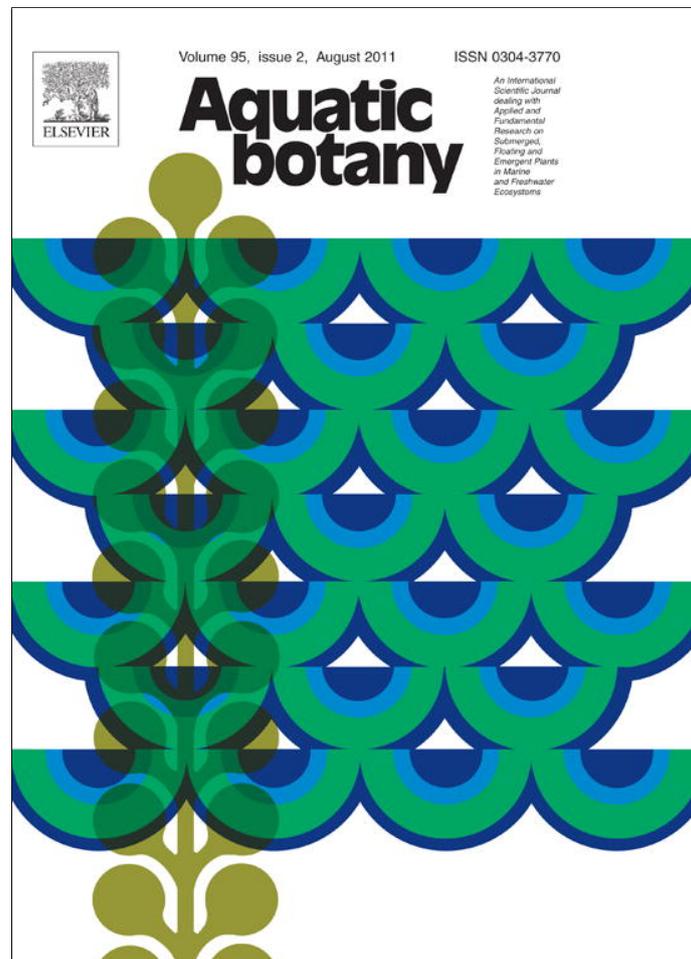


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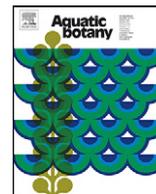
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Distribution of clonal growth traits among wetland habitats[☆]

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ABSTRACT

Clonality resulting from the growth of specialized organs is common among plants in wetland habitats. We hypothesize that different wetland habitats select for different attributes of clonal traits. This hypothesis is based on studies of individual species but has not been previously tested at the level of habitat. We compared the functional diversity of clonal growth traits of plants in bogs, fens, wet heathlands, floodplains, river beds, open fresh water habitats, salt marshes, and open marine habitats. Clonal traits (including number of offspring, lateral spread, persistence of connections between ramets, and shoot life span) were analysed with multivariate techniques using species frequency data and with permutation tests using presence/absence data. Based on species frequencies, clonal plants in aquatic habitats (open fresh water habitats, open marine habitats, and river beds) were characterized by the abundant production of freely dispersible propagules, annual shoots, and splitting clones. Species of daily flooded salt marshes were characterized by bi-annual connections between ramets and medium dispersability. In contrast, plants in permanently wet bogs were characterized by polycyclic shoots and low offspring production. The specificity of river beds and open freshwater habitats was also confirmed by permutation tests, which gave equal weight to rare and abundant species. However, species in all other wetland habitats were characterized by the entire range of clonal traits, suggesting weak environmental filtering of analyzed traits by habitat at the present scale.

