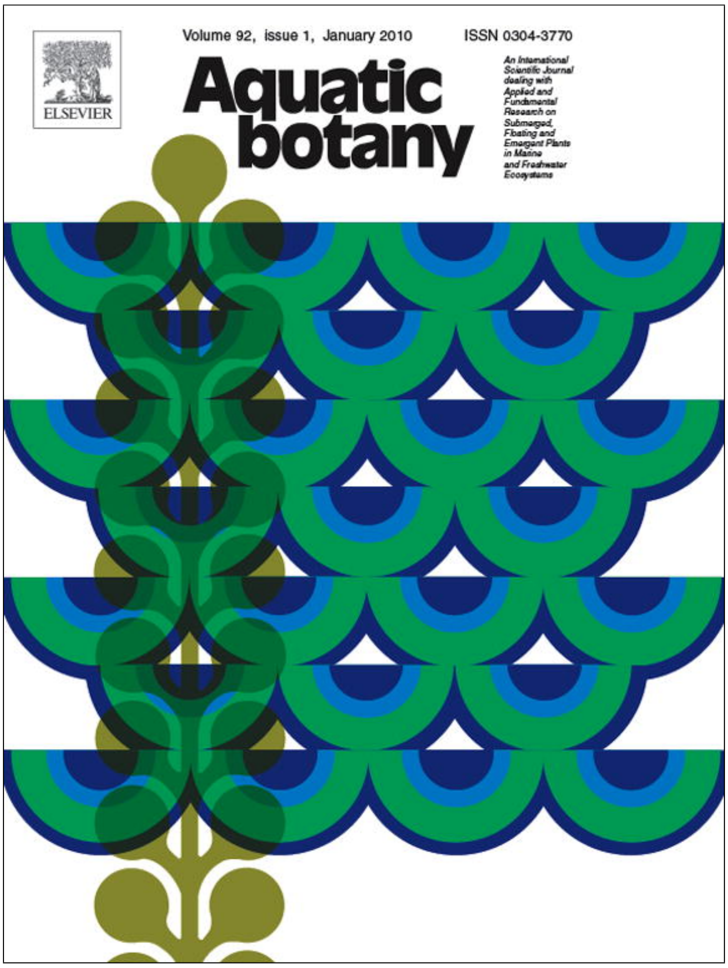
Volume 92, issue 1, January 2010
ISSN 0304-3770
ELSEVIER
Aquatic botany
An International Scientific Journal dealing with Applied and Fundamental Research on Submerged, Floating and Emergent Plants in Marine and Freshwater Ecosystems

Aquatic Botany 92 (2010) 33–39

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Distribution of clonal growth forms in wetlands☆

Monika Sosnová [a,b,*], Rudy van Diggelen [c,d,e], Jitka Klimešová [b]

[a] *Department of Botany, Faculty of Science, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic*
[b] *Institute of Botany, Academy of Sciences of the Czech Republic, Dukelská 135, CZ-379 82 Třeboň, Czech Republic*
[c] *Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands*
[d] *Faculty of Spatial Sciences, University of Groningen. P.O. Box 800, 9700 AV Groningen, The Netherlands*
[e] *Ecosystem Management Research Group, Department of Biology, University of Antwerp, Universiteitsplein 1c, B2610 Antwerpen, Belgium*

ARTICLE INFO

Article history:
Received 27 January 2009
Received in revised form 13 September 2009
Accepted 14 September 2009
Available online 19 September 2009

Keywords:
Clonal growth organ
The Netherlands
Wetland plant community
Functional trait

