most biological processes proceed rapidly, as the delta grows and enlarge annually due to the river-

*Corresponding author: kai.aulio@hotmail.fi

borne deposition. The deltas are especially suitable grounds for biota, whose competitive abilities are weak, and whose establishment would not be possible in stable environmental conditions (Phillips, 1978).

The macrophytic vegetation – typical for shallow-water estuaries and river deltas – is of paramount importance for all ecosystems, including other biological taxa and man (Orth *et al.*, 2006; Hughes *et al.*, 2009). Estuarine and coastal wetlands provide a wide variety of natural services, and thus the preservation and proper management of these ecosystems should be the primary goal in the active natural conservation. Both the coastal and estuarine vegetation can serve “as the canary bird of the coasts”, reflecting the health of the whole community and concretizing the ongoing changes – of which majority are harmful or even dangerous to all living creatures (Orth *et al.*, 2006).

The continuous, and often directed and anticipated changes in morphology and vegetation of river deltas are a real challenge for follow-up studies. Just a sample of particular date can produce results, that when evaluating the values of real nature of an estuarine system can be dangerously misleading (Livingston, 1987; Timoney, 2008).

The continuously changing environmental conditions in river deltas are reflected in rapid – and often predictable variations in macrophytic vegetation. The changes are most rapid in the phase, when the aquatic, open-water flora is replaced by the littoral wetland communities through competition and due to environmental changes (Timoney, 2008). The subject of the present study, the common reed *Phragmites australis* is a universal example of the plant species being able to utilize such quickly changing natural habitats and resources (Phillips, 1978).

The worldwide success of *Phragmites australis* is based on the co-operation and sharing of resources in the clonal plant. Utilization and efficient transport of stored energy and nutrients from underground storages (rhizomes) to the growing shoots enable rapid growth and development of its flowers. Within-plant allocation of resources within the clone enhances the capacity of *Phragmites* to conquer suitable littoral grounds and form wide monocultures, reedswamp wetlands (Dobson and Frid, 2009; Hara *et al.*, 1993). The uniform and dense communities of *Phragmites* modify extensively their habitats by enhancing the sedimentation and deposition of autochthonous organic matter reducing the effects of water currents and winds. Like other strong competitors, it also restricts the colonization or even existence of other plant species (Dobson and Frid, 2009). On the other hand, in the modified microhabitats near and outside the reed stands, the species composition of other aquatic plants and the diversity and total number of aquatic animals is influenced (Gabriel and Bodensteiner, 2011).

River deltas are usually characterized by rapid changes in environmental conditions, continuous creation of new rooting grounds for vegetation, and thus dynamic changes in biota. The changes are most clearly seen in successional changes in macrophytic vegetation. Its development is often directional and predictable (Tilman, 1990; Grime, 2001). In estuaries, where the deposition takes place irregularly – for example due to occasional floods – the successional trends can be unpredictable and irregular (Zweig and Kitchens, 2009). Successional trends (Dobson and Frid, 2009; van der Valk, 2012) – adaptations to changing environments – are a characteristic feature in *Phragmites australis*. Typically the common reed invades and colonizes non-vegetated areas near the average water level (in shallow water or a few centimetres above the level), and spreads effectively through vegetative underground rhizomes (Amsberry *et al.*, 2000).

In the Kokemäenjoki River delta, a wide variety of growth forms and great variations in the biometric parameters can be found in the common reed. Obvious similarities and generalizations could be made, however, between the three distinct successional phases of *Phragmites australis* (Aulio, 1979).

Materials and methods

Study area

The succession of the macrophytic vegetation was studied in the Kokemäenjoki River estuary, in western Finland (Northern Europe; 61°34'N, 21°40') in 1990's and again in 2013 (figure 1). The estuary, discharging into the Baltic Sea, is a shallow sedimentation basin, which is nearly thoroughly covered with rich and exceptionally productive macrophytic vegetation (Aulio, 1979). The delta in the

estuary is proceeding very quickly due to the deposition of sediments carried by the River Kokemäenjoki, the accumulation of autochthonous organic (plant) matter, and due to land uplift, typical to the shores of the Baltic Sea. At present, the extent of the land uplift in the area is 5.5 millimeters a year. The deltaic deposits (formation of new sandbanks and islands), as well as the distribution of the vegetation zones are today moving towards the sea at the average speed of 30 meters a year (Aulio, 1979).



