Physiology of a plant invasion: biomass production, growth and tissue chemistry of invasive and native *Phragmites australis* populations

Fyziologie rostlinných invazí: produkce biomasy, růst a chemismus pletiv invazních a původních populací *Phragmites australis*

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Differentiation within *Phragmites australis,* one of the world's most cosmopolitan and globally important wild plants, and invasions by individual lineages outside of their native ranges is attracting the interest of scientists worldwide. We compared the physiological performance of 89 populations representing distinct genotypes from six phylogeographic groups from Australia, Europe, North America (two groups including native and invasive populations introduced from Europe), South Africa and Far East in a common garden experiment. We show that the populations cluster into two distinct groups: one that includes populations from Europe and Far East together with the North American invasive, and the second the North American native populations with those from Australia and South Africa. Populations within the former group exhibited superior performance in the following traits: they were more vigorous in terms of higher shoot number per pot, greater belowground biomass, longer rhizomes, had greater specific leaf area (SLA), higher N and P concentrations in tissues, and greater investment into generative reproduction. Pooled across phylogeographic groups, *P. australis* has higher values of maximal photosynthesis (A_{max}), higher N and P concentrations in tissues, and greater SLA than most vascular plants, represented by the GLOPNET dataset. Whether due to a weak environmental match or genetic differences, the results indicate that invasion by Australian and African populations in the Northern Hemisphere seems unlikely at present. However, it is not possible to exclude the invasion of genotypes of European origin into Southern Hemisphere or other temperate regions.

K e y w o r d s: below- and aboveground biomass, climate, common reed, growth traits, intraspecific differentiation, N and P concentrations, photosynthesis, *Phragmites australis*, phylogeography, physiological traits, plant invasion, specific leaf area

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Introduction

Extending from the tropics to cold temperate regions in both hemispheres, *Phragmites australis* is among the world's most cosmopolitan and globally important wild plants (Meyerson et al. 2016b, Eller et al. 2017). Its wide geographic distribution and history of introductions make it ideally suited as a model species for studying biogeographical aspects of plant invasions (van Kleunen et al. 2015, Meyerson et al. 2016b, Pyšek et al. 2017). In its native range, it is an important component of wildlife habitats, a keystone species with often substantial effects on ecosystem composition and functioning, and provider of ecosystem services (Packer et al. 2017). However, where introduced, it becomes a noxious invader diminishing biodiversity and altering ecosystem functions but also providing some ecosystem services. This is true namely for North America, where it has rapidly spread over the last two centuries and has converted botanically diverse wetlands into low-diversity stands (Meyerson et al. 2000). Introduced *Phragmites* is a highly successful invasive grass that has overwhelmed coastal and inland ecosystems across much of the United States and southern Canada (see Meyerson et al. 2009 for a review of the situation in North America).

Four distinct lineages of *P. australis* are present in North America (Meyerson et al. 2010, Lambertini et al. 2016): (i) native *P. australis* subsp. *americanus* (Saltonstall 2002) is found throughout the United States and much of Canada, where it has been present, inferred from fossil evidence, for at least 40,000 yr (Hansen 1978). Three other lineages have been identified: (ii) one from Eurasia first appeared in the herbarium record in the 19th century and has invaded throughout North America, (iii) the second, *P. australis* var. *berlandieri*, is found in the southern United States from Florida to California and also extends into Central America and (iv) the third is another recent introduction from the Mediterranean region, so far established only in the Mississippi River delta and in a few more spots in Florida (Lambertini et al. 2012a). Overall, North America is the most studied region in terms of genetics and much less attention has been paid to other parts of the world where the species is also widely distributed, in particular Australia, Far East and South Africa.

The genetic evidence suggests that there are differences in the biogeographic niches among haplotypes (Lambertini et al. 2006, 2012a, Guo et al. 2014, Cronin et al. 2015). This makes *P. australis* a useful model species for understanding differences between the performance in native and non-native biogeographic ranges of population groups represented by different genotypes (Kueffer et al. 2013, Meyerson et al. 2016a, Packer et al. 2017). However, little is known about how genetic differences among haplotypes translate into ecological and physiological differences that determine the vigour of individual populations, an attribute that is likely to play a key role in this species' invasion.

Besides an extensive body of literature on the ecology of *P. australis* from all over the world (see Eller et al. 2017, Packer et al. 2017 for recent reviews), and intensive research into the mechanisms of its invasion in the United States (e.g. Saltonstall 2002, Guo et al. 2013, 2016, 2018, Meyerson et al. 2016b, Pyšek et al. 2018), comparative ecological studies on trait variation under standard conditions have provided valuable knowledge concerning the role of phylogeographic diversity in adaptation processes (Hansen et al. 2007, Eller et al. 2013, 2014, Nguyen et al. 2013, Guo et al. 2014, Tripathee & Schäfer 2014, Allen et al. 2016, Bhattarai et al. 2016, Bui et al. 2016, Mozdzer et al. 2016,

Mozdzer & Caplan 2018, Ren et al. 2018). However, these studies used mainly clones from Europe and North America, and to a limited extent from Australia. We are not aware of any study that would compare these clones with those from other parts of the world.

Here we present data on six *P. australis* phylogeographic groups, covering the species temperate distribution range. Based on a several-year common-garden experiment, we aimed to find the among population-group differences and within population-group variation in traits related to growth, above- and belowground biomass, concentrations of chemical elements in tissues, and the relationships between the main leaf economics traits. The variation in traits and differences among phylogeographic groups are then interpreted with respect to patterns of *Phragmites* global distribution, with a focus on their invasiveness. We also explored bivariate relationships between some of the traits measured and tested for the isometric or allometric growth of individual populations.

Materials and methods

Study species

The taxonomy of the genus *Phragmites* has developed rapidly over the past decade, and five species are currently accepted: *P. australis*, *P. frutescens*, *P. japonicus*, *P. mauritianus* and *P. karka* (Lambertini et al. 2006, Meyerson et al. 2012). *Phragmites australis* (Cav.) Trin. ex Steud. (*Poaceae*) is tall, helophytic, wind-pollinated perennial grass with shoots up to 4 m tall (but see Rodewald-Rudescu 1974 who report up to 6 m), forming an extensive system of rhizomes and stolons (runners), with a single inflorescence developing on each fertile shoot, producing 500–2000 seeds (see Packer et al. 2017 and references therein). *Phragmites australis* represents one of the most ploidy-variable species known, with published cytotypes from 4x to 12x, based on x = 12 (te Beest et al. 2012), and there is marked phylogeographic genetic diversity within the species and the whole genus (Saltonstall 2002, Lambertini et al. 2006).

This is relevant from the perspective of the global *P. australis* invasion: there are a number of phylogeographic groups delimited based on an increasing knowledge of the worldwide distribution of haplotypes (Saltonstall 2002, Lambertini et al. 2006, 2012b, Meyerson & Cronin 2013, Lambertini 2016). The knowledge on the worldwide distribution and status of populations is still incomplete; insights into the presence of non-native genotypes in the well-researched area of North America (Saltonstall 2002, Lambertini et al. 2012a, b) suggest that the distribution of alien genotypes is a much more widespread phenomenon. In North America, there is evidence of multiple introductions of *P. australis* to this continent (Lambertini et al. 2012a, b, Meyerson et al. 2012, Meyerson & Cronin 2013), with the European haplotype M being the first lineage recorded, as evidenced by an herbarium record ~150 years ago (Saltonstall 2002). Alien lineages of *P. australis*, including haplotypes M and Delta, are expanding in North America and sometimes form monospecific stands.

The recent account on the global distribution of *P. australis* revealed that this species is on all continents except Antarctica, and although in many regions of the world the origin status is unclear and requires further study, there is evidence of weedy populations being present in North America, Australia, and Madagascar (Packer et al. 2017). The species is now naturalized on islands in the Pacific (New Caledonia, Cook Islands and

Hawaii) and the Caribbean Sea (Bahamas, Dominican Republic, Haiti, Leeward Islands, Puerto Rico, Trinidad-Tobago and Windward Islands; see Fig. 2 in Packer et al. 2017). Whether alien genotypes of *P. australis* have been introduced to other places such as South America requires further study (Packer et al. 2017).