ABSTRACT

Clonal multiplication is a predominant type of reproduction in wetland species. However, both wetlands and plant organs of clonal growth are diverse, thus due to different stress factors operating in various wetlands preponderance of plants with specific clonal growth organs (CGOs) can be expected. To test this hypothesis the CGO spectra of wetland communities of the Netherlands were analysed, including a bog, a fen, heathland, a floodplain, river beds, fresh water pools, open salt water and a salt marsh. Moreover, it was evaluated whether different CGOs are characterised by different functional traits (shoot cyclicity, persistence of connections between ramets, number of offspring produced per year and lateral spread per year) in wetland species. Data on types of CGO, i.e., epigeogenous and hypogeogenous rhizomes, fragments and budding plants, stolons, tubers and bulbs, root-splitters, root-sprouters and special adaptations (turions) as well as their functional traits, were taken from the CLO-PLA 3 database. CGO spectra of wetland communities were analysed using two methods: comparison of observed vs. expected CGO spectra based on the presence/absence data and multivariate analysis (CCA) for inter-community differences considering species frequency. Moreover, relationships between CGOs and their functional traits were tested using multidimensional contingency tables. Apart from 26% of non-clonal species, the majority of wetland species was rhizomatous (51%). Other types of CGO were represented in less than 10% of species and root-derived CGOs were underrepresented ($<$2%) in comparison with terrestrial habitats. Among communities, fresh water pools and open salt water hosted higher proportion of species with fragments ($\sim$10%) and turions ($\sim$30%). Multivariate analysis divided wetland communities along the disturbance and hydric (water) gradients. Highly disturbed communities (salt marshes) were characterised by non-clonal species and species with root-derived CGOs. Aquatic communities (fresh water pools and open salt water) hosted species with the ability to spread by fragmentation and turions, contrary to permanently wet communities (bog and wet heathland) with the prevalence of species with epigeogenous rhizomes. It was also confirmed that the CGOs of wetland species differed in their traits. The most important functional trait characterising individual CGOs in the wetland flora was the degree of lateral spread (explained variability: 53%) followed by duration of persistence of connections between ramets (explained variability: 74%), which is in accordance with earlier distinguished strategies of clonal growth: integrator/splitter and spreading/non-spreading clones.

1. Introduction

Clonal multiplication is a set of attributes which enables a plant to produce genetically identical offspring with the potential to become independent of the mother organism (Klimeš et al., 1997). Plants using vegetative spreading for their growth and reproduction are found across all types of habitats. van Groenendael et al. (1996) found clonality to be frequent under cold, shaded, wet and nutrient-poor conditions and less frequent under dry and disturbed conditions. The proportion of clonally growing species in wetlands, and particularly in aquatic habitats, is large and in most aquatic taxa vegetative propagation predominates over sexual reproduction (Grace, 1993; Boedeltje et al., 2003, 2004; Combroux and Bornette, 2004; Dorken and Barrett, 2004). This phenomenon was supposed to be due to phylogenic reasons (Eckert, 2002), life-history constraints (Charpentier et al., 2000), or simply a consequence of an adaptation of plants to wet or aquatic habitats (Johansson and Nilsson, 1993). However, focusing on wetlands, a large diversity in habitat types as well as in clonal

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☆ Nomenclature sources: Kubát et al. (2002), phytosociological alliances according to Schaminée et al. (1995, 1996, 1998).

* Corresponding author at: Institute of Botany, Academy of Sciences of the Czech Republic, Dukelská 135, CZ-379 82 Třeboň, Czech Republic. Tel.: +420 384 72 11 27; fax: +420 384 72 11 36.

E-mail address: sosnova@butbn.cas.cz (M. Sosnová).

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doi:10.1016/j.aquabot.2009.09.005

growth forms can be seen, so the pattern of clonal growth modes and particular wetland types is obscured.

Wetlands are a heterogeneous group of communities ranging from peat forming habitats and floodplains to open-water and saline environments. In these communities plants must cope with various stress factors such as temporal and spatial heterogeneity in oxygen, various disturbance regimes, different nutrient and light availability and uneven connectivity with similar habitats (Bornette et al., 1994). Even one type of community can largely differ in environmental conditions and consequently species composition (stress factors operating throughout the season, Bornette et al., 2008). Also modes of clonal growth are diverse, since clonal spread and multiplication are realised by growth of specialised organs of root, stem or even leaf origin. These organs of clonal growth presumably differ in the distance they can spread, in the period of time for which clonal offspring are connected, in number of clonal offspring produced and other functional traits (Grace, 1993; Klimešová and Klimeš, 2008). Although this assumption was postulated, it has not been tested so far. However, comparative studies of species possessing similar growth forms often found different strategies to cope with disturbance and stress (Bornette et al., 1994, 2008).

Grace (1993) presumed the existence of specific selective forces operating in particular wetland types on clonal growth organs (CGOs) according to their function. In his conceptual work he distinguished six of these functions, i.e., numerical increase in ramets, dispersal, resource acquisition, storage, protection and anchorage, and showed that different types of clonal multiplication differ in terms of these functional traits. Moreover, he presumed that these traits are not independent, but form certain syndromes.

The aim of this study was to test the conceptual model by Grace (1993) by asking: (1) if certain types of CGO tend to prevail in some wetland communities and (2) whether certain CGO types are characterised by certain syndromes of characteristics (functional traits). The vegetation of the Netherlands was used as an example for this study, because the majority of European wetland types are found in this country.

