Quantitative Characteristics and Dynamics of Rhizomes in Reed Populations in Different Habitats of Zhalong Wetland: Postprint

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Abstract

Employing unit soil sampling and survey-statistical methods to measure length and biomass, a comparative analysis was conducted on the rhizome quantitative characteristics of Phragmites australis populations in four habitats of Zhalong Wetland Reserve. The results showed that after Phragmites australis greened up around May 10th and entered the vegetative growth period, rhizome length increased slowly from June to August, and increased significantly from August to October, with the later period being 3.5-10.3 times that of the earlier period. The mid-to-late growth season was the main period for new rhizome supplementation and growth in the population, which not only achieved spatial expansion of the population but also reserved more reproductive buds for vegetative propagation. Rhizome biomass and dry matter storage gradually decreased from June to August, and then gradually increased from August to October, with both reaching their maximum in October at the end of the growth season, significantly higher than other months ($P < 0.05$). The consumption of rhizome nutrients was mainly allocated to rhizome bud germination and seedling growth, while the storage of rhizome nutrients provided material guarantee for population renewal and expansion in the following year. The population exhibited a significant nutrient "super-compensatory" storage phenomenon in underground rhizomes. Population rhizome length and biomass were highest in wet habitats, followed by dry habitats and aquatic habitats, with saline-alkali habitats being the lowest. Rhizome dry matter storage was highest in dry habitats, followed by wet habitats and aquatic habitats, with saline-alkali habitats being the lowest. Population rhizome length showed a good linear relationship with actual growth time after green-up, while population rhizome biomass and dry matter storage showed a good quadratic relationship with growth time, with R^2 values between 0.804-0.997. All fitting equations reached significant or highly significant levels ($P < 0.01$). The Phragmites australis populations in the four habitats exhibited relatively stable seasonal dynamic patterns in quantitative characteristics such as rhizome length, biomass, and dry matter storage, which were controlled by genetic factors. The differences among habitats and their ranking order were also basically stable, all exhibiting obvious soil factor environmental effects. Among them, soil water content, organic matter, and available nitrogen were positive drivers, while pH and available phosphorus were negative drivers. The driving effects of soil water content and pH on rhizome quantitative characteristics were more prominent.

Full Text

Preamble

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Quantitative Characteristics and Dynamics of the Rhizome of *Phragmites australis* Populations in Heterogeneous Habitats in the Zhalong Wetland

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Abstract

This study compared the quantitative characteristics of rhizomes in *Phragmites australis* populations across four habitats in the Zhalong Wetland Reserve using unit soil volume sampling to measure rhizome length and biomass. The results revealed that *P. australis* returned green around May 10 and entered the vegetative growth period. Rhizome length showed a slow increasing trend from June to August, followed by a significant increase from August to October, with late-season lengths reaching 3.5–10.3 times those of the early season. The middle and late growth seasons represented the primary period for new rhizome supplementation and growth, during which spatial expansion was achieved and abundant reproductive buds were reserved for vegetative propagation.

Rhizome biomass and dry matter storage gradually decreased from June to August, then increased from August to October, peaking at the end of the growing season in October at values significantly higher than other months ($P < 0.05$). Rhizome nutrient consumption primarily supported bud germination and young plant growth, while storage provided material support for population renewal and expansion in the following year, demonstrating obvious "super-compensatory" storage in rhizomes.

Both rhizome length and biomass were greatest in wet habitats, followed by xeric and aquatic habitats, and lowest in saline-alkali habitats. Conversely, dry matter storage was greatest in xeric habitats, followed by wet and aquatic habitats, and lowest in saline-alkali habitats. Significant linear correlations existed between rhizome length and actual growth time after greening, while biomass and dry matter storage showed significant quadratic relationships, with goodness-of-fit values (R^2) of 0.804–0.997 ($P < 0.01$).

The length, biomass, and dry matter storage of rhizomes across all habitats exhibited relatively stable seasonal dynamics controlled by genetic factors. Inter-habitat differences and their rank order remained basically stable, showing significant environmental effects of soil factors. Soil water content, organic matter, and available nitrogen were positive drivers, while pH and available phosphorus were negative drivers, with soil water content and pH having the most prominent effects.