Ecology of Phragmites invasion

In its invaded range in North America, *P. australis* subsp. *australis* has converted botanically diverse wetlands into low-diversity ecosystems and outcompetes the North American native *P. australis* subsp. *americanus* (Meyerson et al. 2000). The invasion is facilitated by disturbance (Chambers et al. 1999, Meyerson et al. 2000, Silliman et al. 2014), but invasive populations also readily colonize undisturbed ecosystems. Invading populations can be locally limited by poor drainage, lack of burial opportunities for seed and rhizome fragments, or by salinity during the early stages. However, naturalized alien populations are reported to extend into less favourable anoxic and highly saline areas (Bart & Hartman 2002). Among reported predictors of invasiveness, such as vigorous growth, sexual reproduction, long-distance dispersal and genetic diversity (Belzile et al. 2010, McCormick et al. 2010, Kettenring et al. 2011, Kirk et al. 2011), an important role is played by genome size as a trait relating to competitiveness (Pyšek et al. 2018). Smaller-genome plants of the alien haplotype M outcompete native haplotypes with larger genomes in North America (Suda et al. 2015, Meyerson et al. 2016a, Pyšek et al. 2018).

Phylogeographic groups used in the experiment

Plants were grown in the Experimental Garden of the Institute of Botany of The Czech Academy of Sciences in Průhonice, Czech Republic (49°59'39"N, 14°33'58"E), 320 m a.s.l., with a mean annual temperature of 8.6 °C and precipitation of 610 mm. We distinguished six phylogeographic groups (see Fig. 1 for their global distribution). We used *P. australis* clones obtained from the collections of the University of Rhode Island, Kingston, Rhode Island, USA and University of Aarhus, Denmark, and also included some field-collected clones. The phylogeographic groups were represented by populations from (i) Australia; (ii) Europe; North America, with two groups including (iii) native (coded as 'NAmerica-nat') and (iv) invasive populations introduced from Europe ('NAmerica-inv'); (v) South Africa ('SAfrica'); and (vi) Far East. There were 17, 21, 17, 19, 8, and 7 genotypes planted for each group, respectively, grown in a total of 372 pots. We used *P. australis* genotypes representing distinct populations (see Electronic Appendix 1 on the localities from which the clones used in the study were sampled).

Data collation: experimental set up

The clones were grown in round pots 60 cm in diameter at the top, 36 cm in height (effective pot size 80 l), filled with sand and mixed with 480 g of slow-release (release time 12–14 months) fertilizer Osmocote Pro (16% N, 11% P, 10% K). A piece of young rhizome (standard size of 20–30 cm) with an emerging shoot was planted in each pot on 7–8 July 2012. Two to six replicates per clone, depending on the availability of the plant material and early survival were used, giving a total of 273 pots with experimental plants. The plants were watered daily in the morning and in the evening using tap water delivered by

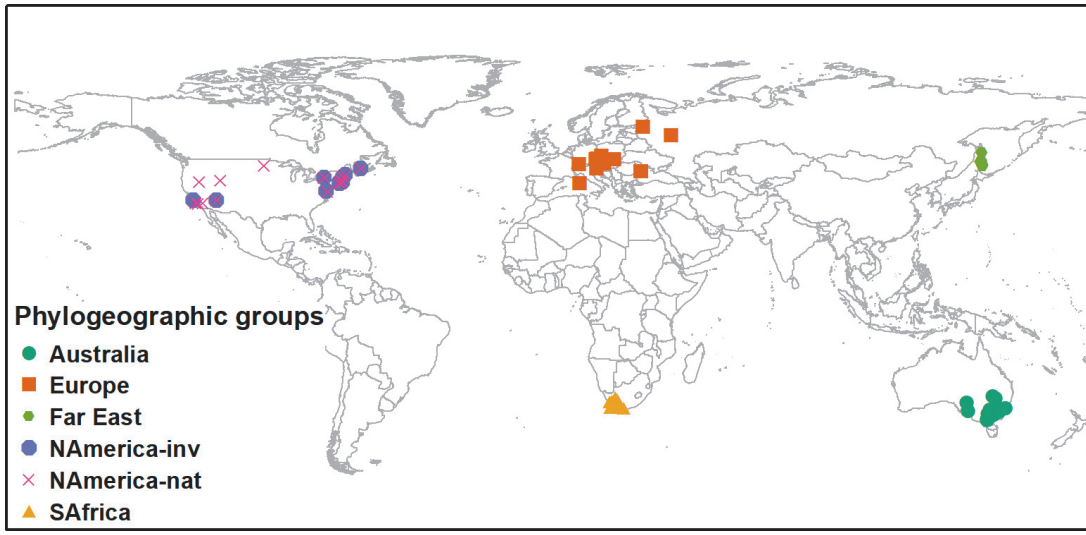


Fig. 1. Global distribution of the six phylogeographic groups with sampling location of populations used in the present study.

an automatic watering system (Hunter Industries, San Marcos, USA). To ensure comparable water supply to all plants, three holes were drilled in each pot 25 cm from the bottom to allow drainage of excessive water and achieve the same water level in each pot. In September when some plants started to exhibit signs of iron-deficiency (yellowing), 0.2 g Fe as iron in chelation complex of DTPA dissolved in 300 ml of tap water was added to all pots. Plants grew until full senescence (November), and the pots were covered over winter to protect the plants from frost. In early April of the following year, the frost protection was removed, and 200 g of slow-diluting Osmocote and 0.2 g Fe were added to each pot, and an addition of the same Fe dose was repeated in May/June. The experiment was terminated after 2.5 yrs, in autumn 2014. For harvest, the aboveground biomass was cut about 3 cm above the sand surface, when shoots were senescent (turning tan coloured) in late November/early December of 2012 and 2013. During the final harvest in October 2014, belowground biomass was also harvested, excavated from the substrate, rinsed and separated into roots and rhizomes, and the length of each rhizome was measured. The root and rhizome biomass was oven-dried at 60 °C and weighed in the same way as for aboveground biomass (see Pyšek et al. 2018 for more details).

Traits measured

During the experiment we recorded information about a wide range of traits functionally related to growth, physiology, tissue chemistry, reproduction, and herbivory (for a complete list of all traits recorded and details on methods of recording, see Table 1). Here we focus on exploring the differences among the above phylogeographic groups in their performance with respect to the following traits: shoot height; shoot basal diameter; shoot number per pot; aboveground dry biomass; belowground dry biomass separated into

Table 1. – Variables measured within the experiment and used in the analyses.

Variable name (unit)	Description	Month/Year
Aboveground biomass (g)	Aboveground biomass clipped at 3 cm above the sand surface when shoots were senescent, oven-dried at 60 °C for 12 hours and weighed. In the analysis, we used only 2013 harvest data.	11/2013+ 9/2014
Shoot height (cm)	Shoot height at harvest measured from the sand surface up to the tallest point of the shoot	11/2013+9/2014
Shoot number	Shoot number at harvest	11/2013+9/2014
Belowground biomass (g)	Belowground biomass, excavated from the pots, rinsed and separated into roots and rhizomes that were oven-dried at 60 °C and weighed	9–10/2014
Below/aboveground biomass (%)	Below- and aboveground biomass ratio	9–10/2014
Rhizome biomass (g)	Rhizome biomass measured separately, see belowground biomass	9–10/2014
Root biomass (g)	Root biomass measured separately, see belowground biomass	9–10/2014
Rhizome length (cm)	Total length of rhizomes	9–10/2014
Shoot diameter (mm)	Shoot diameter measured below the bottom leaf in three randomly selected stems per pot using electronic calipers	9–10/2014
Reproductive allocation (%)	Proportion of the biomass of all panicles in the total aboveground biomass (per pot)	8/2013
SLA ($m^2 \cdot kg^{-1}$)/LMA ($kg \cdot m^{-2}$)	Specific leaf area measured in the 3rd or 4th fully developed top leaf in four randomly selected shoots per pot using LICOR planimeter (LI-3100, LI-COR, Lincoln, Nebraska, USA); leaves were then oven-dried at 60 °C, weighed individually, and SLA calculated as leaf area/dry weight; inversed used as LMA	9–11/2013
LWC (%)	Leaf water content measured in the same leaves as used for SLA estimate, as the ratio of the fresh weight measured immediately after the leaf was harvested and its dry weight	7/2013
Leaf area per shoot (cm^2)	Assessed for three randomly selected shoots per pot, from which all leaves were cut and their total area per stem measured using the LICOR planimeter; total leaf area per pot was assessed by multiplying per shoot average leaf area × shoot number in the pot	7–8/2013
Photosynthetic capacity ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	Maximum photosynthesis A(max) measured in randomly selected 2nd or 3rd undamaged full developed top leaf using IRGA licor 6400 Portable Photosynthesis System (Li-Cor, Nebraska, USA) equipped with a standard 6 cm^2 leaf chamber CO_2 400 ppm, leaf temperature of 26°C, air flow rate of 500 $\mu mol \cdot s^{-1}$ and mean relative humidity of about 60 %, photosynthetically active radiation irradiance at 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$	8/2013