2. Methods

To assess if certain types of CGO prevail in some wetland communities, two methods were used: (i) comparison of observed CGO spectra for each alliance (belonging to a particular community) with expected CGO spectra (based on 500 permutations of all species) by contingency tables and (ii) comparison of communities by means of multivariate analysis (CCA). Additionally it was tested (iii) how individual CGOs are characterised by their functional traits, i.e., shoot cyclicity, persistence of connections between ramets, number of offspring produced per year and lateral spread per year by multidimensional contingency tables.

2.1. Plant communities

According to the treatise vegetation of the Netherlands (Schaminée et al., 1995, 1996, 1998) the following main wetland communities were selected: a bog, a fen, wet heathland, a floodplain, river beds, fresh water pools, a salt marsh and open salt water. Each wetland community was characterised by its phytosociological alliances. In the treatise, all species occurring with a frequency of more than 10% in at least one of the alliances of an order are included and species rare in all alliances are left out. The amount of relevés per alliance differs, ranging from several hundreds to even several thousands of relevés. For our comparison all alliances (except the very rare ones) typical of a given wetland community were selected and all recorded species were included.

2.2. Wetland species pool

Into the wetland species pool all higher plants of the Netherlands with Ellenberg indicator values for moisture equal to or higher than six (Botanisch Basisregister, CBS, 1993) were included. This wetland species pool was used to assess CGO spectra for all wetland plants of the region and to test how individual clonal growth organs are characterised by their functional traits using multidimensional contingency tables.

2.3. Classification of clonal growth

Using the CLO-PLA 3 database of clonal growth in plant (Klimešová and Klimeš, 2006) types of CGOs for each species from all alliances and wetland species pool were assessed. Also the following functional traits related to clonality were recorded: shoot cyclicity (categories: 1/2/>2 years), persistence of connections between ramets (categories: 1/2/>2 years), number of offspring produced per year (categories: <1/1/2–10/>10) and lateral spread per year (categories: <0.01/0.01–0.25/>0.25 m/dispersable).

The majority of clonally growing species often use more than one type of CGO (e.g., *Potamogeton* species, which often employ up to four modes of clonal growth: turions, plant fragments, rhizomes and stem tubers, Klimeš and Klimešová, 1999). Therefore all CGOs listed as necessary in the database were used (but see Section 2.4.3). The record with the most filled cells related to clonality was used. If there were not any CGOs classified as necessary, the species was considered non-clonal.

Types of CGOs were reduced from the 17 distinguished in the CLO-PLA 3 database to 8 types, i.e., epigeogenous rhizome, hypogeogenous rhizome, fragments and budding plants, stolons, tubers and bulbs, root-splitters, root-sprouters, and special adaptations. CGOs were arranged by their origin (root, stem) and function (storage or dispersal organs). Mostly ecologically similar CGOs with a relatively low number of species, such as tubers and bulbs, fragments and budding plants, and special adaptations, were combined. For example turions, which represent a way of overwintering connected with multiplication, fell into one category (special adaptation); plant fragments and budding plants, as a way of multiplying during the vegetative season, fell into another category (fragments and budding plants).

2.4. Data analyses

2.4.1. Contingency tables

Types of CGOs found in species across alliances were permutated (500 permutations) and its random sample of the same number of observations (expected values) was compared with that from an individual alliance (observed values) by contingency tables (Pearson Chi-square test).

2.4.2. Multivariate analysis (CCA)

CGOs found in different wetland communities were compared using a direct method of canonical analysis, i.e., canonical correspondence analysis (CCA). The difference between wetland communities characterised by frequencies of species found in alliances typical of a given community and CGOs was examined in this analysis. The frequency of species in the alliance was used as the species data set and the data on CGOs were standardised by samples before starting the analysis and used as explanatory (environmental) variables. The weight of alliances containing species with an unknown type of CGO, i.e., not listed in the CLO-PLA3 database, was proportionally lowered. The CCA was performed by using CANOCO (ver. 4.5, ter Braak and Šmilauer, 2002) and differences between wetland communities were tested using the Monte Carlo permutation test (499 permutations under the reduced model).

2.4.3. Multidimensional contingency tables

Relationship between types of CGO and their functional traits (shoot cyclicity, persistence of the connection between ramets, number of offspring produced per year and lateral spread per year) was tested on the wetland species pool using multidimensional contingency tables by R Development Core Team (2005). In this analysis only one type of clonal growth organ, i.e., the one with the highest production of offspring and the largest lateral spread, respectively, was used. Non-clonal species were omitted from this analysis. The analysis started by testing the null model, which presumes random organisation of the data set. In the next step it was tested if addition of any of the explanatory variables (functional traits) improves the quality of the model (by decreasing deviance) and after that a stepwise selection searching for the best combination of explanatory variables was followed.