Figure 1. Location of the study area.

The delta of the Kokemäenjoki River at Pihlavanlahti Bay shows the most rapid change in any landscape in the Northern Europe. The water of the estuary is essentially fresh water carried by the River Kokemäenjoki. The water of the river and of the estuary were highly polluted and eutrophicated during past decades, but due to effective water purification and conservation efforts, the aquatic environment of the area is today considered clean and healthy (Aulio, 2010).

On the basis of water quality, the Pihlavanlahti Bay is eutrophic. Biologically the estuary is very rich, and from 2004 on the site has been part of the *Natura 2000* conservation network of the European Union. The estuary is also part of the international *Ramsar Convention on Wetlands* network of valuable bird sanctuaries. The penetration of sea water into the estuary is restricted by road embankments, and even naturally. The water of the adjacent, northern reach of The Baltic Sea is brackish water with a salt concentration of only 0.1–0.5 ‰.

The study target: common reed (*Phragmites australis*)

Phragmites australis (Cav.) Trin ex Steudel (= *P. communis* Trin.) is the tallest grass growing in the Northern Europe. The common reed can extend as high as over 4 meters, and the production of aboveground biomass often reaches several kilograms dry matter per square meter during a growing season. In the Kokemäenjoki River delta,

Phragmites is one of the dominant macrophytes, covering extensive areas in the shallow sections of the estuary. In the interspecific competition – an essential feature in the vegetation succession in varying environments – the common reed is a strong contender during the succession. With the course of terrestrialization, i.e. water depth shallowing, the common reed is pushing away the species that dominate deeper water habitats. On the other hand, terrestrial plant taxa will replace *P. australis* as the shallowing of the estuary is advancing near the average water level.

In this study, the communities of *Phragmites australis* in the Kokemäenjoki River delta were divided into three classes according to the successional phases of the estuarine macrophytic vegetation (Aulio, 1979). The successional phases described and compared were as follows:

Pioneer stage: The stands growing primarily along the open-water channels of the estuary.

Mature stage: The monocultural communities covering tens or hundreds of hectares in the shallow and sheltered waters out of the direct influences of the primary river flow and wind surge. The exchange of water is continuous, and thus the supply of nutrients via the river water is guaranteed.

Regressing stage: The final phase of *Phragmites* succession in the estuary. The water depth is very shallow or the ground has risen above the mean water level through sedimentation and principally through accumulation of the self-produced plant material. In this phase, the competitive ability of *Phragmites* is weak, and the taxa – such as cattails (*Typha latifolia* L. and *T. angustifolia* L.) and sedges (*Carex* spp.) occupying and withstanding also dry littoral grounds – replace the decades-old dominant communities of the common reed (Dobson and Frid, 2009).

The common reed spreads most efficiently vegetatively through transport of fragmented rhizomes. Through vegetative propagation and expansion, the *Phragmites* stands usually consist of monocultural clones. However, in reality there are minor variations in the genetic pools of the reed stands (Engloner and Major, 2011). Those variations cannot be seen or realized in field studies, and so in the present study the stands are supposed to consist of only genetically uniform ramets. In recent decades, *Phragmites australis* has gained significant advantage all over the world due to the climatic change and eutrophication, especially the increase in nitrogen emissions and discharges (Rickey and Anderson, 2004).