Keywords: Zhalong Wetland; *Phragmites australis* population; rhizome; heterogeneous habitats; quantitative characteristics

Introduction

Plant rhizomes serve not only as nutrient storage organs but also as important reproductive structures [1]. Rhizomes fulfill critical functions in vegetative reproduction and population spatial expansion [2] while acting as channels for physiological integration among different modules of clonal plants [3]. Persisting in soil, rhizome lifespan varies by species depending on genetic characteristics [4]. Some plants possess short-lived rhizomes, such as *Hierochloe glabra* [5] and *Hemarthria altissima* [6], whereas others have long-lived rhizomes, like *Leymus chinensis* [7] and *Phragmites australis*, whose rhizomes can survive for many years [8]. Even in long-lived rhizomes, individual lifespan depends not only on nutrient output and consumption but also on whether nutrients can be re-imported for storage [9–10].

Clonal plants can adjust rhizome length to facilitate population migration and habitat selection, avoiding intraspecific competition for space and nutrients by establishing ramets in habitats distant from the mother plant [11]. The growth of clonal modules exhibits foraging characteristics and population expansion behavior [12]. Among rhizome quantitative characteristics, rhizome buds represent the potential population for vegetative reproduction, length encodes information about growth and spatial expansion, and biomass reflects nutrient storage status [1]. Investigating the quantitative characteristics and spatiotemporal dynamics of rhizomes in heterogeneous habitats holds important theoretical and practical significance. Through surveys across growth periods in the Zhalong Wetland Reserve, this study compared inter-habitat differences in rhizome length, biomass, and dry matter storage, as well as their changing patterns throughout the growth period, to reveal the biological characteristics and ecological significance of rhizome growth, material consumption, and storage in *P. australis* populations, providing a scientific basis for understanding divergent adaptation mechanisms at the population level and theoretical guidance for wetland conservation and management.

1. Study Area

This research was conducted in the core area of Zhalong National Nature Reserve, located on the northern Songnen Plain, 23 km southeast of Qiqihar City. The region features a mid-temperate continental monsoon climate (46°52 -47°32 N, 123°47 -124°37 E), with 2,700-3,000 annual sunshine hours and a frost-free period of 128 days [13-14]. The mean temperature of the hottest month (July) is 22.9°C, while the coldest month (January) averages -19.4°C. The accumulated temperature 10°C ranges from 2,600 to 3,000 degree-days.

2. Sample Plot Setup

Four habitats were established in the reserve core area based on soil moisture conditions and salinization levels:

H1 (Xeric habitat): Meadow soil with no standing water year-round or brief waterlogging during the rainy season, typically forming *Leymus chinensis* communities with scattered *Phragmites* patches [15].

H2 (Wet habitat): Swamp soil with normally no or minimal standing water, gradually accumulating water after the rainy season began (depth generally <30 cm), forming single-dominant *Phragmites* stands.

H3 (Aquatic habitat): Humic swamp soil forming the largest *Phragmites* community in the wetland, with water depth varying by <100 cm.

H4 (Saline-alkali habitat): Saline-alkali soil with no standing water year-round, completely desalinated surface layer, obvious saline patches, and some alkaline patches. All plots had been harvested in winter for paper production or domestic use for many years. Inter-habitat distances ensured similar light and temperature conditions.

3. Research Methods

During four growth stages—early vegetative growth, vigorous vegetative growth, early reproductive growth, and vigorous reproductive growth—rhizomes were collected using unit volume sampling. In each plot, soil blocks (1 m × 1 m × 1 m) were excavated, all rhizomes extracted, and each rhizome measured for length to calculate cumulative length per unit soil volume. Rhizomes were bagged separately, transported to the laboratory, dried at 80°C to constant weight, and weighed for biomass. Aboveground ramets were sampled using unit area quadrats (1 m × 1 m). Soil samples were collected with an auger at each plot, mixed, sieved, and analyzed for water content (drying method), organic matter (K Cr O heating method), available nitrogen (alkali-hydrolysis diffusion method), and available phosphorus (Mo-Sb colorimetry) [17-18].