To filter out the possibility that the results are just a combination of the most common traits from abundant species (e.g., *Carex*, *Juncus*, *Potamogeton*), the analysis was performed not only for the whole data set, but also took into account the phylogenetic proximity of the species. The level of genus was used, and according to the "majority vote", species of one genus were grouped into one record. In case of inconsistency the whole genus was omitted (this occurred in less than 10% of genera).

3. Results

3.1. Clonal growth of wetland species of the Netherlands

In the wetland species pool (580 species), consisting of all species of the Dutch flora, 26% of species were classified as non-clonal. The highest proportion of clonal species was rhizomatous (25% epigeogenous rhizomes and 26% hypogeogenous rhizomes), whereas plants with other types of clonal growth organs (i.e., stolons, fragments and budding plants, tubers and bulbs, root-splitters, root-sprouters, and special adaptations) represented up to 10% of species (Fig. 1). Characteristics of CGOs and its typical wetland representatives are given in Table 1.

Comparison between the observed spectra of types of CGOs of individual alliances with their expected spectra showed a different representation in one alliance from floodplains (Calthion palustris: $\chi^2 = 16.6, p < 0.05$) and river beds (Sparganio-Glycerion: $\chi^2 = 18.5, p < 0.05$). In fresh water pools five out of nine alliances were found to have a significantly different spectrum of CGO types and in open salt water 2/3 of alliances were different (Table 2 and Fig. 2). In these communities (fresh water pools and open salt water) a lower proportion of non-clonal species and a higher proportion of plants using special adaptations (turions), budding and fragmentation were found (Fig. 2).

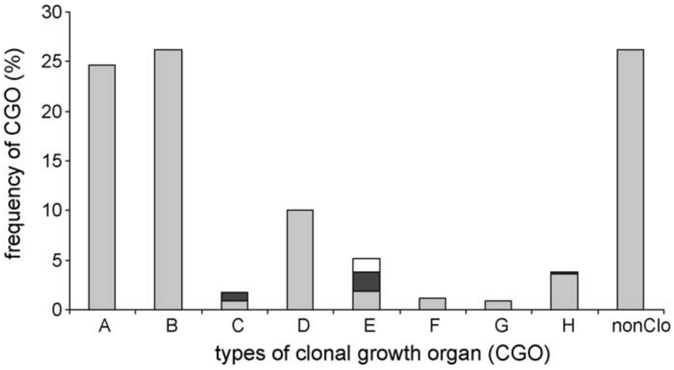

Fig. 1. Frequency of types of CGO in the wetland species pool (defined as all species from the Dutch flora with Ellenberg's indicator value for moisture >6, $n = 580$). (A) Epigeogenous rhizome, (B) hypogeogenous rhizome, (C) fragments and budding plants (fragments in grey, budding plants in black), (D) stolons, (E) tubers and bulbs (stem and offspring tubers in grey, bulbs in black, root tubers in white), (F) root-splitters, (G) root-sprouters, (H) special adaptations (turions in grey, bulbils in black), and (nonClo) non-clonal species.

In the canonical correspondence analysis (CCA), where the type of CGO was used as an explanatory variable for species distribution between the wetland plant communities, 26% of the variability was explained on the first canonical axis (499 permutations under the reduced model—Eigenvalue: 0.844, *F*-ratio: 2.65, *p*-value: 0.002), which correlated with non-clonal species and root-sprouters abundantly found in salt marshes. The second axis explained 20.8% of the variability (Eigenvalue: 0.685). Along this axis, budding and special adaptations prevailed in fresh and salt water communities at one extreme and epigeogenous rhizomes in bogs and wet heathlands at the opposite side. However, rhizomatous species and species with stolons were found in many types of wetland communities with no clear pattern (Fig. 3).

3.2. Clonal traits typical of a given type of CGO

Using multidimensional contingency tables it was tested if individual types of CGO can be characterised by specific functional traits. Adding all traits (shoot cyclicity, persistence of connections between ramets, number of offspring produced per year and lateral spread per year) to the model resulted in a decrease of unexplained variability. Following the stepwise selection, each variable was tested against the whole model (1st class interaction) and the best combination according to decrease in deviance was selected. After adding the trait of lateral spread per year the model explained

Table 1
Types of clonal growth organs (CGOs), their characteristics and typical wetland representatives. Numbers in parentheses denote relevant types in the CLO-PLA 3 database.