Collection and analyses of the plant materials

The plant samples of *Phragmites australis* were collected by the time of the maximum biomass of reeds (late August, during several successive years in 1990's and again in 2013). The sampling was made randomly in the middle of the uniform, monocultural stands at three succession stages (Aulio, 1979). In this study, the height of the individual shoots (or ramets, as the definition is in the clonal plants) was determined from the water/sediment interface up into the tip of the uppermost leaf axil (Haslam, 1973). The biometric measurements as well as the frequency of the flowering ramets were taken for 25 – 50 randomly sampled individuals at each of the

successional stages. The water depth of the sites was determined by 10 measurements in each site. The samplings and the number of replicates are considered a reliable in describing the growth and production characteristics of tall helophytic plants like *Phragmites australis* (Goraud *et al.*, 2008). The sampling and measurement policy of the study followed the international standards commonly used in hydrobiological studies (Vollenweider, 1969).

Determination of the nutrient contents of the plant and sediment samples followed standard methods described in detail in the manual by Allen (1974). Dried and pulverized samples were digested with sulphuric acid-hydrogen peroxide reagent. The concentrations of nitrogen were determined by semi-micro Kjeldahl distillation and titration with 0.01 N sulphuric acid. Mixed acid reagent was used in the digestion for phosphorus analyses. The concentrations of phosphorus were determined colorimetrically by using the ammonium molybdate method (Allen, 1974).

The content of organic matter of the sediment samples was determined after dry ashing (at 475 °C, 4 h). All the results are expressed on a dry weight basis. For plant and sediment material dry matter determinations, the samples were oven-dried at 60°C for 24 h (Vollenweider, 1969).

Statistical analyses and terminology

The parametric (mean ± standard error of the mean and standard deviation of the mean, one-way analysis of variance; ANOVA), and non-parametric (Kruskal–Wallis one-way analysis of variance) statistical analyses of the numerical data were performed by using the *Analyse-it for Microsoft Excel* (version 2.12) program package (Analyse-it Software, 2008). The terminology of biological concepts and principles follows the latest edition of the *Oxford Dictionary of Plant Sciences* (Allaby, 2012).

Results

Description of the study sites

The environmental characteristics of the sampling sites varied widely over the study area. The estuary of the Kokemäenjoki River has an area of about 38 km², and the average water depth is less than three meters. In the vegetated parts of the delta, the range of the water depth is between 2.3 meters and above the average water level. In the present study, the average water depth in each of the succession phases of *Phragmites australis* was measured in 15–20 stands in each of the three successional phases. In the monocultures, the mean water depths were quite uniform, although solitary individuals are growing in waters as deep as two meters. The mean water depth characteristics in the successional phases are presented in table 1. The variation in the water depth was largest in the regressing stands. This variation is later reflected in several biometric measurements of the plants.

Shoot length

The common reed, *Phragmites australis* is the dominant macrophytic plant in the middle sections of the Kokemäenjoki River delta at Pihlavanlahti Bay. The morphological characteristics vary widely between the

successional stages, but marked variation is seen also within the classes (table 2). In the comparison between the successional stages, the mature and established communities consist of the tallest reed shoots (or *ramets*, if judged by the clonal characteristics of the reed). In the whole material throughout the delta, the average shoot length in the mature community class was 278 cm (range between the stands 169–326 cm). The environmental conditions vary a lot, and this is reflected in the shoot parameters of *Phragmites*.

The pioneer stage, i.e., the youngest successional class gains significant advantages of continuous nutrient supply via the river water as well as unlimited space to expand without interspecific competition. The shoots of *Phragmites* are nearly as tall as in the mature communities; the average shoot height determined in this study was 266 cm (range 145–311 cm). The coefficient of variation of 6.9% was almost the same as in the pioneer stage. In the final stage of *Phragmites* in the succession, the average height of reed shoots was 219 cm (range 131–259 cm), and the coefficient of variation was high as compared to the other two stages, i.e., 11.4%.

The eight biometric parameters determined in the *Phragmites* stands are – as expected – mostly correlated with each other. But the general trend according to the phases in the decades-long vegetation succession shows marked and statistically significant differences (table 2), thus emphasizing the importance of a detailed characterization and description of the sampling sites in field studies of *Phragmites australis*.