Variable name (unit)	Description	Month/Year
Leaf toughness (N)	Leaf toughness measured as force necessary for penetrating the leaf using an Imada PS-20N push/pull mechanical force gauge with a 5 mm diameter blunt tip (Imada, Inc., Northbrook, Illinois) approximately 5 cm from the leaf base of a top, mid and basal leaf in two randomly selected shoots per pot	8/2014
Leaf C (%)	Leaf C concentration assessed in four leaves, from one randomly selected shoot per pot, that were dried, homogenized, and milled on particle size < 0.1mm, weighed in tin vials (10–30 mg) and delivered into combustion tube via autosampler of Carlo Erba NC 2500 elemental analyser where they were burned in the pure oxygen flow (combustion temperature of 1000 °C and the Cr oxide used as catalyser); C and N oxides were than led through reduction tube (temperature 800 °C, pure Cu filling) into the separation column using He as the carrying gas; the total concentration of the oxides determined by conductivity detector and the signal is analysed by software Clarity Lite of DataApex.	7–8/2014
Leaf C/N	Leaf C/N ratio	7/2014
Leaf N (%)	Leaf N (see leaf C for methods)	7/2014
Leaf P ($mg \cdot kg^{-1}$)	Leaf P concentration assessed in four leaves, from one randomly selected shoot per pot, that were dried, homogenized and milled on particle size < 0.1mm, mineralized using 4ml HNO_3 and 1 ml 30% H_2O_2 for 0.5 g biomass in microwave units Milestone Standard 2500. P was estimated in the filtrate photometrically according to Olsen (1982).	7/2014
Rhizome C (%)	Rhizome C concentration was measured in three 5–10 cm long pieces of rhizomes taken from different positions within the pot; the samples were homogenized and same methods as for leaf C were applied	9–10/2014
Rhizome C/N	Rhizome C/N ratio	9–10/2014
Rhizome N (%)	Rhizome N concentration (for details see rhizome C and leaf C)	9–10/2014
Rhizome P ($mg \cdot kg^{-1}$)	Rhizome P concentration (for details see rhizome C and leaf P)	9–10/2014
Root C (%)	Root C concentration was ascertained in five pinches of roots taken from different positions within each pot, homogenized and further treated as biomass for leaf C	9–10/2014
Root N (%)	Root N concentration (for details see root C and leaf C)	9–10/2014
Root P ($mg \cdot kg^{-1}$)	Root P concentration (for details see root C and leaf P)	9–10/2014

roots and rhizomes; total length of rhizomes in the pot (growth traits); proportional allocation of biomass to generative reproduction (panicle weight, a reproductive trait); leaf water content; specific leaf area (SLA); leaf area per shoot; leaf toughness measured as the force necessary to penetrate the leaf; photosynthetic capacity measured on fully developed top leaf (physiological traits); C, N, P concentration determined separately in leaves, roots and rhizomes, and used to calculate ratios (tissue chemistry). The overview of the traits measured with details on how and when they were sampled is in Table 1. For the majority of growth traits, we used data from the 2013 growing season to avoid the effect of possible space limitation (including the aboveground biomass), with the exception of traits related to belowground harvest in 2014 (including the belowground / aboveground biomass).

Statistical analysis

All analyses were carried out in R (v. 3.4.0, R Core Team 2017). First, we used linear mixed-effect models to test the performance of individual traits, with phylogeographic groups as the fixed factor and genotype identity as a random factor. Second, the same data was averaged per genotype and the averaged values were used in a one-way analysis of variance (ANOVA) to test for the significance of differences among the phylogeographic groups. As the results from these two analyses were identical, only the one-way ANOVA results based on the clone mean data are shown. Bonferroni post-hoc correction was used for traits that showed significant differences in ANOVA. The normality and homogeneity of the trait variances were checked, and log-transformation was applied when needed. For variables not meeting the assumptions of ANOVA, non-parametric Kruskal-Wallis rank sum test was used, followed by a Dunn post-hoc test if a significant difference was detected.

As shoot number and shoot height were measured more than once during 2013 and 2014, linear mixed models were applied to these two traits, with years and phylogeographic groups as main factors, and the measurement times and genotype identities as random factors. Linear mixed models were applied via "lmer" function from the lmerTest package (Kuznetsova et al. 2017). We ran pairwise post-hoc comparisons using least-squared (LS) means with Bonferonni corrections applied to ensure the global Type I error rate remained at 0.05 via the 'emmeans' package (Lenth et al. 2018). All previous models were examined by diagnostic plots to check if they met the assumptions of linear regression.

To investigate the bivariate relationships between traits, in particular those related to the leaf economics spectrum (LES) and biomass allocation, the standardized major axis (SMA) analysis (Wright et al. 2004) was implemented with the smatr package in R (Warton et al. 2012) using clone means. SMA line fitting minimizes residual variance in both x and y dimensions and is preferred in analysing bivariate allometric relationships (Warton et al. 2006). We specifically focused on the leaf economics traits, i.e. leaf N, leaf P, leaf mass per area (LMA), and A_{max}, to test whether bivariate trait relationships of *P. australis* populations are similar to the corresponding ones from the Global Plant Trait Network (GLOPNET) dataset (Wright et al. 2004). The GLOPNET dataset reports values of photosynthetic capacity (A_{max}), dark respiration rate, nitrogen (N) and phosphorus (P) concentrations, leaf life span (LL), and LMA, and covers 2222 species from 175 sites

on six continents. We ran a similar analysis on the biomass allocation to different organ parts to test for the isometric or allometric growth of the *P. australis* populations (Komiyama et al. 2008).

Principal components analysis (PCA) with all traits measured in this study was applied to examine the pattern of the six phylogeographic groups, and how close they are to each other. PCA was run via the FactoMineR package (Lę et al. 2008).

Results

European native populations and those originating from Europe that are invasive in North America were the most productive, with the former producing the greatest belowground and the latter aboveground biomass. These values were markedly greater than those recorded for populations from other phylogeographic groups (with the exception of Far Eastern populations that exhibited comparable values), and those populations also produced a great root biomass. Consequently, European populations had the greatest belowground / aboveground biomass ratio and root / aboveground biomass ratio, which were, however, not significantly different from that obtained for Far Eastern populations. The three groups mentioned above also invested a great proportion of biomass into generative reproduction. North American native populations were less productive than both European-related groups and were similar in this respect to South African and Australian populations. South African populations produced rather thick shoots with a large leaf area and tough leaves. Far Eastern populations had the longest rhizomes, while North American native, African and Australian populations the shortest. The Far Eastern populations had also the greatest SLA (see Table 2 for values and significances of these differences). No significant differences among phylogeographic groups were found in photosynthesis.

These results indicate that there are differences among populations that were also manifested in shoot number per pot and partly height (Fig. 2). European native and Far Eastern populations produced more shoots than other groups except North American invasive that produced comparable numbers of shoots. Of the three most vigorous phylogeographic groups, European native produced more shoots per pot than North American invasives, although this difference was less pronounced (Fig. 2). The differences in shoot height among phylogeographic groups were generally non-significant with the only exception being that Australian populations performed poorly in comparison with European and both groups of North American plants (Fig. 2).