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1. Introduction

Most wetland and aquatic plants largely propagate by vegetative means (Sculthorpe, 1967; Grace, 1993). Compared to clones of plants inhabiting drier habitats, clonal growth of wetland plants is characterized by extensive lateral spread and lower persistence of connections among ramets (Van Groenendael et al., 1996; Klimešová et al., 2010). Although this pattern is obvious when comparing clonal growth forms along the whole moisture gradient in various regions (e.g., Central Europe: Van Groenendael et al., 1996; Western Himalayas: Klimeš, 2008), it is lost when phylogenetic relationships of species are considered. The correlation between the wetness of the habitat and the nature of clonal growth is probably caused by early specialization of monocots for wetland habitats

(Grace, 1993; Duarte et al., 1994) and their shared inherent capability of clonal growth due to a lack of secondary thickening and the ease with which they form adventitious roots. Moreover, clonality itself is thought to be important for successful radiation of monocots in wetlands (Duarte et al., 1994; Philbrick and Les, 1996).

The term wetland describes a heterogeneous set of habitats where soil is saturated with moisture either permanently or seasonally (Keddy, 2000; Schaminée et al., 1995). Wetlands include habitats with permanent water columns (i.e., open water habitats), periodically flooded river margins, or waterlogged mires. While the previously cited studies examined wetlands in general and compared them to terrestrial habitats, numerous studies focusing on the role of clonal growth have dealt with small spatial and temporal scales of one wetland community, where various and possibly counteractive selection pressures affect the success of different growth strategies (Bornette et al., 1998, 2008; Puijalon et al., 2005; Dunn et al., 2006). An evaluation of the role of different clonal growth traits over the whole spectrum of wet habitats, as proposed by Grace (1993), has yet to be reported.

In our previous work (Sosnová et al., 2010), we asked whether different kinds of wetland habitats support plants with different kinds of clonal growth organs. We found that open water habitats are rich in plants with turions or easily fragmented stems, that

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

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Table 1

Wetland habitats of the Netherlands with descriptions of their characteristic environmental factors and relevant phytosociological alliances (according to Schaminée et al., 1995, 1996, 1998).

Habitat	Environmental characteristics	Alliances
Bogs	Mire community with low vegetation. Water table at the soil surface. Nutrient-poor, small-scale variability (hummocks and hollows). Undisturbed, but acidic (pH <5.5).	Rhynchosporion albae, Caricion lasiocarpae, Ericion tetralicis, Oxycocco-Ericion
Wet heathlands	Rather short dwarf-shrub vegetation. Fluctuating water table during wet/dry season. Nutrient poor. High spatial variation. Disturbed by herbivory or fire.	Littorellion uniflorae, Hydrocotylo-Baldellion, Eleocharition acicularis
Fens	Mire community with low vegetation. Rather stable water table below soil surface. Nutrient rich. Rather homogeneous. Undisturbed, acidic to neutral (pH >5.5), fed by ground/surface water.	Caricion nigrae, Caricion davallianae
Floodplains	Dynamic systems with tall vegetation. Intensive flooding (winter/spring) and dry summer periods. High nutrient availability due to flooding deposits and internal (re)mobilisation of nutrients. High spatial variability. Intense disturbance.	Phragmition australis, Caricion gracilis, Caricion elatae, Lolio-Potentillion anserinae, Calthion palustris, Alopecurion pratensis
River beds	Littoral zones with submerged and emergent macrophytes. Fluctuating water table. High nutrient availability. High spatial variation. High disturbance.	Sparganio-Glycerion, Oenanthion aquatica, Cicution virosae
Open freshwater habitats	Emergent, submerged, and floating vegetation. Slight fluctuation of (deep) water. High nutrient availability. Spatially homogeneous. Low disturbance, but oxygen stress.	Lemnion minoris, Lemnion trisulcae, Nymphaeion, Hydrocharition morsus-ranae, Parvopotamion, Ranunculion peltati, Nitellion flexilis, Charion fragilis, Charion vulgaris
Salt marshes	Low vegetation. Regularly flooded by salt water. High nutrient availability. Heterogeneous and frequently disturbed. Salt stress.	Spartinion, Thero-Salicornion, Puccinellion maritima
Open marine habitats	Submerged vegetation. Deep fluctuating water. High nutrient availability. Spatially homogenous. Highly disturbed and also salt and oxygen stress.	Zosterion, Charion canescentis, Zannichellion pedicellatae, Ruppion maritima