In ANOVA, the different letters in the horizontal rows indicate significant difference ($P < 0.01$).

Shoot weight

As with the length of the ramets of *Phragmites australis*, the weight of the individuals differed markedly according to the successional phases. The two components of ramet dimensions correlate, and so it is logical that the trend with weight is absolutely the same as with the height comparisons, showing statistical significant trend: *pioneer* > *mature* > *regressing*. In the analysis of variance, all the comparison of the three successional phases differed highly significantly from each other (table 3).

Variations in the ramet weights were greater than the differences in the shoot heights. The individuals in the pioneer stage are robust, i.e. the stems are thicker and thus significantly heavier than in the other two stages. The individual ramets in the pioneer stage weigh more than twice as much as those in the final stage of *Phragmites* succession (table 3). The correlations between the shoot height and the shoot weight were statistically highly significant in each of the three successional stages. The Pearson correlation coefficients in the Kokemäenjoki River delta were as follows: In the pioneer stage, $r = 0.945$ ($P < 0.001$), in the mature stage, $r = 0.919$ ($P < 0.001$) and in the regressing stage, $r = 0.844$ ($P < 0.001$). About 125 individuals were measured in each of the classes.

In a separate analysis, the allocation of biomass into different plant organs was determined. In all the three successional stages combined, the average share of leaf blades and leaf bases was 24.9% (range 17.4–38.9%), the share of the stems was 72.2% (range 58.3 – 81.9%), and the average share of inflorescences/fruits was 2.9% (range 0.8 – 6.1%).

In ANOVA, the different letters in the vertical columns indicate significant difference ($P < 0.01$).

Density of ramets

In the tall and rapidly growing helophytic littoral grasses such as the common reed, the density of the communities is of paramount importance for the species maintenance and for the success in the interspecific competition. In the Kokemäenjoki River delta, the stands of *Phragmites australis* are very wide and exceptionally productive (Amsberry *et al.*, 2000). The densities of the monocultures vary, however, widely due to the course of vegetation succession. The differences between the three successional classes are marked. Comparisons of the shoot densities are shown in figure 2.

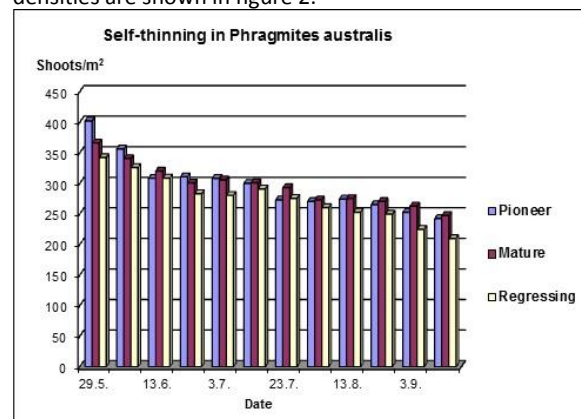


Figure 2. The averages shoot densities (individuals per square meter) of *Phragmites australis* during the growing season (late May to mid-September) in the three successional phases in the Kokemäenjoki River delta. $N = 10$ separate communities per each successional phase per date.

The comparisons show clearly the intra-clonal or self-thinning phenomenon at all the three successional stages. In all phases, the densities show clear and consistent declining trend from spring towards the autumn. And secondly, in the comparisons between the stages, the densities of *Phragmites* ramets were clearly lowest at the regressing stage, whereas the highest densities were measured at pioneer stage at the start of the growing season, but later the mature communities had the most ramets per unit area.

Discussion

The communities of *Phragmites australis* in the Kokemäenjoki River estuary are exceptionally productive, as compared to similar communities throughout the Northern Europe (Björk, 1967; Andersson, 2001) as well as in the Western and Central Europe (Rodewald-Rudescu, 1974). This is certainly true, even though the recent trends in strengthening of the reed communities due to climatic change and enhanced availability on nutrients are considered (Pitkänen *et al.*, 2013).