4. Data Processing

Rhizome length and biomass were expressed as actual observed values. Dry matter storage was calculated as biomass per unit length (g/100 cm). Excel 2007 and SPSS 19.0 were used for one-way ANOVA to test differences among months and habitats (= 0.05). Linear and quadratic regressions were performed to model relationships between rhizome characteristics and actual growth time after greening, selecting the best-fitting equation as the quantitative model. Goodness-of-fit was assessed using R^2 tests and significance by F tests. Pearson correlation analysis evaluated relationships between rhizome characteristics and soil factors, as well as between ramet density and rhizome length (aquatic habitat excluded from soil water content analysis).

5. Results

5.1 Dynamics of Rhizome Length in Different Habitats

Rhizome length is a crucial indicator of growth and spatial expansion. In the Zhalong Wetland, rhizome length across all habitats peaked in October (14,330 cm/m^3), significantly higher than other months ($P < 0.05$). Wet habitats showed the greatest length (13,754-17,446 cm/m^3), followed by xeric (9,676-13,027 cm/m^3) and aquatic habitats (7,898-9,877 cm/m^3), with saline-alkali habitats significantly lower (5,870-7,873 cm/m^3). Inter-habitat differences were significant throughout the growing season, with stable rank order.

Rhizome length increased gradually from June, slowly at first then significantly from August to October, with late-season values 3.5-10.3 times greater than early-season values. This reflects a prolonged period of new rhizome supplementation and growth in mid-to-late season, enabling spatial expansion and reserving abundant reproductive buds. Regression analysis showed significant linear relationships between rhizome length and actual growth time after greening across all habitats ($R^2 = 0.804$-0.920, $P < 0.05$) [FIGURE:1, FIGURE:2].

5.2 Dynamics of Rhizome Biomass in Different Habitats

Rhizome biomass represents the primary nutrient reserve and material basis for vegetative reproduction. Biomass was greatest in wet habitats (1,063.6–1,379.6 g/m^3), followed by xeric (939.3-1,247.0 g/m^3) and aquatic habitats (624.6-952.2 g/m^3), with saline-alkali habitats lowest (587.0-787.3 g/m^3). Inter-habitat differences were significant, with stable rank order maintained throughout the season.

Biomass decreased gradually from June to August, then increased from August to October, peaking at season' s end at values significantly higher than other months ($P < 0.05$). This pattern reflects a prolonged nutrient consumption process in early-to-mid season, when stored materials were used for new rhizome and bud formation, followed by a prolonged storage process in mid-to-late season when photosynthates were translocated underground for next year' s bud germination. Significant quadratic relationships existed between biomass and actual growth time after greening ($R^2 = 0.984\text{-}0.997$, $P < 0.05$) [FIGURE:3, FIGURE:4].

5.3 Dynamics of Rhizome Dry Matter Storage in Different Habitats

Dry matter storage (biomass per unit length) measures nutrient storage/consumption and determines rhizome longevity. Xeric habitats showed the greatest storage (8.0-9.6 g/100 cm), followed by wet (6.7-8.3 g/100 cm) and aquatic habitats (5.9-7.3 g/100 cm), with saline-alkali habitats lowest (5.4-6.6 g/100 cm). Inter-habitat differences were significant ($P < 0.05$) with stable rank order.

Storage decreased from June to August, then increased from August to October, with end-of-season values significantly exceeding other months. The storage in mid-to-late season exceeded early-season consumption, reflecting both nutrient loss between season end and sampling, and demonstrating clear nutrient "supercompensation" —the material basis for rhizome longevity and direct evidence of strong vitality [2, 26]. Significant quadratic relationships with growth time were observed ($R^2 = 0.990\text{-}0.993$, $P < 0.05$) [FIGURE:5, FIGURE:6].

5.4 Relationship Between Rhizome Length and Ramet Density

In Zhalong Wetland, *P. australis* ramets primarily originate from rhizome buds, making rhizome production crucial for vegetative reproduction. Correlation analysis revealed a significant linear relationship between ramet density and rhizome length ($y = 5355 + 19.8x$), indicating that each additional ramet per m^2 requires at least 19.8 cm/m^3 of rhizome extension. Longer rhizomes support greater ramet density.