There were few significant differences in C, N, P concentrations in leaves, rhizomes and roots (Table 3). European native and the Far Eastern populations were often among those with the highest concentrations and North American natives often had the lowest concentrations of these elements.

The trait values we recorded for the *P. australis* populations were distributed within the range of the GLOPNET dataset (Fig. 3). Compared to this global species dataset, *P. australis*, pooled across phylogeographic groups, tends to have higher A_{max}, N and P concentrations, and lower LMA. Bivariate trait relationships were generally consistent with the results from the GLOPNET dataset (Wright et al. 2004), with the exception of LMA–N and N–P relationships the slopes of which were significantly different from global species data.

Table 2. – Mean values (±1 SD) of biomass, growth and physiological traits of *Phragmites australis* by phylogeographic groups. F-values and P-values of ANOVA tests are given; different superscripts row-wise indicate significant differences between the respective phylogeographic groups ($P < 0.05$). Note that n for leaf toughness is 20, and 7 for Europe and South Africa, respectively. SLA, specific leaf area; A_{max}, photosynthetic capacity. Reproductive allocation is not shown for Australian and South African populations due to poor generative reproduction at the end of the experiment. The bold values indicate the group with the highest values in the respective trait, regardless of the significance of the difference.

Traits	Australia (n = 17)	Europe (n = 21)	Far East (n =7)	NAmerica-inv (n =17)	NAmerica-nat (n = 19)	SAfrica (n = 8)	F-value	P-value
Rhizome biomass (g)	411.3±274.1^{a}	**1296.5±390.4^{c}**	1063.0±229.8^{bc}	923.5±190.7^{b}	538.3±301.1^{a}	452.0±212.8^{a}	25.15	< 0.001
Root biomass (g)	162.6±128.2^{a}	496.5±149.5^{c}	**509.2±171.0^{c}**	378.6±133.3^{bc}	227.5±134.9^{a}	203.2±120.0^{ab}	17.16	< 0.001
Belowground biomass (g)	573.9±390.0^{a}	**1792.9±488.7^{c}**	1572.2±334.2^{bc}	1302.1±262.6^{b}	765.8±428.3^{a}	655.2±316.0^{a}	26.44	< 0.001
Aboveground biomass (g)	271.3±219.7^{a}	1231.3±353.4^{cd}	842.52±126.5^{bc}	**1304.0±199.8^{d}**	624.8±446.5^{b}	616.2±282.6^{ab}	27.80	< 0.001
Below:aboveground biomass	0.62±0.29^{a}	**2.19±1.00^{d}**	1.88±0.55^{cd}	1.25±0.30^{bc}	0.92±0.35^{ab}	0.69±0.16^{ab}	20.09	< 0.001
Root:aboveground biomass	0.18±0.08^{a}	**0.57**±0.28^{d}	0.55±0.25^{cd}	0.35±0.13^{bc}	0.26±0.09^{b}	0.21±0.09^{ab}	18.41	< 0.001
Rhizome length (cm)	4003.5±2628.3^{a}	15199.8±4362.7^{b}	**22607.8±3934.2^{c}**	14653.0±3963.0^{b}	5708.5±3356.8^{a}	3880.1±2098.2^{a}	51.05	< 0.001
Stem diameter (mm)	4.87±1.05^{b}	4.62±0.86^{b}	3.53±0.33^{a}	4.64±0.49^{b}	5.68±0.61^{c}	**6.85±1.02^{d}**	18.38	<0.001
A_{max} (µmol CO_2 $m^{-2}{\cdot}s^{-1}$)	20.3±5.3	21.7±2.7	19.0±2.7	20.9±1.9	18.5±3.2	**21.7±2.9**	2.40	0.044
SLA ($m^2{\cdot}kg^{-1}$)	12.7±1.6^{a}	13.0±1.2^{a}	**15.0±1.4^{c}**	13.3±0.8^{ab}	13.4±1.8^{ab}	12.2±1.1^{a}	3.75	0.004
Leaf area (mm^2)	2849.6±1413.5^{a}	3755.5±1259.2^{abc}	3025.0±559.2^{ab}	4279.9±620.4^{bc}	**4585.4±1157.1^{c}**	4434.3±737.1^{bc}	6.35	< 0.001
Leaf area per shoot (cm^2)	231.5±105.5^{ab}	311.9±148.5^{bc}	147.2±23.3^{a}	354.6±93.5^{c}	330.5±120.0^{bc}	**374.1±93.3^{c}**	5.50	< 0.001
Leaf water content (%)	65.7±1.7^{c}	60.6±2.5^{a}	62.0±1.6^{ab}	59.3±1.5^{a}	63.1±3.7^{b}	**67.0±1.4^{c}**	20.20	< 0.001
Reproductive allocation (%)	–	4.42±3.95^{ab}	5.41±2.78^{ab}	**7.60±4.28^{b}**	1.97±4.06^{a}	–	6.12	0.001
Leaf toughness (N)	4.18±1.36^{a}	3.98±1.21^{a}	3.06±0.84^{a}	3.81±0.56^{a}	4.36±1.10^{a}	**6.24±1.17^{b}**	73.52	0.006

Table 3. – Mean values (±1 SD) of C, N, P and their ratios in leaf, root, and rhizome tissues of *Phragmites australis* by phylogeographic groups. F-values and P-values of ANOVA tests are given; different superscripts row-wise indicate significant differences between the respective phylogeographic groups ($P < 0.05$). The bold values indicate the group with the highest values in the respective trait, regardless of the significance of the difference.

Trait	Australia (n = 17)	Europe (n = 21)	Far East (n =7)	NAmerica-inv (n = 17)	NAmerica-nat (n = 19)	SAfrica (n = 8)	F-value	P-value
Leaf C ($mg \cdot g^{-1}$)	438.5±6.9	440.1±4.5	438.2±4.8	437.6±2.9	**442.0±5.4**	437.2±4.6	2.05	0.080
Leaf N ($mg \cdot g^{-1}$)	$34.9±3.6^{bcd}$	**$37.9±3.0^{d}$**	$38.8±5.6^{d}$	$34.4±2.9^{abc}$	$31.0±4.3^{a}$	$31.2±1.6^{ab}$	10.79	< 0.001
Leaf P ($mg \cdot g^{-1}$)	$2.11±0.36^{abc}$	$2.11±0.20^{bc}$	**$2.27±0.46^{c}$**	$1.86±0.22^{ab}$	$1.82±0.33^{a}$	$2.00±0.27^{abc}$	4.36	0.001
Leaf C:N	$12.8±1.5^{ab}$	$11.7±0.9^{a}$	$11.6±1.6^{a}$	$13.0±1.1^{ab}$	**$14.8±2.3^{c}$**	$14.2±0.9^{bc}$	10.33	< 0.001
Leaf N:P	$17.0±2.63^{ab}$	$18.2±0.8^{bc}$	$17.4±2.3^{abc}$	**$18.8±1.2^{c}$**	$17.5±1.2^{abc}$	$15.9±1.5^{a}$	4.13	0.002
Root C ($mg \cdot g^{-1}$)	$412.8±19.6^{a}$	$438.7±9.3^{b}$	$426.0±13.1^{ab}$	**$439.7±15.5^{b}$**	$432.2±13.4^{b}$	$430.6±10.9^{ab}$	8.22	<0.001
Root N ($mg \cdot g^{-1}$)	14.2±4.9	14.1±2.8	**14.7±1.0**	12.0±1.9	12.3±1.6	13.3±3.4	2.01	0.086
Root P ($mg \cdot g^{-1}$)	**$1.41±0.53^{c}$**	$1.02±0.19^{ab}$	$1.28±0.10^{bc}$	$0.84±0.16^{a}$	$1.17±0.27^{bc}$	$1.22±0.19^{bc}$	7.45	< 0.001
Root C:N	32.8±9.0	33.4±7.0	29.8±2.18	**39.0±7.1**	37.1±4.8	36.9±9.8	2.46	0.040
Root N:P	$11.2±3.7^{a}$	$14.1±2.1^{ab}$	$12.0±1.19^{ab}$	**$15.1±2.6^{b}$**	$11.4±2.3^{a}$	$11.1±2.1^{a}$	7.12	< 0.001
Rhizome C ($mg \cdot g^{-1}$)	$430.6±10.7^{b}$	$430.1±5.4^{b}$	**$435.0±5.5^{b}$**	$423.8±9.8^{ab}$	$418.1±18.5^{a}$	$417.8±8.8^{ab}$	4.74	< 0.001
Rhizome N ($mg \cdot g^{-1}$)	$18.0±3.8^{a}$	**$23.0±3.4^{c}$**	**$23.0±3.6^{bc}$**	$19.0±2.4^{ab}$	$17.5±3.0^{a}$	$19.5±3.1^{abc}$	8.65	< 0.001
Rhizome P ($mg \cdot g^{-1}$)	$2.05±0.39^{ab}$	**$2.29±0.38^{b}$**	2.19±0.33	$2.04±0.30^{ab}$	$1.87±0.30^{a}$	$2.01±0.34^{ab}$	3.36	0.008
Rhizome C:N	**$26.9±6.6^{b}$**	$19.7±3.4^{a}$	$19.7±3.1^{a}$	$24.1±4.2^{ab}$	$26.5±3.9^{b}$	$22.7±4.1^{ab}$	6.69	< 0.001
Rhizome N:P	9.19±2.19	10.21±1.68	**10.58±0.88**	9.59±1.30	9.58±1.32	10.06±1.31	2.48	0.038