Clonal growth organ (CGO)	Characteristics	Example (relevant type in CLO-PLA3)
Epigeogenous rhizome	Perennating rhizome formed above-ground but later buried or pulled by root contraction below ground. It commonly serves as a bud bank and storage organ. Usually slow vegetative spread.	*Acorus calamus* (9)
Hypogeogenous rhizome	Perennating rhizome formed below-ground. Vegetative spread may be fast.	*Calamagrostis epigejos* (10)
Fragments and budding plants	Detached parts of shoot or an extremely reduced plant body of aquatic plants.	*Elodea nuttallii* (5, 6)
Stolons	Creeping axes of a plant. Serves as bud bank and storage organ. Vegetative spread may be fast.	*Stratiotes aloides* (1)
Tubers and bulbs	Root or stem origin. Below-ground storage and regenerative organ.	*Ranunculus ficaria* (12, 13, 16, 17)
Root-splitter	Plant fragmentation due to senescence and decay of the tap root. Poor vegetative spread. Adventitious roots and buds missing.	*Armeria maritima* (14)
Root-sprouters	Plants with ability to form adventitious buds on roots (spontaneously or after injury). Buds can be formed on tap root or on horizontal roots.	*Rorippa sylvestris* (15)
Special adaptations	Turions, bulbils, plantlets (pseudovivipary), gemmipary and root tubers formed at or above soil surface.	*Ceratophyllum demersum* (2, 3, 4, 7, 8)

Table 2
Wetland communities of the Netherlands with its environmental characteristics and relevant phytosociological alliances used in this study (according to Schaminée et al., 1995, 1996, 1998). Species lists of a particular alliances (observed spectra) were compared to expected spectra of clonal growth organs (based on 500 permutations of all species).

Wetland communities	Alliances	DF	Chi	*p*-Value
Bog				
Mire community with water table at the surface. Bogs are acid (pH < 5.5), nutrient-poor habitats fed by precipitation water.	Rhynchosporion albae	7	4.90	0.67
	Caricion lasiocarpae	8	9.10	0.33
	Ericion tetralicis	8	9.26	0.32
	Oxycocco-Ericion	7	7.57	0.37
Wet heathland				
Nutrient-poor habitat consisting mainly of dwarf shrubs. The water table is fluctuating during wet/dry season.	Littorellion uniflorae	8	4.76	0.78
	Hydrocotylo-Baldellion	8	7.28	0.51
	Eleocharition acicularis	8	5.23	0.73
Fen				
Mire community fed by ground/surface water. Fens are base-rich, slightly acidic to neutral (pH > 5.5).	Caricion nigrae	8	8.51	0.39
	Caricion davallianae	8	7.23	0.51
Floodplain				
Hydrologically very dynamic systems with intensive flooding, which may occur in winter or spring, and dry summer periods. High nutrient availability due to flooding deposits and internal (re)mobilisation of nutrients.	Phragmition australis	8	6.77	0.56
	Caricion gracilis	8	8.24	0.41
	Caricion elatae	8	9.17	0.33
	Lolio-Potentillion anserinae	8	12.95	0.11
	Calthion palustris	8	16.64	**0.03**[*]
	Alopecurion pratensis	8	12.46	0.13
River beds				
Euthrophic to mesotrophic littoral zones. Usually mudy, with fluctuating water table.	Sparganio-Glycerion	8	18.50	**0.02**[*]
	Oenanthion aquaticae	8	14.85	0.06
	Cicution virosae	8	13.43	0.10
Fresh water pools				
Deeper water and oxygen stress. In this study open fresh water includes emergent communities and truly open-water communities (submerged or floating species).	Lemnion minoris	7	16.24	**0.02**[*]
	Lemnion trisulcae	7	13.73	0.06
	Nymphaeion	8	29.10	**0.00**[***]
	Hydrocharition morsus-ranae	8	17.17	**0.03**[*]
	Parvopotamion	8	18.47	**0.02**[*]
	Ranunculion peltati	8	20.32	**0.01**[**]
	Nitellion flexilis	7	6.94	0.44
	Charion fragilis	7	10.20	0.18
	Charion vulgaris	8	10.52	0.23
Salt marsh				
The habitat between mainland and sea, which is regularly flooded by the sea, i.e., species must cope with mechanic and salt stress.	Zosterion	3	1.58	0.67
	Spartinion	6	5.06	0.54
	Thero-Salicornion	7	7.88	0.34
	Puccinellion maritimae	8	10.73	0.22
Open salt water				
Open salt water is characterised by deeper water, salt and oxygen stress and low nutrient availability.	Charion canescentis	5	3.15	0.68
	Zannichellion pedicellatae	8	19.43	**0.01**[*]
	Ruppion maritimae	6	14.59	**0.02**[*]

[*] $p < 0.05$.
[**] $p < 0.01$.
[***] $p < 0.001$.