habitats with waterlogged soils host a high portion of rhizomatous species, and that daily flooded sea-shore habitats disturbed by wave action often contain species with root-derived clonal organs (Sosnová et al., 2010). Although that research confirmed that clonal growth organs can be characterized to a great extent by a specific set of functional traits (Sosnová et al., 2010), their functions may partially overlap. For example, both rhizomes and horizontal roots capable of adventitious sprouting may provide lateral spread of up to 0.5 m per year, but rhizomes, turions, and fragmenting stems (but not horizontal roots) enable plants to multiply clonally at a high rate (Klimešová and Klimeš, 2008). On the other hand, plant fragments of different species may have variable regeneration and colonization capacity (Barrat-Segretain and Bornette, 2000). Because of the functional redundancy of clonal growth organs, we are not able to assess the role of clonal traits (like persistence of connections between ramets, extent of lateral spread, shoot life span, or multiplication rate) on the basis of the distribution of clonal growth organs across wetland habitats as described by Sosnová et al. (2010). Determining the role of clonal traits requires a direct analysis.

To determine whether plants with certain clonal traits are selected for in particular wetland habitats, we used two approaches. In the first, we considered only species presence in certain wetland habitats, and both rare and abundant species had the same effect (or weight). In the second approach, we considered species frequencies. The use of both approaches facilitates the understanding of habitat assemblies, because the first approach reveals the spectrum of trait attributes exhibited by plants that are able to grow in a particular habitat, whereas the second approach reveals the trait attributes of the frequent species.

2. Methods

To evaluate the spectra of trait attributes of plants growing in different wetland habitats, we used contingency tables and multivariate analysis. With contingency tables (which account only for the presence or absence of trait attributes), we compared trait attribute spectra of a given alliance (observed spectra) with random trait attribute spectra made up from permutations of all trait

attributes (expected spectra). Multivariate analysis (canonical correspondence analysis, CCA), in contrast, compared trait attribute frequencies among different habitats.

In this study we used the vegetation of the Netherlands as an example. This wet country contains examples of most types of wetlands that occur in Europe. These include rather extreme habitats such as acidic bogs and halophytic salt marshes, but also many wetland types with less extreme conditions. In addition, the vegetation of the country is described in detail relatively recently by Schaminée et al. (1995–1998) and extensive tables are available with species composition of all vegetation types.

2.1. Studied plant communities

We selected all wetland alliances of the Netherlands that are not uncommon and attributed them to the habitat in which they occurred most. The habitats included bogs, wet heathlands, fens, floodplains, river beds, open freshwater habitats, salt marshes, and open marine habitats. Environmental characteristics of each habitat are listed in Table 1. To characterize the species composition of each habitat type, we adapted the typology of Schaminée et al. (1995, 1996, 1998) and used alliances considered typical for these habitats. We included all listed species that were considered characteristic for the alliances (Table 1, see the Appendix for a list of the species). The amount of relevés per alliance differed, ranging from several hundreds to several thousands. The use of alliances enabled us to reasonably approximate the species composition of various habitat types and to identify the potential environmental filters differing at the scale of alliances. Working at the level of alliances also enabled us to consider the diversifying effects of environmental gradients (such as water depth or flooding regime) that determine species composition of floodplains, salt marshes, and other wetland habitats.

2.2. Clonal growth traits

We obtained the data on traits related to clonality from the database of clonal growth in plants (CLO-PLA 3, Klimešová and

Table 2
Descriptions and attributes (separated by slashes) of clonal traits used in this study. Data were extracted from the CLO-PLA3 database (Klimešová and Klimeš, 2006).