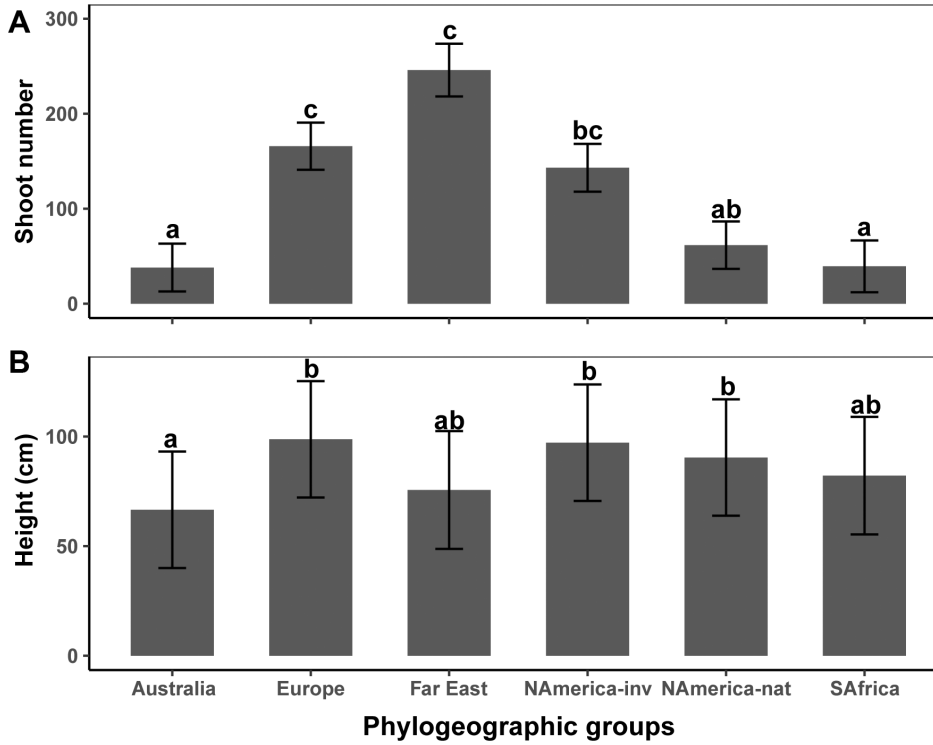


Fig. 2. – Least squared (LS) means and SEs of the (A) shoot number and (B) shoot height of the six phylogeographic groups of *Phragmites australis*, based on the linear mixed models. As there was no significant difference between years, the values were pooled together. Different letters above the error bars indicate significant differences among groups ($P < 0.05$), tested via Bonferroni post-hoc correction.

There were significant differences in biomass allocation to different organs and across all the studied *P. australis* populations with plants showing an allometric growth (Fig. 4). The plants allocated more biomass to belowground than aboveground organs.

The PCA of phenotypic traits for the six phylogeographic groups revealed that European native, Far Eastern and North American invasive populations were least distinct from each other, forming a group that almost does not overlap with the other three. North American native populations cannot be separated from South African and Australian populations based on their traits (Fig. 5A). The factor loadings of the PCA generally fitted the previous analyses, i.e., the former three groups tend to have more shoots, longer rhizome, higher belowground biomass, and higher leaf N than the latter three groups, which showed larger stem diameter (Fig. 5B)

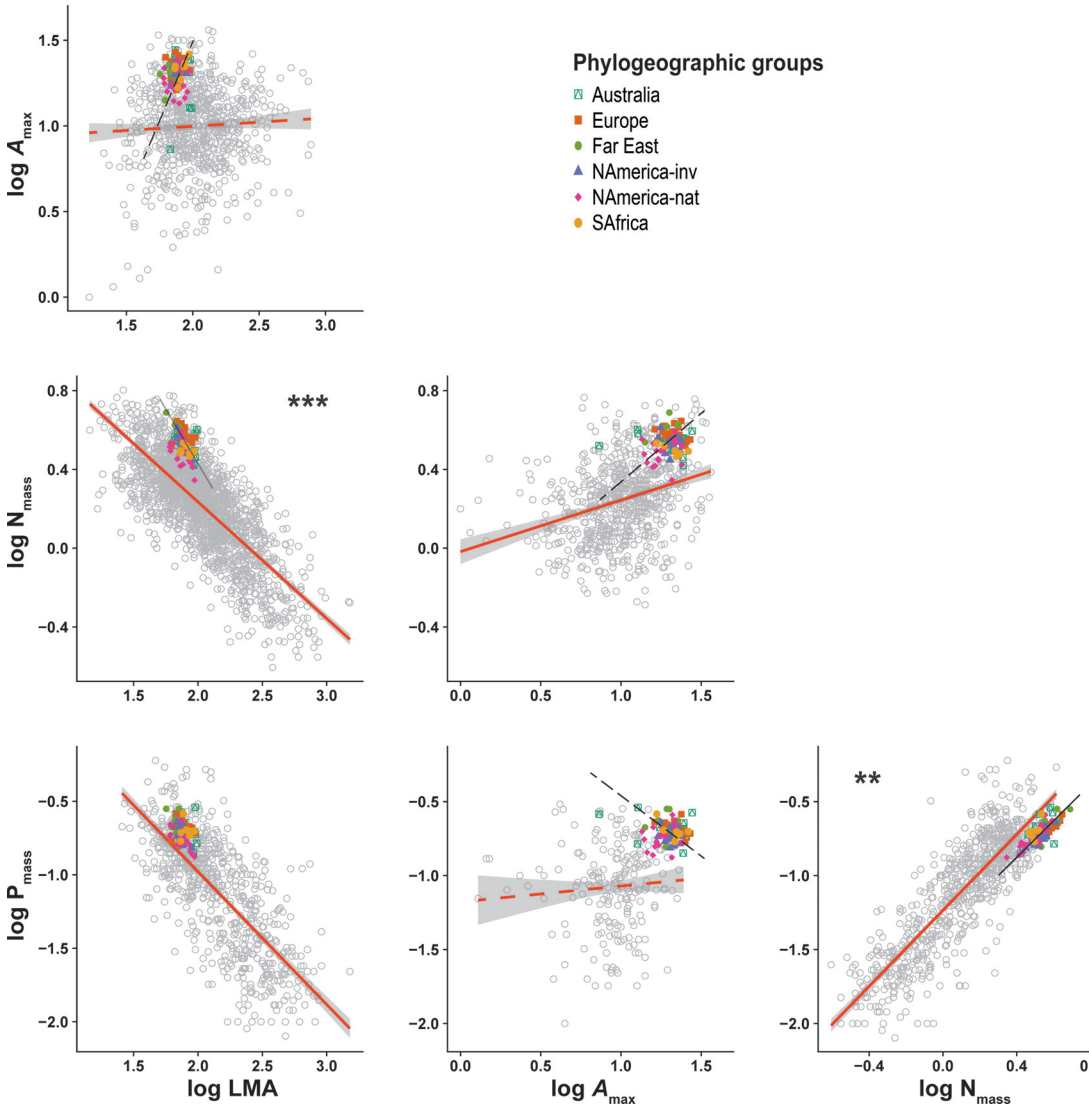


Fig. 3. – Slope tests in standardized major axis (SMA) lines for the bivariate allometric relationship between leaf economics spectrum (LES) traits for *P. australis* populations and the GLOPNET datasets (Wright et al. 2004). The circles in background are data from GLOPNET (Wright et al. 2004). Dashed lines represent non-significant relationship between the traits ($P > 0.05$) and solid lines are significant ($P < 0.05$); if the relationship between traits is non-significant ($P > 0.5$), no SMA test was run.* indicates significant difference between the two slopes: ** $P < 0.01$, *** $P < 0.001$. LMA: Leaf mass per area, the inverse of SLA; N_{mass} and P_{mass}, phosphorus and nitrogen concentration on mass bases, respectively; A_{max}, photosynthetic capacity.