One of the most important external determinants of the plant growth is the availability of nutrients. In the estuary of a river heavily loaded with anthropogenic discharges of waste waters and agricultural runoff, the levels of the major and minor nutrients are usually sufficient to maximize the plant production. For the tall, rooted helophytic grasses such as *Phragmites australis*, the amount and availability of nutrients in the rooting

medium is of paramount importance. In the Kokemäenjoki River delta, the concentrations of the major nutrients nitrogen and phosphorus are high throughout the study area. There were, however, significant differences between the successional stages of *Phragmites* (table 4). The accumulation and contents of organic matter in the sediment (rooting zone of the reed) is a major determinant for the retention of nitrogen and phosphorus in the bottom deposits. The contents of the organic matter show a clear trend according to the successional stages (table 4).

The stands of *Phragmites australis* in the Kokemäenjoki River delta are dense and very productive, and so the amount of biomass produced during each growing season is also very high. Thus the deposition and accumulation of the autochthonous organic mass produced is also a major factor in the shallowing process of the delta. Due to the river flow, the deposition of the plant mass is slight in the pioneer stage, where majority of the overwintering plant mass is wiped out by ice mass and transported further away by the river. But in the very dense and uniform stands of the mature and regressing stages, the majority of *Phragmites* mass is deposited at the sites. This trend is clearly reflected in the contents of the organic matter of the sediments at the three successional stages of *P. australis* (table 4).

The total amount and availability of nutrients is the main background for growth and biomass production of plants. The most important growth regulators are the major nutrients nitrogen (N) and phosphorus (P). Their concentrations in the sediments and especially in the rhizosphere of the reeds are strongly correlated with the contents of organic matter of the bottom deposits. In the Kokemäenjoki River delta, the levels of the major nutrients in the successional stages of *P. australis* are presented in table 4. The levels of growth-promoting nutrients, as well as the organic matter varied markedly between the successional stages.

In the studied sediments, a highly significant correlation was found between the contents of organic matter and the levels of the major nutrients. In the Pearson correlation analysis $r = 0.934$ ($P < 0.001$) between nitrogen and organic matter, and $r = 0.853$ ($P < 0.001$) between phosphorus and organic matter, $df = 15$.

In the plant production ecology, the ratio between the major nutrients nitrogen and phosphorus (N/P-ratio) in plant tissues as well as in the environment is usually characterized as a crucial determinant. At the present study, the N/P-ratio in the rhizosphere deposits varied widely in the three successional stages of *P. australis*. In the pioneer stage, the average value of N/P-ratio was 5.97, in the mature stage the N/P-ratio was 5.66, and finally at the regressing phase of the *Phragmites* succession the mean N/P-ratio of the sediments was 6.64. The continuous supply of nutrients via the eutrophicated river water enables optimal production conditions throughout the study area. And the accumulation of nutrient-rich organic matter in the regressing communities can compensate the reduced availability of nitrogen, lost through the denitrification in the occasionally anaerobic conditions during warm summers (Minchinton and Bertness, 2003). Hence, the availability of nutrients seems not to limit the growth and production of *Phragmites* in the Kokemäenjoki River delta. On the other hand, the unlimited supply and availability of major nutrients, especially nitrogen,

enhance the production and also directs the biomass allocation (Rickey and Anderson, 2004, Martin and Blossey, 2013). So it can be concluded that the high production of aboveground ramet biomass of *Phragmites australis* in the Kokemäenjoki River delta is largely based on the availability of nitrogen.