Trait	Description	Attributes
Lateral spread	Distance between parent and offspring ramet (m/year).	<0.01 (slow)/0.01–0.25 (medium)/>0.25 (fast)/dispersable
Shoot life span	Life span of a shoot in years, i.e., until shoot flowers.	1 (annual)/2 (bi-annual)/>2 (perennial)
Persistence of connections	Persistence of connections between parent and offspring ramets (in years).	1 (annual)/2 (bi-annual)/>2 (perennial)
Number of offspring	Offspring ramets produced per year and per mother ramet.	<1/1/2–10/>10

Klimeš, 2006). We used the following traits: lateral spread, shoot life span, persistence of connections between ramets, and number of offspring produced per year (Table 2). In the case of multiple records per species in the database, the record with the most-filled cells was used. Because most clonally growing species use more than one type of clonal growth organ (e.g., *Potamogeton* spp. can spread via turions, fragmentation, rhizomes, and stem tubers; Klimeš and Klimešová, 1999), clonality may also be represented by different trait attributes. However, we used only one attribute for each species, i.e., the one providing the highest offspring production and lateral spread (but see Section 2.4.2).

2.3. Wetland species pool

For illustration of typical trait spectra found in wetland plants of the region, we made a wetland species pool. This pool consisted of all higher plants of the Netherlands with Ellenberg indicator values for moisture ≥ 6 (Botanisch Basisregister, CBS, 1993). Ellenberg indicator values are empirically determined preferences based on the occurrence of the species in plant communities along environmental gradients, with preferences generally assessed as ranging from 1 (lowest preference) to 12 (highest preference) on an ordinal scale. The wetland species pool contained more species than the alliance species pool that was used for comparison by contingency tables (as indicated in Section 3, the wetland pool contained 533 species while the alliance pool contained 397 species). Species composition of the two pools, however, mostly overlapped.

2.4. Data analysis

2.4.1. Contingency tables

Occurrence of trait attributes within all species of all examined alliances (alliance species pool) was permuted (500 permutations), and the average of a random sample (expected value: mean across all the species trait attributes; n always being identical to the species number in the corresponding alliance) was compared with the trait attribute occurrence within an individual alliance (observed value) by contingency tables (Pearson χ^2 test). The achieved P -level was adjusted according to Bonferroni's correction ($P_{\text{corrected}} = P/34$). We followed the same procedure for all traits. Rare species in this analysis had the same weight as common ones.

2.4.2. Multivariate analysis

Trait attributes found in different alliances were also compared using the direct method of ordination analysis (canonical correspondence analysis, CCA). This approach accounted for species frequencies and recognized that many plant species possess several types of clonal growth organs (see above) and thus may have more than one attribute of a particular clonal trait. The data on clonal traits were coded as dummy variables, standardised by samples before entering the analysis, and used as explanatory variables. We used the frequency of species per alliance as the species data set. The CCA was performed with CANOCO (ver. 4.5; Ter Braak and Šmilauer, 2002), and differences between alliances were tested

with Monte Carlo permutation tests (499 permutations under a reduced model).

3. Results

3.1. Clonal traits of wetland species

We found slow or medium lateral spread ($<25 \text{ cm year}^{-1}$) in 84% of the wetland species (i.e., species with Ellenberg values for moisture >6) and fast lateral spread ($>25 \text{ cm year}^{-1}$) in 8% of wetland species. Only 7% of the species produced freely dispersible propagules (Fig. 1a). Most plants produced annual or bi-annual shoots (59% and 30% of species, respectively; Fig. 1b). Perennial connections between ramets prevailed over annual or bi-annual connections (54% vs. 22%, respectively; Fig. 1c). Most wetland species produced at least one clonal offspring per year (44% of the species produced just one offspring, 41% produced 2–10 offspring cohorts per year); few species produced more than 10 or less than 1 clonal offspring generation per year (Fig. 1d).

3.2. Spectra of trait attributes based on presence/absence data

Particular wetland habitats differed in observed spectra of trait attributes, but significant results were never found for all alliances ascribed to a particular habitat type, i.e., attributes spectra of some but not all alliances belonging to a particular habitat were different from an expected trait spectra (Table 3). Observed and expected spectra of attributes frequently differed in the incidence of lateral spread. River beds and open freshwater habitats had distinct spectra of trait attributes (Table 3).