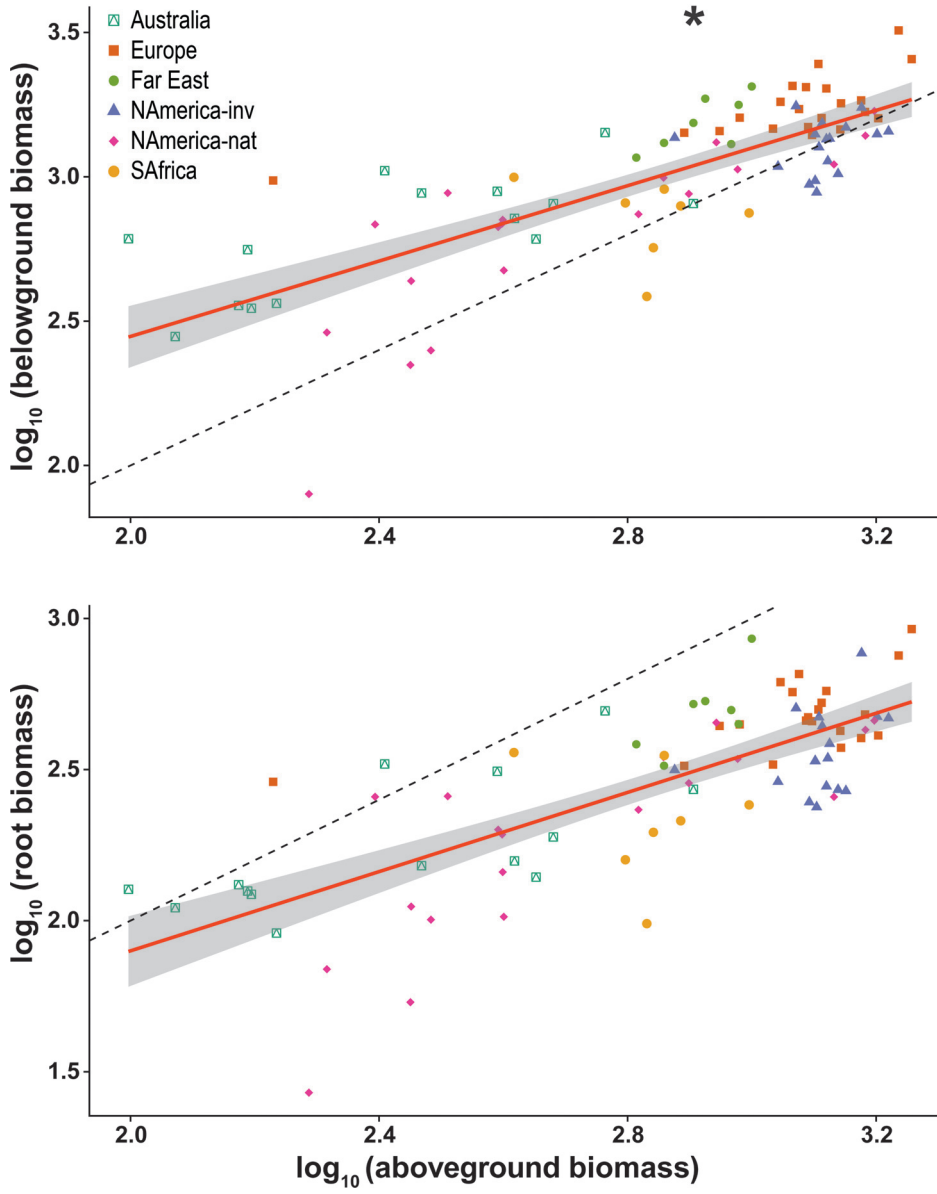
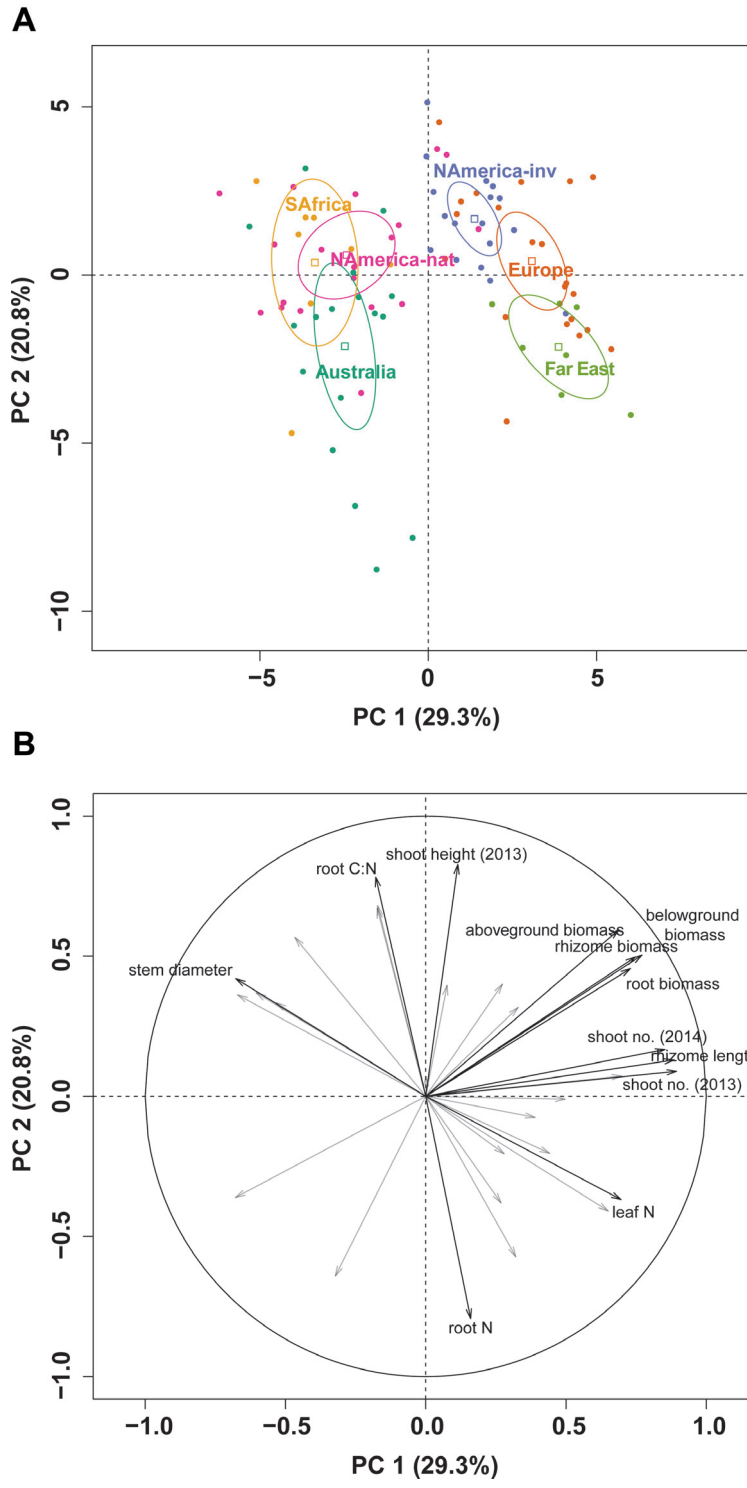


Fig. 4. – Allometric relationships between biomass of different organ parts. Dashed lines represent isometric line (slope = 1), solid red lines represent significant relationships between variables; significant differences between the two slopes are indicated: * $P < 0.05$.