Phragmites australis is a very strong contender in the biological – both intraspecific as well as interspecific – competition. Especially in North America, the originally European invasive subspecies of *P. australis* is nowadays a huge problem. However, its management efforts have gained only minor results in spite of several projects and investments of millions dollars (Kettenring and Mock, 2012, Martin and Blossey, 2013). When established, the monocultures of *Phragmites australis* are stable for decades, owing to the vegetative distribution. The dense communities thus established prevent other plants of penetrating into the stands (Haslam, 1973). As in the present study area, *Phragmites australis* has markedly increased both occurrence and distribution on other shores and estuaries in the Baltic Sea. Eutrophication is the most important reason for the enhanced production – denser and wider communities – of the common reed in the sheltered coastal habitats (Pitkänen *et al.*, 2013)

The present results of the dynamics in the growth of *Phragmites australis* show that there are no such things as “one truth fits for all”. Although both experimental and model investigations have emphasized that the height and density of the *Phragmites* shoot remain fairly stable throughout the growing season (Hara *et al.*, 1993), the biometric parameters show significant trends at least in rapidly varying environments such as river deltas. Rapid and unexpected changes in environmental conditions – such as the birth of new deltaic sandbanks and islands due to deposition of flood-borne sediments – creates unvegetated grounds for helophytes such as *Phragmites australis* and cattails (*Typha* spp). And when these plants are established, the superior competitive abilities ensure that other plants cannot push them away, and hence the succession can start and proceed unexpectedly (Tulbure *et al.*, 2007, Dobson and Frid, 2009).

Previous studies have demonstrated that both stochastic and deterministic control can maximize the resource utilization in the common reed, thus guaranteeing the survival of even the smallest and weakest individual ramets. However, this study in the Kokemäenjoki River delta showed that self-thinning (Hutchins, 1979) reduces the density, and at the end of the growing season the weight of the ramets declines due to breakdown of leaves and inflorescences. As in experimental studies published earlier (Ekstam, 1995), the thinning was most prevalent in the smallest individuals and in the early phase of the growing season.

Conclusions

As a conclusion, the variations between the successional phases in one rather uniform river delta were so marked that a detailed description and characterization of sampling sites is necessary in any analysis of wetland macrophytic vegetation.