52.8% of the variability (the deviance decreased from 618.56 in the null model to 292.11, $p < 0.001$, df = 21). After including the trait of persistence of connections between ramets the deviance decreased to 158.05 (explained variability 74.4%, $p < 0.001$, df = 14), and then to 123.91 by including the number of offspring produced per year (explained variability 79.9%, $p < 0.05$, df = 21). The final addition of shoot cyclicity to the model decreased the deviance to 99.85 (explained variability 83.8%, $p < 0.05$, df = 14).

After including phylogenetic relationships to the analysis, all functional traits were found to be good predictors of types of CGO. Adding lateral spread per year, the model explained 42.9% of the variability (the deviance decreased from 344.76 in the null model to 196.98, $p < 0.001$, df = 21) and including the trait of persistence of connections between ramets finally explained 65.6% of the variability (deviance 118.58, $p < 0.001$, df = 14). No other addition significantly improved the model.

4. Discussion

Both hypotheses of our study were supported: (1) certain types of CGO tend to prevail in some wetland communities and (2) certain CGO types can be characterised by particular syndromes of characteristics (functional traits). Particularly open-water communities were characterised by a higher ratio of species producing turions, plant fragments or multiply by budding. These CGOs were characterised by a high degree of lateral spread, low persistence of connections between ramets, their low longevity and high potential for multiplication. Moreover, salt marshes were characterised by a high proportion of non-clonal plants and root-sprouters. The remaining wetland communities hosted a universal set of CGOs with lower lateral spread, higher persistence of connections between ramets, their higher longevity and lower potential for multiplication (Fig. 3).

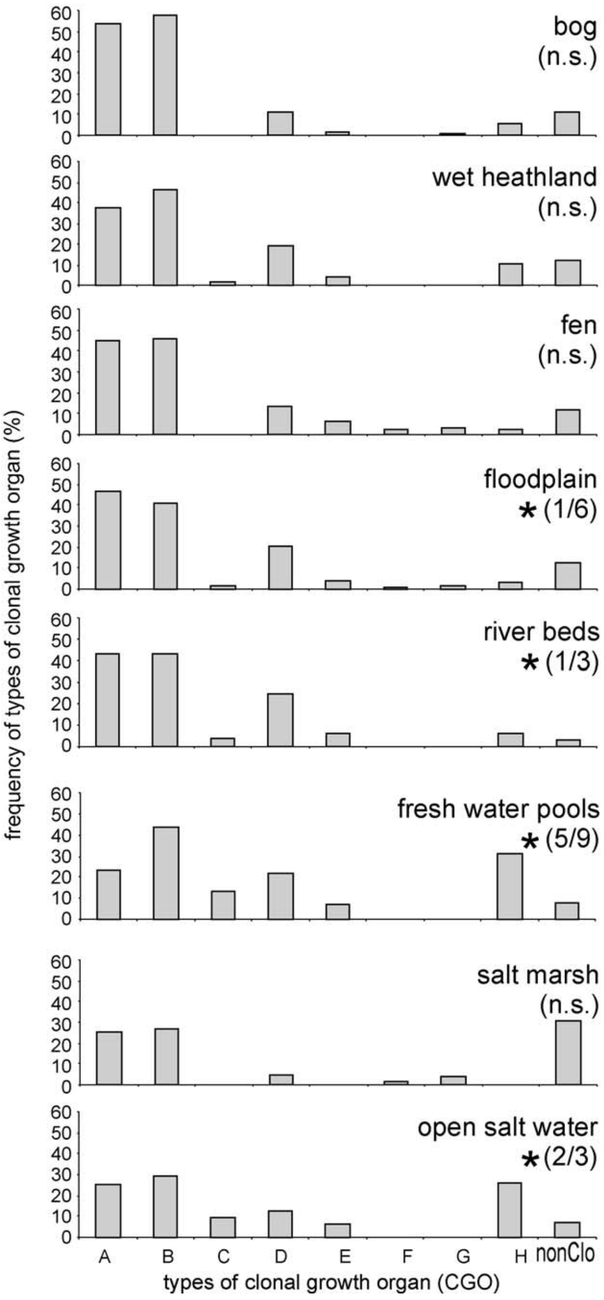

Fig. 2. Frequency of types of CGO in wetland communities of the Netherlands. Columns denote the mean percentage of species possessing a particular CGO in a given community. In parentheses the proportion of significant results is indicated (No. significant alliances/all alliances belonging to particular community; for results of tests, see Table 2). (A) Epigeogenous rhizome, (B) hypogeogenous rhizome, (C) fragments and budding plants, (D) stolons, (E) tubers and bulbs, (F) root-splitters, (G) root-sprouters, (H) special adaptations, and (nonClo) non-clonal species. (n.s.) Non-significant, (*) $p < 0.05$ in at least one alliance.