Fig. 5. – (A) Principal components analysis (PCA) using all measured phenotypic traits for the six phylogeographic *Phragmites australis* groups. The square and circle with the same color as surrounding points is the centroid and 95% confidence ellipse of the specific phylogeographic group. (B) Factor loadings of the PCA. The black arrows with names are the traits with coefficients of higher than 0.6, whist the gray arrows are traits with low coefficients (lower than 0.6). ▶


A
NAmerica-inv
SAfrica
NAmerica-nat
Europe
Australia
Far East
PC 2 (20.8%)
PC 1 (29.3%)
5
0
−5
−10
−5
0
5
B
shoot height (2013)
root C:N
belowground biomass
aboveground biomass
rhizome biomass
stem diameter
root biomass
shoot no. (2014)
rhizome length
shoot no. (2013)
leaf N
root N
PC 2 (20.8%)
PC 1 (29.3%)
1.0
0.5
0.0
−0.5
−1.0
−1.0
−0.5
0.0
0.5
1.0

Discussion

Differences among phylogeographic groups

In the previous paper based on the same dataset, we found a distinct relationship between genome size and invasiveness at the intraspecific level; monoploid genome size was the only significant variable that clearly separated the North American native plants from invading populations of European origin. The latter had a smaller genome that was associated with plant traits favoring invasiveness such as long rhizomes, early emerging abundant shoots, low aphid attack and low C / N ratio (Pyšek et al. 2018). In this study the main focus is on characterizing a broader range of phylogeographic groups by their physiological traits.

In general, both phylogeographic groups with origins in Europe – be it those that grow as native in this continent or as invaders in North America – are more vigorous than all other groups, with the exception of the Far Eastern populations that reached the highest values in some characteristics. They produced high biomass, tall shoots and dense stands. The native European populations had the greatest belowground / aboveground biomass ratios, while the North American invasives allocated a greater proportion of biomass into generative reproduction, measured as the relative weight of the panicle. On the other hand, North American native populations performed rather poorly in terms of biomass production and were similar in this respect to South African populations. Australian plants were on average even shorter and less vigorous. However, their poor performance could also be at least partly due to fact that the environmental conditions in which the plants were grown might have been suboptimal for these plants – the performance of this group need therefore to be interpreted with caution.

Overall, these results correspond with the invasion success of European plants in North America and suppression of the native North American populations in direct competition with the invader (Meyerson et al. 2000). Based on the performance of various lineages in our experiment, invasion by Australian and African populations in the Northern Hemisphere due to weak environmental match or genetic differences seems unlikely at present. However, it is not possible to exclude the invasion of genotypes of European origin into Southern Hemisphere or other temperate regions. Unfortunately, reciprocal transplant experiments that could either support or contradict this hypothesis are missing.

A novel result of the present study is the vigour of the Far Eastern populations, which is comparable to that of the European and North American invasive populations. Besides the high biomass of the Far Eastern populations, their invasion potential may be enhanced by extensive lateral spread by long rhizomes. Achenbach et al. (2012) demonstrated that the Far Eastern populations grew even taller and performed better than the European genotypes in a common garden study in Denmark. However, the superior performance of the Far Eastern genotypes over the Australian populations (their close relatives) in several traits was not expected. In Lambertini et al. (2006) the Far Eastern populations appeared as a monophyletic group within the Australian clade of *P. australis*, with which it shares also the chloroplast DNA (haplotype P) (Lambertini et al. 2012b). Such a phenotypic divergence in traits, related to competitiveness and fitness between the two closely related groups, would be a new wrinkle in *Phragmites* evolutionary history. Possible explanations could be that the Far Eastern populations acquired the competitive traits and became similar to the European populations by hybridization. Far East Asia is

a hot spot of *Phragmites* lineages, including European haplotypes (An et al. 2011), and recombination between lineages may have occurred. However, for our experimental conditions the more probable explanation seems to be the better environmental match for the Far Eastern populations as well as for those of the Northern Hemisphere. The poor performance of the North American native populations does not contradict this explanation as these populations are generally less competitive than European populations (Pyšek et al. 2018). Nevertheless, these new insights of the present study require further testing, ideally by reciprocal transplants of Eurasian and Australian plants, and should stimulate further genetic research both in the Far East and North American native populations.

A pattern seems to emerge if the position of the *Phragmites* populations in the ordination space, and their geographical distribution, is interpreted with respect to the latitude (reflecting solar radiation) and climatic conditions of the sites of origin. The PCA analysis shown in Fig. 5 indicates that the phylogeographic groups are divided into two distinct clusters, one being Australia, South Africa and North American native clones, the other the Far-East clones, European ones and North American invasives. With the exception of North American populations, where native and invasive grow together, populations from the former group tend to originate from relatively low-latitude and warmer regions, while the latter from higher-latitude colder regions (Electronic Appendix 1). The warmer conditions and high solar radiation appear to be associated with lower shoot densities and, in the case of Australian populations, with relatively low aboveground biomass, compared to belowground. One explanation of the weaker performance of these populations in our experiment could be that populations adjusted to warm conditions and high solar radiation, such as Australian or South African, need to allocate more biomass to rhizome system for the survival during winter if they are growing under cold climate and low solar radiation of the Czech Republic. This would be supported by previous research on the variation in growth response of *Phragmites* with changing geographical conditions (Granéli et al. 1992, Clevering et al. 2001, Karunaratne et al. 2003, Cronin et al. 2015, Allen et al. 2016, Bhattarai et al. 2016).

Biomass production

Phragmites australis is among the most thoroughly researched plant species (Meyerson et al. 2016b) and a great body of information on growth and biomass production under a wide range of conditions has accumulated over last decades, including belowground production (e.g. Dykyjová & Hradecká 1976, Fiala 1976, Granéli et al. 1992, Čížková et al. 2001, Šantrůčková et al. 2001). Although none of the studies systematically compared these characteristics for such a high number of lineages under standardized conditions of an experimental garden, it is of interest to review this information here and compare with our data.

Except belowground production recorded in Australia (see Packer et al. 2017 and citations therein) and in a hypertrophic lake in the United States (Boyd et al. 2015), the above- and belowground biomass recorded in our experiment was generally high and especially values for European clones exceeded field values reported from Europe (Čížková et al. 1996, Kuhl et al. 1997, Soetaert et al. 2004, Gribsholt et al. 2007); the same was true for belowground / aboveground biomass ratio (Coops et al. 1996, Soetaert et al. 2004). The North American clones in our experiment, namely the invasive, also pro-

duced more above- and belowground biomass (Minchinton & Bertness 2003, Emery & Fulweiler 2014) and higher belowground / aboveground ratio than North American field populations (Farnsworth & Meyerson 2003, Achenbach & Brix 2014), and similar biomass to those reported from cultivation (Hellings & Gallagher 1992). The greater biomass in the experiments indicates that plants were not limited by the lack of resources. These results further support the high resource-use efficiency, when resources are available, of the European populations and their resilience at the high levels of our fertilization, at least in this European common garden.

Nitrogen, phosphorus and carbon in leaves, rhizomes and roots

High nutrient content in the tissues of European native and Far Eastern populations agree with their high invasive potential indicated by their vigorous growth, and also with the invasion success of European clones in North America (Meyerson et al. 2009). The leaf-nitrogen values in our experiment were close to the maxima found in plants cultivated under high supply of nutrients (Clevering 1998) and to the maxima found in the field (Kohl et al. 1998, Farnsworth & Meyerson 2003, Baldantoni et al. 2004, Soetaert et al. 2004, Elvisto 2010). The pattern of the highest leaf-nitrogen values in European clones followed by North American invasive and North American native genotypes (Guo et al. 2014) was confirmed in our experiment. Also the leaf-carbon values were close to maxima of 455–465 $mg \cdot g^{-1}$ reported from the field for European (Csatari et al. 2015) and North American invasive plants (Schaefer et al. 2014). The leaf phosphorus was comparable with the values, including maxima of 2.5–2.9 $mg \cdot g^{-1}$, reported from the field in Europe (Baldantoni et al. 2004, Elvisto 2010, Flury & Gessner 2014, Marchand et al. 2014).