References

- Abell R. 2002. Conservation biology for the biodiversity crisis: a freshwater follow-up. *Conservation Biology*, **16(5)**: 1435–1437.
- Allaby M (Ed.). 2012. **Oxford Dictionary of Plant Sciences**. Third Edition. Oxford University Press, Oxford. p. 565.
- Allen SE (Ed.). 1974. **Chemical analysis of ecological materials**. Blackwell, Oxford. p. 565.
- Amsberry L, Baker MA, Ewanchuck PJ and Bertness, MD. 2000. Clonal integration and the expansion of *Phragmites australis*. *Ecological Applications*, **10(4)**: 1110–1118.
- Andersson, B. 2001. Macrophyte development and habitat characteristics in Sweden's large lakes. *Ambio*, **30**: 503–513.
- Analyse-it Software, Ltd, **Analyse-it for Microsoft Excel** (version 2.12). 2008. <http://www.analyse-it.com>
- Aulio K. 1979. Mataloitumisen vaikutus kasvillisuuteen Kokemäenjoen suistoalueella. (In Finnish, with Summary in English: Effects of decrease in water depth on the aquatic and littoral vegetation in the Kokemäenjoki River delta). Publications Instituti Geographici Universitatis Turkuensis, **90**:1–30.
- Aulio K. 2010. The Kokemäenjoki River: A success story in water conservation. *Baltic Cities Environmental Bulletin*, **2/2010**: 7.
- Björk, S. 1967. Ecologic investigations of *Phragmites communis*. Studies in theoretic and applied limnology. *Folia Limnologica Scandinavica*, **14**: 1–248.
- Dobson M and Frid C. **Ecology of Aquatic Systems**, Second Edition. Oxford University Press, Oxford, 2009; pp. 321.
- Ekstam B. 1995. Ramet size equalization in a clonal plant, *Phragmites australis*. *Oecologia*, **104(4)**: 440–446.
- Engloner AI and Major Á. 2011. Clonal diversity of *Phragmites australis* propagating along water depth gradient. *Aquatic Botany*, **94(4)**: 172–176.
- Gabriel AO and Bodensteiner, LR. 2011. Ecosystem functions of mid-lake stands of common reed in Lake Poygan, Wisconsin. *Journal of Freshwater Ecology*, **26(2)**: 217–229.
- Goraud C, Giroux JF, Mesléard F and Desnouhes L. 2008. Non-destructive sampling of *Schoenoplectus maritimus* in southern France. *Wetlands*, **28(2)**: 532–537.
- Grime JP. 2001. **Plant strategies, vegetation processes, and ecosystem properties**, Second Edition. John Wiley & Sons, Chichester. p. 417.
- Hara T, van der Toorn J and Mook JH. 1993. Growth dynamics and size structure of shoots of *Phragmites australis*, a clonal plant. *Journal of Ecology*, **81**: 47–60.
- Haslam S. 1973. Some aspects of the life history and outecology of *Phragmites communis* Trin. A review. *Polskie Archiwum Hydrobiologii*, **20**: 79–100.
- Hughes AR, Williams SL, Duarte CM, Heck Jr KL and Waycott M. 2009. Associations of concern: declining seagrasses and threatened dependent species. *Frontiers in Ecology and the Environment*, **7**: 242–246.
- Hutchings MJ. 1979. Weight–density relationships in ramet populations of clonal perennial herbs, with special reference to the $-3/2$ power law. *Journal of Ecology*, **67**: 21–33.
- Kettenring KM and Mock KE. 2012. Genetic diversity, reproductive mode, and dispersal differ between the cryptic invader, *Phragmites australis*, and its native conspecific. *Biological Invasions*, **14(12)**: 2489–2504.
- Livingston RJ. 1987. Field sampling in estuaries: The relationship of scale to variability. *Estuaries*, **10(3)**: 194–207.
- Martin LM and Blossey B. 2013. The runaway weed: Costs and failures of *Phragmites australis* management in the USA. *Estuaries and Coasts*, **36(3)**: 626–632.
- Minchinton TE and Bertness MD. 2003. Disturbance-mediated competition and the spread of *Phragmites australis* in a coastal marsh. *Ecological Applications*, **13(5)**: 1400–1416.
- Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck Jr KL, Hughes, AR, Kendrick GA, Kenworthy WJ, Olyarnik S, Short FT, Waycott M and Williams, SL. 2006. A global crisis for seagrass ecosystems. *BioScience*, **56**: 987–996.
- Phillips JD. 1987. Shoreline processes and establishment of *Phragmites australis* in a coastal plain estuary. *Vegetatio*, **71**: 139–144.
- Pitkänen H, Peuraniemi M, Westerborn M, Kilpi M and von Numers M. 2013. Long-term changes in distribution and frequency of aquatic vascular plants and charophytes in an estuary in the Baltic Sea. *Annales Botanici Fennici*, **50 (Supplement A)**: 1–64.
- Rickey MA, Anderson RC. 2004. Effects of nitrogen addition on the invasive grass *Phragmites australis* and a native competitor *Spartina pectinata*. *Journal of Applied Ecology*, **41(5)**: 888–896.
- Rodewald-Rudescu, L. 1974. Das Schilfrohr *Phragmites communis* TRINIUS. *Die Binnengewässer*, **27**: 1–302.
- Silva JP, Philips L, Jones W, Eldridge J and O'Hara E. 2007. **LIFE and Europe's wetlands: Restoring a vital ecosystem**. Office for Official Publications of the European Communities, Luxembourg. p. 68.
- Tilman D. 1990. Constraints and tradeoffs: Towards a predictive theory of competition and succession. *Oikos*, **58(1)**: 3–15.
- Timoney K. 2008. Rates of vegetation change in the Peace-Athabasca delta. *Wetlands*, **28(2)**: 450–463.
- Tulbure MG, Johnston CA and Auger DL. 2007. Rapid invasion of Great Lakes coastal wetland by non-native *Phragmites australis* and *Typha*. *Journal of Great Lakes Research*, **33 (Supplement 3)**: 269–279.
- van der Valk AG. 2012. **The Biology of Freshwater Wetlands**, Second Edition. Oxford University Press, New York. p. 280.
- Vollenweider RA (Ed.). 1969. **A manual on methods for measuring primary production in aquatic environments**. IBP Handbook 12, London, p. 213.
- Zweig CL and Kitchens WM. 2009. Multi-state succession in wetlands: a novel use of state and transition models. *Ecology*, **90(7)**: 1900–1909.