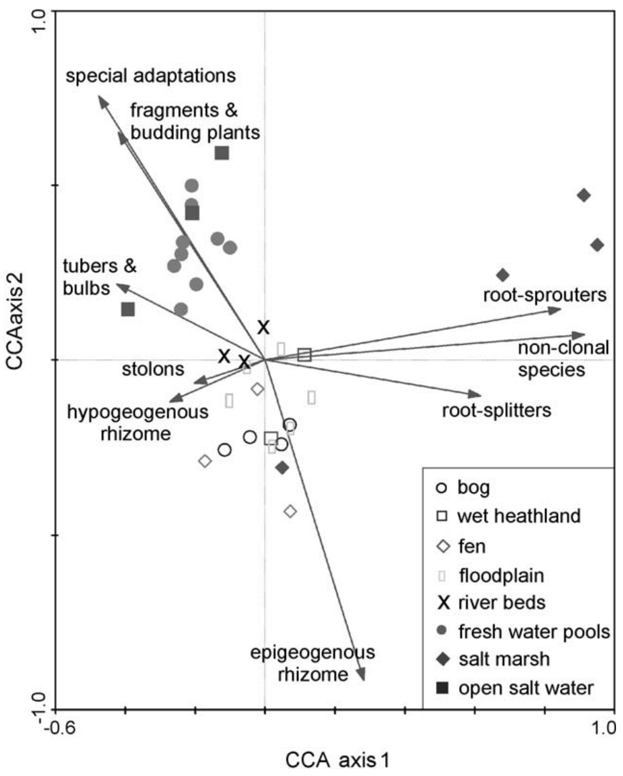

Fig. 3. Canonical correspondence analysis (CCA) ordination diagram of types of CGO used as explanatory variable for species composition in wetland communities. Arrows show clonal growth organ correlations. For explanation of clonal growth organs, see Table 1. Wetland communities are represented by different symbols. CCA axis 1 explained 26% of the variability (Eigenvalue: 0.844, F-ratio: 2.65, p-value: 0.002), CCA axis 2 explained 20.8% of the variability (Eigenvalue: 0.685).

4.1. CGOs of wetland species

The most common CGOs in Dutch wetlands were rhizomes, which is similar to the regional flora of the Czech Republic (Klimešová and Klimeš, 2008). These types of CGO were at least two times more common than other ones. Similarly, the ratio between epigeogenous and hypogeogenous rhizomes (1:1) was the same as in the whole regional flora, regardless of the more permeable waterlogged soil of wetland habitats, which might be more suitable for longer internodes of hypogeogenous rhizomes than the soil of terrestrial habitats (Philbrick and Les, 1996). The proportion of plants having stolons (10% of wetland species of the Netherlands, 8.6% in the Czech flora) and tubers and bulbs (approx. 5% in both datasets) did not differ much either.

On the other hand, there was a lower proportion of root-splitting and root-sprouting species in wetland habitats compared to terrestrial ones (less than 2% in wetland species of the Netherlands, more than 12% in the Czech flora), which had been reported earlier (Klimeš et al., 1997; Santamaría, 2002). This underrepresentation may be caused by the costly maintenance of extensive root systems and a lower R/S ratio in nutrient-rich conditions, where nutrients can be acquired directly from water (Duarte et al., 1994). Another factor hindering root growth in waterlogged soil is oxygen deficiency causing injury to the root apex (Pezeshki, 2001). However, the scarcity of species relying on root-sprouting can also be explained by the dominance of monocots in wetlands (Grace, 1993; van Groenendael et al., 1996), since this ability is in monocots restricted to several members of the Orchidaceae family (Klimešová and Martínková, 2004).

CGO typical for wetlands may thus include fragments, budding plants and turions, which were not found outside of nutrient-rich open-water communities and are typical of plants occurring in the water column or floating on the water surface.

4.2. Wetland communities

The distribution of CGOs across wetland communities of the Netherlands was tested by contingency tables and multivariate analysis. The first analysis, in which the observed frequency of CGOs was tested against its general background with contingency tables, enabled us to filter out the unequal distribution of clonal growth organs in the flora, as rare and common types of CGO are of equal importance, whereas in the multivariate analysis (CCA) species were weighted by their frequency. However, both analyses revealed similar patterns and the Grace's presumption (Grace, 1993) was partly supported. According to the multivariate analysis the studied wetland communities were spread along two gradients (see Fig. 3).