Open freshwater habitats were occupied by species producing freely dispersible propagules, whereas species in river beds often placed their ramets up to 25 cm from the mother ramet (Fig. 1a and Table 3). Salt marsh species of the alliance of *Thero-Salicornion* were characterized by medium dispersal ability.

We found a short local persistence, i.e., a prevalence of annual shoots, in *Cicution virosae*, an alliance generally present in river beds (Fig. 1b and Table 3). River bed species were also characterized by the equal distribution of perennial and short-lived connections among ramets. The *Nymphaeion*, an alliance of open freshwater habitats, was characterized by splitting clones, i.e., a short persistence of the connection among ramets (Fig. 1c and Table 3). Offspring production did not differ among habitats (Fig. 1d and Table 3).

3.3. Spectra of trait attributes considering species frequency

The whole multivariate model (CCA) was significant at $P=0.002$. The first canonical axis explained 18% of the variability (499 permutations; eigenvalue = 0.785, $F=2.25$, $P=0.002$), and the second axis explained an additional 15% of the variance in the data. The first axis was positively correlated with production of freely dispersible propagules, annual shoots, and short-lived connections between ramets, which were typically found in open freshwater habitats and open marine habitats. The second axis assigned perennial shoots to bogs and medium offspring production together with

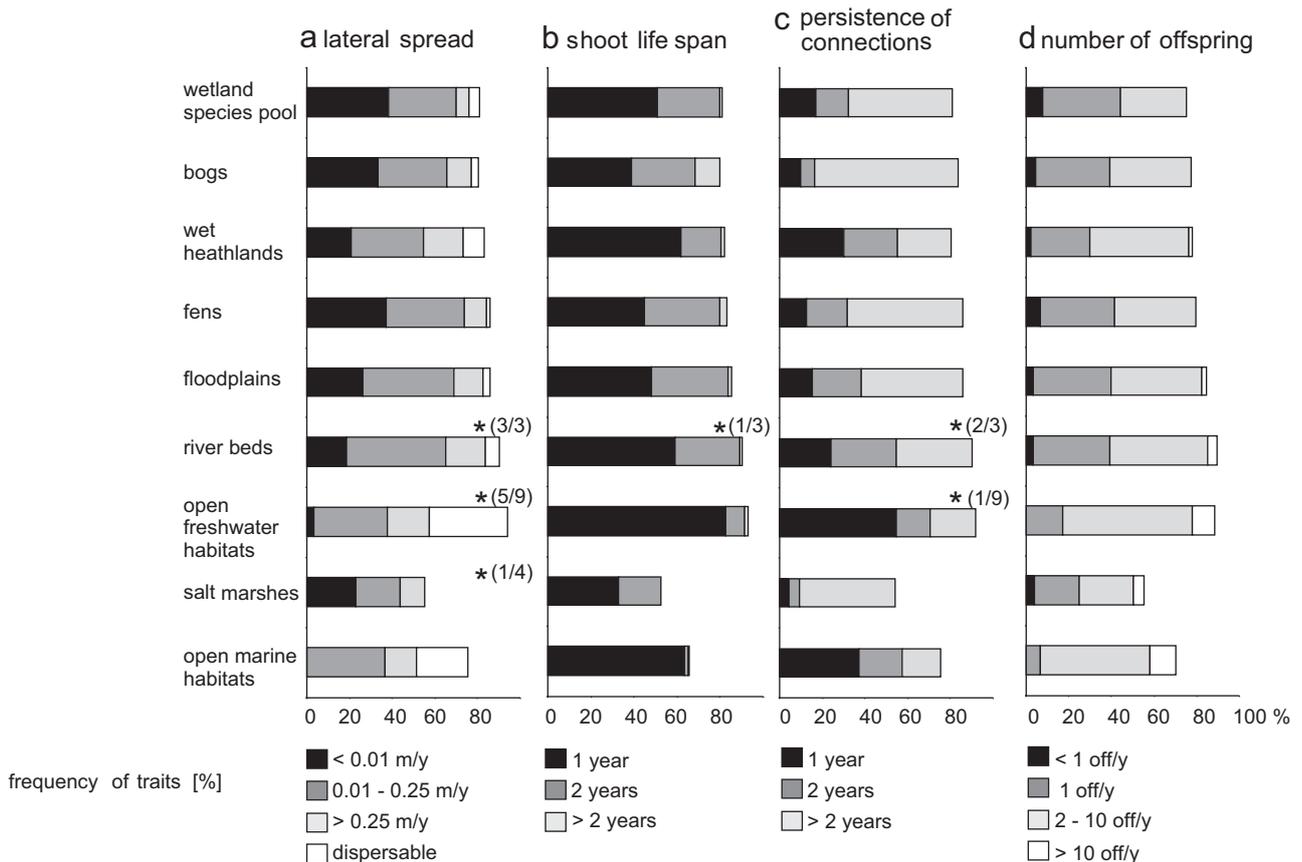


Fig. 1. Frequency of clonal trait attributes among species in wetland habitats of the Netherlands: (a) lateral spread, (b) shoot life span, (c) persistence of connections between ramets, and (d) number of offspring. The wetland species pool was defined as all species from the flora of the Netherlands with Ellenberg's indicator values for moisture >6 ($n = 428$). Columns represent the mean percentage of a particular trait in a given habitat type. The