Table 1. The water depth in the three successional phases of *Phragmites australis* in the Kokemäenjoki River delta, western Finland. *N* = 15 in each phase.

Successional phase	Mean ± S.E. (cm)	Range (cm)	Coefficient of variation (%)
Pioneer stage	14.14 ± 3.11	15 – 33	82.32
Mature stage	17.50 ± 4.33	6 – 44	92.69
Regressing stage	10.79 ± 3.12	0 – 20	108.34

Table 2. Biometric measures in *Phragmites australis* in the three successional phases in the Kokemäenjoki River delta, western Finland. Mean ± standard error of the mean (S.E.), coefficient of variation (CV, %), and the statistical significance of the differences analyzed by ANOVA. *N* = 10 communities in each successional phase, and 25 randomly sampled shoots in each community.

	Successional phase		
	Pioneer stage	Mature stage	Regressing stage
Shoot length (cm)	266.47±5.42 ^a	278.40±6.05 ^a	219±7.94 ^b
CV (%)	6.43	6.87	11.42
Length of inflorescence (cm)	26.80±1.64 ^a	25.04±0.64 ^a	21.35±2.50 ^b
CV (%)	19.37	8.03	36.96
Length of the uppermost leaf (cm)	43.57±0.92 ^a	41.57±3.68 ^a	36.16±4.49 ^b
CV (%)	6.70	28.02	32.27
Breadth of the uppermost leaf (cm)	2.87±0.06 ^a	2.37±0.16 ^b	2.11±0.20 ^c
CV (%)	6.62	21.94	29.86
Length of the broadest leaf (cm)	49.83±0.77 ^a	41.15±1.02 ^b	38.07±1.62 ^c
CV (%)	4.90	7.85	13.53
Breadth of the broadest leaf (cm)	4.05±0.12 ^a	3.29±0.13 ^b	2.92±0.28 ^c
CV (%)	9.88	12.16	30.14
Number of leaves/shoot	11.20±0.23 ^a	8.70±0.25 ^b	8.60±0.29 ^b
CV (%)	6.70	8.97	10.58
Thickness of the stem (cm)	0.65±0.02 ^a	0.98±0.05 ^b	0.62±0.05 ^a
CV (%)	10.77	15.31	25.81

Table 3. Shoot weight (in grams dry weight) of *Phragmites australis* in the three successional phases in the Kokemäenjoki River delta by the time of the maximum biomass (late August). Mean ± standard error of the mean (S.E.) and the coefficient of variation (CV, %). *N* = 20–30 individuals in each phase.

Successional phase	Weight (g, dry wt)	Coefficient of variation (%)
Pioneer stage	14.48±1.06 ^a	29.21
Mature stage	10.89±1.19 ^b	39.49
Regressing stage	6.63±0.58 ^c	35.14

Table 4. Contents of organic matter, nitrogen, and phosphorus in the sediments in stands of *Phragmites australis* in the three successional stages in the Kokemäenjoki River delta, western Finland.

	Pioneer stage	Mature stage	Regressing stage
Organic matter (% dry wt)	2.84 (±1.17) ^a	10.18 (± 1.09) ^b	21.41 (±1.21) ^c
Nitrogen (mg/g, dry wt)	1.79 (± 0.40) ^a	5.21 (± 0.41) ^b	6.57 (± 0.35) ^b
Phosphorus (mg/g, dry wt)	0.30 (± 0.05) ^a	0.92 (± 0.09) ^b	0.99 (± 0.54) ^b

Mean ± standard error of the mean (S.E). *N* = 15–20 stands in each successional stage. Statistical significance of the differences: In ANOVA, different letters in the horizontal rows indicate highly significant difference (*P* < 0.01).