The first gradient (along CCA axis 1) can be interpreted as a gradient of disturbance from floodplain habitats to salt marshes. The high ratio of non-clonal plants and root-sprouters in salt marshes provides a pattern similar to a rather contrasting habitat—arable fields, where annuals and perennial root-sprouters play a significant role (Klimešová and Klimeš, 2007). This surprising similarity might be due to the nature of disturbance typical of those two habitats: ploughing similarly as wave activity disturbs the soil and leads to fragmentation of the plant root system (Bertness and Ellison, 1987). Only a few perennial plants are able to cope with such disturbance regime, thus species richness is low and some root-sprouting species (e.g., *Artemisia maritima*, *Limonium vulgare*) are relatively abundant. Clonal growth by means of lateral roots is regarded to be typical of opportunistic species growing in disturbed habitats, as this produces a potentially high number of buds on lateral roots (Klimešová and Klimeš, 2007). Although disturbed habitats can also be found among fresh water pools, river beds and floodplain communities (Barrat-Segretain, 2001; Bornette et al., 2008), they were not distinguishable due to a limited resolution caused by our *a priori* definition of a community (see Section 2).

The second gradient (CCA axis 2) can be interpreted as a hydric (water) gradient from permanent stagnating water (open-water communities) through fluctuating conditions (river floodplains) to stable waterlogged conditions (fen and bogs). CGO preferences changed in the same direction, from special aquatic adaptations (turions, fragments and budding) through CGO spectra typical of terrestrial habitats towards epigeogenous rhizomes. This water gradient also correlates with the nutrient status of eutrophic conditions in open-water communities (nutrient-poor open-water communities are rare in the Netherlands, Schaminée et al., 1995) to nutrient-poor bogs. In nutrient-rich aquatic communities plants with spreading and splitting clones, low longevity of shoots and high multiplication rate prevail, whereas in nutrient-poor bogs plants with non-spreading integrated clones, high longevity of shoots and low multiplication rate prevail. This correlation of nutrients and clonal traits support some concepts of clonal growth strategies described earlier (van Groenendael et al., 1996; Jónsdóttir and Watson, 1997). van Groenendael et al. (1996) found splitting and spreading clones being abundant under nutrient-rich, shaded and wet conditions, whereas non-spreading integrators were abundant under nutrient-poor, full-light and dry conditions. Jónsdóttir and Watson (1997) similarly assigned splitters to nutrient-rich and integrators to nutrient-poor conditions. This has also been demonstrated in a few case studies (Halassy et al., 2005; Klimeš, 2008).

4.3. Functional traits

Clonal growth organs can to a great extent be characterised by a specific set of functional traits, as presumed by Grace (1993). All of our traits (i.e., offspring production, lateral spread, persistence of connections between ramets and shoot cyclicity) were found to be good predictors in the model. However, the best predictors were lateral spread per year and persistence of connections between ramets—the traits already suggested to be essential in a characterisation of clonal growth strategies (see above). While fragments and turions (special adaptations) were characterised by fast lateral spread, tubers and bulbs together with epigeogenous rhizomes moved few centimetres a year only. Long-lived connections between ramets were typical of rhizomes and root-derived CGOs, whereas in stolons, fragments and turions ramets were connected for 1 year.

The least predictable function of clonal multiplication, on the other hand, was offspring production, ranging from nearly zero to tens of ramets produced per year. Thus, the same organ of clonal growth may provide different functions in various species and/or in the same species in different conditions (Klimešová and Klimeš, 2006). This is in accordance with numerous observations that species with the same type of CGO may differ in offspring production depending on plant size (Boedeltje et al., 2003), fertility of the habitat (Greulich et al., 2001), variation in local environmental conditions (Combroux et al., 2001; Pollux et al., 2007), and genetic factors (Brown and Eckert, 2005).

The relationships between wetland communities, CGOs and clonal functional traits assessed in our study, operated on the studied scale. However, these findings do not preclude the possibility of different strategies of plants possessing the same growth form (Bornette et al., 1994, 2008) or phenotypic plasticity of a plant growing along an environmental gradient (Puijalon and Bornette, 2006; Puijalon et al., 2008).

Acknowledgements

We are grateful to Petr Šmilauer and Petr Macek for help with statistics and to Jan W. Jongepier for language corrections. This study was supported by the Grant Agency of the Czech Republic, grant no. GD206/08/H044 and grant AV 0Z60050516 from the Academy of Sciences of the Czech Republic. M.S. was supported by the Erasmus/Socrates programme during her stay in the Netherlands.

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