frequency of traits is not equal to 100% due to presence of non clonal species and missing values. Asterisks denote significantly different results (χ^2 tests, $P < 0.05$ after applying Bonferroni's correction) between observed and expected trait spectra. The proportion of significant results is indicated in parentheses (i.e., number of significant alliances/all alliances occurring in a particular habitat; for results of tests, see Table 3).

bi-annual connections of ramets to floodplains and salt marshes (Fig. 2).

4. Discussion

The wetland habitats of the Netherlands differed in spectra of clonal growth trait attributes. Studied open freshwater and marine habitats hosted plants with a low local persistence (i.e., high offspring production, good dispersability, fast-splitting clones, and annual shoots). Periodically flooded habitats showed intermediate persistence, and waterlogged habitats (i.e., bogs) were characterized by the highest local persistence (i.e., slow lateral spread, perennial shoots, and long-lived connection between ramets). This pattern was found when the analysis considered species frequencies. When the analysis was based solely on species presence, however, there was an association between specific trait attributes and species presence only in the wettest habitats. This indicates that the trend was caused by the higher frequencies of species with particular clonal attributes rather than by prevalence of species in the examined alliances. The results do support the idea that wetter habitats host species with more extensive lateral spread and easily splitting clones (Van Groenendael et al., 1996; Klimešová et al., 2010).

We realize that our selection may exaggerate existing differences between habitats somewhat by only attributing the selected alliances to their optimal habitat, although they may occur (less frequently) in other habitats as well. The results of this broad analysis could be refined by further subdividing habitats or using more