The rhizome nitrogen values were comparable with the highest values measured on plants in the field and in cultivation in Europe (Čížková & Lukavská 1999 and Clevering 1998, respectively). Rhizome carbon in the experimental garden was within the range of values known from Europe (Engloner et al. 2004, Csatari et al. 2015) and rhizome phosphorus reached values comparable with the highest values found in the field in this continent (Čížková & Lukavská 1999).

The root nitrogen values corresponded to the maxima of 24–26 $mg \cdot g^{-1}$ found in cultivation in Europe (Clevering 1998) and root carbon was within the range of values measured there (Hartmann 1999, Csatari et al. 2015). Unlike the other elements the values of root phosphorus rather compared to lower values found in Europe (Duan et al. 2004, Engloner et al. 2004, Stamati et al. 2010).

The high values of leaf and rhizome nitrogen and phosphorus, as well as of the root nitrogen, indicate a very good nutrient supply to the cultivated plants which, together with the generally high biomass values recorded in this experiment, indicate that the plants were not limited by space and nutrients. However, it needs to be kept in mind that the plants in our experiment were cultivated under optimal conditions and actual field performance may be limited by low resource availability, disturbance or stress.

Leaf traits

The photosynthetic capacity (A_{max}) values in our experiment can be compared to the maxima reported in the literature, for some European and North American invasive clones of *P. australis* cultivated in a common garden (Hansen et al. 2007 and Mozdzer et al. 2016).

In a previous study, Guo et al. (2014) compared the photosynthesis of North American invasive and native clones with native European plants and found the highest values in the first of the three groups. We did not find significant differences between these lineages in our study, but the American native clones had considerably lower photosynthesis than the other two groups of European origin. Plants in the previous study had rather low leaf-nutrient content (Guo et al. 2014), which can limit the photosynthetic output and might have thus generated the differences between the three groups.

In a previous study from China, leaf economics traits of *P. australis* showed large intraspecific variation (Hu et al. 2015). The specific leaf area (SLA) values recorded in our experiment are within the upper half of the range reported for European, Asian and North American plants (Farnsworth & Meyerson 2003, Soetaert et al. 2004, Colmer & Pedersen 2008, Jiang et al. 2009, Shi et al. 2010, Eller et al. 2014, Li et al. 2014, Zhong et al. 2014). Such relatively high values are probably due to a high nutrient supply as increased nitrogen availability was revealed to increase SLA (Minchinton & Bertness 2003).

Higher A_{max}, N and P concentrations, and higher SLA of *P. australis* compared to other GLOPNET plants is probably the reason for it growing so vigorously and being generally successful throughout the temperate zone. In accordance with this, the most productive European and North American invasive clones are at the positions most distant from the LMA–N and N–P relationships within the GLOPNET plants (Fig. 3).

Post-introduction changes in the Phragmites complex

Within our study system, the natural experiment created by the historical intercontinental introductions of *P. australis* provided an opportunity to address not only the ecological differences between native North American populations and invasive populations introduced from Europe, but also to explore post-introduction evolutionary change in the latter (Pyšek et al. 2018). This can be achieved by comparing North American invasive populations originating from Europe with their ancestors that still occur as natives in Europe. In fact, the position of populations in the PCA seems to confirm this. European populations, both the native sampled in Eurasia and those that were derived from European ancestors and that now invade in North America (Pyšek et al. 2018), have much in common in terms of the trait space that they occupy in the ordination space; together they form a distinct group not overlapping with populations from other continents. This corresponds to the results of Guo et al. (2014) and Bui et al. (2016) who similarly found the three groups largely separated but used a different method. However, the North American invasives in our experiment were closer to North American natives than they were to their original European ancestors, possibly reflecting the effect of the environment after at least 200 years of invasion (Guo et al. 2018) or interbreeding.

Nevertheless, these inferences are weakened because we do not have exact information that would allow us to relate particular native European genotypes to the specific genotypes introduced to North America. Therefore, the biogeographical comparison among European and North American populations is made by randomly sampling genotypes in the two ranges that represent the three groups defined by origin. Several studies have attempted to identify the source European populations of the introduced populations in North America, but so far none have succeeded, and at present it is very unlikely that source populations can be back-traced. This is because the populations within European

phylogeographic group are very diverse and each genotype has its relatives very far from its population (Lambertini et al. 2008). All of the European common reed is a metapopulation and this genetic pattern is due to the fact that (i) *P. australis* seeds and pollen are dispersed over long distances by wind and birds, (ii) *P. australis* has been used and moved by humans in Europe (thatching, constructed wetlands, etc.), (iii) both the native Eurasian and introduced North-American populations have evolved since their separation, and (iv) the North American invasive population is the result of multiple introductions (Lambertini et al. 2006, 2012a, Meyerson & Cronin 2013). Nevertheless, we are convinced that the comparison of the phylogeographic groups sampled randomly provides valid insights into the physiological differences among *P. australis* phylogeographic groups.

Limitation of the common-garden study and the need for further research

The results were obtained in a standard garden experiment and thus they need to be interpreted with caution resulting from controlled settings. It has been shown that the performance of *P. australis* is influenced by environmental conditions such as water regime, nutrient availability, salinity, temperature and CO_2-levels (see e.g. Engloner 2009, Eller et al. 2017, Packer et al. 2017 and references herein). Also, interaction of the effects of cultivation environment with individual populations on some growth characteristics have been reported (Clevering et al. 2001). This is especially relevant for Australian and South African clones for which the growing conditions in central Europe differ most from the original sites, including the summer/winter switch that may influence biorhythms, potentially manifested in the absence of flowering. However, it was logistically impossible to manipulate growing conditions in such an extensive experiment, where the aim of covering most of the world distribution ranges of *P. australis* was given priority.

See www.preslia.cz for Electronic Appendix 1

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Souhrn

Diferenciace v rámci jednoho ze světově nejrozšířenějších a nejvýznamnějších planě rostoucích kosmopolitních druhů, *Phragmites australis*, i invaze jeho jednotlivých linií mimo jejich domácí areály přitahuje stále větší pozornost. Na základě experimentálního srovnání růstových a fyziologických vlastností 89 populací představujících odlišné genotypy ze šesti fylogeografických linií rákosu, pocházejících z Austrálie, Evropy, Severní Ameriky (dvě skupiny zahrnující domácí populace a invazní populace zavlečené z Evropy), Jižní Afriky a Dálného Východu jsme zjistili diferenciaci populací do dvou velkých skupin. První zahrnuje populace z Evropy, invazní populace ze Severní Ameriky a populace z Dálného Východu, zatímco do druhé skupiny spadají popu-

lace z Austrálie a Jižní Afriky spolu s původními severoamerickými. Pro první skupinu je typický vitální růst, který se projevuje vyšší hustotou stébel v pěstební nádobě, největší podzemní biomasou evropských populací, nejdelšími oddenky a největší specifickou listovou plochou u populací z Dálného Východu, vysokou koncentrací dusíku a fosforu v listech a oddencích a vysokým poměrem N:P v listech a kořenech populací z Evropy a Dálného Východu. Severoamerické populace měly největší nadzemní biomasu a největší podíl biomasy investované do generativní reprodukce. Hodnoty maximální fotosyntézy, koncentrací N a P v pletivech a specifické listové plochy naměřené napříč sledovanými populacemi *P. australis* se pohybují poblíž horní hranice rozsahu hodnot druhů zahrnutých do databáze GLOPNET. Zjištěné výsledky ukazují na nepravděpodobnost invaze populací z Austrálie a Jižní Afriky na severní polokouli bez ohledu na to, zda kvůli genetické odlišnosti populací nebo jejich špatnému přizpůsobení místním podmínkám. Na druhou stranu nelze vyloučit invazi evropských populací do dalších oblastí, zejména na jižní polokouli.

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