5.5 Relationship Between Rhizome Characteristics and Soil Factors

Soil physicochemical properties varied significantly among habitats (TABLE:1). H3 (aquatic) had saturated water content year-round. H1 and H2 showed significantly higher water content than other habitats, with large seasonal fluctuations. Organic matter and available nitrogen were highest in H3, lowest in H4, with significant inter-habitat differences. Available phosphorus was highest in H3 and lowest in H4, decreasing gradually during the growing season.

Correlation analysis (TABLE:2) revealed different driving effects of soil factors on rhizome characteristics. Soil water content, organic matter, and available nitrogen were primary positive drivers of rhizome length and biomass, while pH and available phosphorus were negative drivers. For dry matter storage, water content and pH showed the most prominent driving effects. Soil water content and pH were the dominant factors influencing rhizome quantitative characteristics.

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6. Discussion

6.1 Biological and Adaptive Significance of Rhizome Growth and Production

Clonal plants exhibit specific adaptation strategies in different habitats, including morphological plasticity, physiological integration, and fitness regulation through vegetative reproduction [19-22]. Although plant death occurs at various life stages, rhizome buds show stronger survival capacity than seedlings [23], and vegetative reproduction far exceeds seed-based regeneration in natural communities [24], giving rhizome growth profound significance for population renewal and adaptation.

Rhizomes serve as primary vegetative reproductive modules and major nutrient storage organs. Individual rhizome lifespan depends on both nutrient output consumption and re-input storage [9-10], giving rhizome production important biological and ecological implications for nutrient dynamics [4]. In Zhalong Wetland, rhizomes distributed interwoven in soil showed increasing length throughout the growing season. While new rhizomes formed and elongated, older rhizomes died sequentially. New rhizomes compensated for losses from senescence while extending horizontally, enabling new ramets to avoid direct competition with parent ramets and facilitating horizontal niche expansion [25].

Rhizome biomass and dry matter storage followed a “decrease then increase” pattern, declining from early vegetative growth (June) to early reproductive growth (August), then increasing until season’ s end (October). All habitats showed prolonged nutrient consumption in early-to-mid season followed by prolonged storage in mid-to-late season, with end-of-season storage exceeding early-season consumption. This super-compensation is the material basis for rhizome longevity and direct evidence of strong vitality [2, 26].

While other studies reported significant biomass fluctuations in wetland *Phragmites* populations [27-28], the timing of peaks varied due to regional climate differences. However, within the Songnen Plain, rhizome biomass dynamics showed highly consistent seasonal rhythms determined by genetic factors. Most local grasses have rhizomes surviving 2 years [29-30], whereas *Phragmites* rhizomes can survive 3-5 years or longer [7]. The observed super-compensation in dry matter storage provides macroscopic evidence for nutrient consumption and compensation, contrasting with declining storage patterns in short-lived grasses where nutrients are not replenished. Further research is needed on physiological-biochemical mechanisms underlying these divergent strategies [7].

6.2 Driving Effects of Soil Factors on Rhizome Characteristics

Environmental heterogeneity in essential resources and conditions creates selection pressure for adaptive strategies [31-32]. Rhizomes, with their large storage capacity [33-34], can store and release resources to alleviate resource heterogeneity pressure [11], serving as a bridge between organism and environment [35]. Their unique structure makes them ideal for studying plant-habitat coevolution [35].

The stable inter-habitat differences and rank order in rhizome length, biomass, and storage reflect obvious environmental effects resulting from synergistic interactions among multiple soil factors rather than single-factor effects. Soil water content and pH showed the most prominent driving effects, consistent with previous research showing that moderate water stress benefits rhizome internode elongation while severe stress inhibits it [36]. Under saline-alkali stress, *Calamagrostis pseudophragmites* increases belowground growth to enhance water acquisition and storage capacity [37]. In the Songnen Plain, waterlogged single-dominant *Phragmites* communities have greater rhizome length and biomass than rarely flooded sites [1], though deep-water rhizomes may be shorter and shallower to reduce oxygen transport distance [38]. However, *Typha orientalis* showed increased rhizome length with water depth in stable water bodies [39], indicating species-specific responses.

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