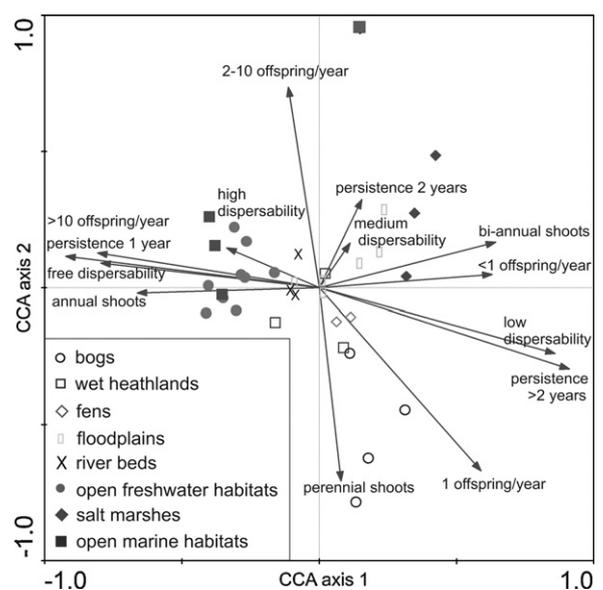


Fig. 2. Canonical correspondence analysis (CCA) ordination diagram of clonal trait attributes used as explanatory variables for species composition in wetland habitats. Arrows show correlations of clonal trait attributes and alliance species composition. For explanation of clonal traits, see Table 2. Wetland habitats are represented by different symbols. CCA axis 1 explained 18% of the variability (eigenvalue = 0.785; $F = 2.25$, $P = 0.002$). CCA axis 2 explained an additional 15.2% of the variability.

Table 3
Comparison based on contingency tables (χ^2 statistics) of observed trait attributes spectra for species of a particular alliance vs. expected trait attributes spectra (based on 500 permutations of trait attributes of all species). n = number of species in each alliance. The values of χ^2 statistics are given. Asterisks denote the level of significance after using Bonferroni's correction ($P_{\text{Bonferroni}} = P/34$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; if not indicated, the compared spectra were not significantly different). DF equals 2 for Shoot life span and Persistence of connections and 3 for Lateral spread and Number of offspring.

Habitat	Alliances	n	χ^2 statistics			
			Lateral spread	Shoot life span	Persistence of connections	Number of offspring
Bog	Rhynchosporion albae	27	1.42	0.45	1.36	2.18
	Caricion lasiocarpae	26	1.01	0.46	0.81	1.13
	Ericion tetralicis	34	2.68	4.91	10.95	1.22
	Oxycocco-Ericion	32	2.69	3.65	10.68	1.80
Wet heathland	Littorellion uniflorae	39	4.88	0.43	1.05	2.65
	Hydrocotylo-Baldellion	52	3.27	1.37	1.48	2.03
	Eleocharition acicularis	40	4.40	0.67	1.63	0.49
Fen	Caricion nigrae	95	4.51	3.57	1.15	1.91
	Caricion davallianae	103	4.08	1.90	0.80	3.23
Floodplain	Phragmition australis	94	6.21	0.81	3.33	2.17
	Caricion gracilis	82	13.33	1.50	6.06	3.94
	Caricion elatae	82	8.77	1.18	6.28	2.39
	Lolio-Potentillion anserinae	64	4.61	0.98	4.15	0.64
	Calthion palustris	153	8.65	1.33	5.57	1.78
River beds	Alopecurion pratensis	105	5.60	1.16	1.74	1.91
	Sparganio-Glycerion	77	24.79***	4.50	13.64*	11.88
	Oenanthion aquaticae	83	18.69*	3.04	10.53	5.84
	Cicution virosae	87	31.51***	13.85*	22.88***	14.49
Open freshwater habitats	Lemnion minoris	26	19.66**	8.68	11.28	9.20
	Lemnion trisulcae	27	20.43**	10.45	12.23	11.22
	Nymphaeion	55	21.97**	11.71	19.92**	11.13
	Hydrocharition morsus-ranae	45	9.10	3.72	3.81	4.10
	Parvopotamion	53	21.37**	9.50	9.09	11.03
	Ranunculion peltati	49	19.01**	11.21	11.38	10.80
	Nitellion flexilis	27	1.14	0.57	1.68	1.99
	Charion fragilis	32	2.27	0.78	2.14	1.28
	Charion vulgaris	36	2.63	4.25	7.14	0.97
	Salt marsh	Spartinion	12	3.53	2.40	1.71
Open marine habitats	Thero-Salicornion	23	17.38*	6.11	6.94	8.80
	Puccinellion maritimae	39	10.43	5.59	9.61	15.32
	Zosterion	4	0.81	0.05	1.93	0.71
	Charion canescentis	8	2.86	1.29	1.96	1.60
	Zannichellion pedicellatae	38	2.26	1.09	2.34	2.67
	Ruppion maritimae	13	7.68	2.42	9.03	5.54

accurate data on frequency distributions of communities over these habitat types. Unfortunately, to the best of our knowledge, such data are not available, not even in a well-investigated country as the Netherlands.

While Sosnová et al. (2010) found similar spectra of clonal growth organs in wetland plant species and all plant species from the Czech Republic, the spectra of clonal trait attributes were shifted towards more extensive lateral spread and higher multiplication rate. Plants of the Dutch wetland species pool were characterized by lateral spread often exceeding 1 cm per year (with the most common category of 0.01–0.25 m per year), but Klimešová and Klimeš (2008) indicate a poorer lateral spread, i.e., <0.01 cm per year, as being typical for all species (including terrestrial species) of the Czech flora. A similar pattern for wetland species has been reported previously by Van Groenendael et al. (1996) and Klimešová et al. (2010). Another trait typical of the Czech flora is a low multiplication rate, i.e., production of 1 offspring shoot per year (Klimešová and Klimeš, 2008), whereas we found a higher multiplication rate (2–10 or >10 clonal offspring per year) for most wetland plant of the Netherlands. As number of offspring is regarded as a measure of the intensity of clonal multiplication, values >1 indicate successful multiplication and support the view that clonal growth is an essential characteristic of wetland species (Grace, 1993; Combroux and Bornette, 2004).

Our analyses revealed that habitats with open water differ from other wetland habitats. Species growing in open water habitats are unique in terms of clonal growth organs (Sosnová et al., 2010) and clonal trait attributes (this study). This is probably attributable

to a set of environmental conditions typical of such aquatic habitats. Among these conditions, the presence of water column is the most important (Duarte et al., 1994; Santamaría, 2002). The water column, which represents substrate as well as support for aquatic plants, also provides optimal conditions for the production of low-cost vegetative propagules (Grace, 1993). Furthermore, these propagules are easily fragmented and can be transported over considerable distances within lakes and among slow-flowing waters in river networks across the landscape (Barrat-Segretain and Bornette, 2000; Boedeltje et al., 2003). The fragmentation of clones may also prevent losses associated with traumatic breakages due to the occasional disturbance in open freshwater habitats (Hay and Kelly, 2008).

Salt marshes and floodplains were characterized by clones with medium lateral spread, long-lived connections between ramets, and medium offspring production. Both habitats are affected by daily or seasonal fluctuations in the water table, and species of salt marshes must also cope with salt stress that may be overcome by clonal integration (Pennings and Callaway, 2000). In both cases, however, clonal traits were typically found in a few frequent species. On the other hand, permanently wet bogs were characterized by a high frequency of species with low multiplication rates and perennial shoots. This confirms the classical idea that the production of perennial connections among ramets is an advantageous clonal growth strategy in resource-poor environments (De Kroon and Schieving, 1990; Jónsdóttir and Watson, 1997) and under dry conditions (Klimešová et al., 2010).

The relatively low specificity of different wetland habitats with respect to the presence of clonal growth organs (Sosnová et al.,

2010) and clonal traits (this study) is probably due to temporal and spatial heterogeneity in key environmental conditions of particular habitats (Santamaría, 2002; Bornette et al., 2008). In floodplains, for example, species strategies are determined by flooding duration and dynamics, which can differ greatly on a small scale within the floodplain of a single river (Bornette et al., 2008). Despite the heterogeneity, plants employ different solutions for specific stresses: spate floods may be overcome by good anchorage and compact growth form (Combroux and Bornette, 2004; Puijalon et al., 2005; Puijalon and Bornette, 2006), or escaped via flexible stems with elongated internodes (Puijalon et al., 2008).

In conclusion, habitats representing both extremes of a hydric gradient hosted species with specific clonal traits, whereas other intermediate wetlands hosted species with a mixture of all trait attributes found in the species pool.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.aquabot.2011.04.001.

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