

Article

Inter-Month Nutrients Dynamic and Plant Growth in *Calamagrostis angustifolia* Community and Soil after Different Burning Seasons

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Abstract: Presently, as human activity and climate warming gradually increase, straw burning leads to more accidental burning in neighbouring wetlands, which threatens wetland carbon stores. Plants are important carbon fixers in wetlands, converting carbon dioxide to biomass through photosynthesis and releasing carbon into the soil as plants die off. Nitrogen and phosphorus limitation in wetlands is a key factor affecting plant growth, and different burning seasons have different effects on mitigating this limitation. To further elucidate the effects of nitrogen and phosphorus distribution on wetland inter-month nutrient dynamics after different burning seasons, we selected a *Calamagrostis angustifolia* wetland in the Sanjiang Plain that was burned in spring and autumn, respectively, and conducted a monthly survey from May to September. We found that the leaf nitrogen content in September at spring burning sites was 3.59 ± 2.69 g/kg, which was significantly lower than that in July, while the difference at the unburned sites was only 0.60 ± 3.72 g/kg, and after the autumn burning, soil nitrogen and phosphorus contents remained higher than at the unburned sites in August, being 0.55 ± 1.74 g/kg and 0.06 ± 0.12 g/kg, respectively. Our results indicate that spring burning immediately increased the nitrogen and phosphorus contents in soil and plants but that these effects only lasted for a short time, until June. In comparison, autumn burning had a long-term effect on soil nitrogen and phosphorus levels and significantly increased the aboveground biomass. Thus, we recommend that conducting autumn burning before the commencement of agricultural burning not only reduces combustible accumulation to prevent fires but also promotes nitrogen and phosphorus cycling in wetlands, and the increase in plant biomass after autumn burning also enhances the carbon fixation capacity of the wetland.

Keywords: wetland; burning season; nitrogen; phosphorus; plant



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1. Introduction

Wetlands are a transition zone between terrestrial and aqueous systems and are the second-largest store of carbon in terrestrial ecosystems after forests [1]. Although wetlands cover only 5–8% of the land area, their carbon stocks account for approximately 12–24% of global terrestrial carbon [2]. Small changes in wetland carbon stores have a greenhouse effect by releasing carbon dioxide and affecting global climate change [3]. Plants are important carbon fixers in mitigating global climate change, absorbing carbon dioxide through photosynthesis and converting it into biomass [4]. After plant senescence, soil microorganisms degrade plant residues and allocate the carbon to microbial biomass, exudate carbon

as microbially derived organic matter, or release carbon through heterotrophic respiration [5,6], which plays a predominant role in regulating the conservation and release of soil organic carbon [7]. The anaerobic environment of wetland soil leads to a decrease in the microbial respiration rate and slows plant residue decomposition, gradually accumulating in the soil as humus, causing carbon storage in wetland soils.

Nitrogen and phosphorus are vital elements for plant growth and stress resistance through the influence of leaf photosynthesis and root growth [8,9]. The increase in soil nitrogen and phosphorus augments the number of plant leaves and their levels of chlorophyll, which promotes plant photosynthesis [10], thereby increasing aboveground biomass. The increase in soil nitrogen and phosphorus also promotes the proportion of carbon allocated to roots, increasing the belowground biomass [11]. Additionally, the input of soil nitrogen and phosphorus facilitates microbial respiration and indirectly promotes soil uptake of CO₂ and CH₄ [12], and soil microorganism populations also increase with soil nitrogen content through promoting the organic carbon stability of plants and soil. However, the special anaerobic environment of wetland soil limits the cycling of nitrogen and phosphorus, thereby affecting plant growth and microbial activity in wetlands [13].

Burning has been indicated as an important ecological disturbance that can ease the nitrogen and phosphorus limitation of wetland ecosystems [14,15]. However, burning has many facets and its effects can be beneficial or harmful to biodiversity conservation and human lives, depending on when and how the burning is conducted [16]. The alleviation of the nitrogen and phosphorus limitation is affected by different burning intensities [17]. Low-intensity burning causes an increased availability of nutrients, especially nitrogen [18,19], which has low stability and volatility and quickly plateaus [20]. In contrast, phosphorus has a high volatility threshold that shows no change after low-intensity burning, and increases linearly with increasing intensity of burning [20]. High-intensity burning will more fully combust biomass, producing more ash and increasing nitrogen and phosphorus production [21–23], as well as resulting in larger areas of bare ground and higher soil temperatures, which promotes microbial activity and thus increases the mineralisation and volatilisation of nitrogen and phosphorus [24].

Burning seasons are a key factor influencing the burn intensity [25]. Presently, as human activity and climate warming gradually increase, more frequent burning tends to occur in spring and autumn [16,26]. The differences in plant and soil water contents, relative air humidity, wind speed, and fuel loads in spring and autumn result in different burn intensities [27], and after spring and autumn burning, the differences in soil temperature recovery, wind, and water erosion result in different effectiveness and losses of nitrogen and phosphorus over time [27]. Therefore, the difference between spring and autumn burning needs to be further explored.

The Sanjiang Plain is one of the largest wetland areas in China and has a special geomorphic distribution, with interspersed farmland and wetland [12]. Because straw burning is often carried out in the farmlands of the Sanjiang Plain in April and October, fire can accidentally spread to nearby wetlands, resulting in seasonal burning in these wetlands. The effect of burning on carbon accumulation and plant growth in the wetlands of the Sanjiang Plain has been explored in the literature [28,29]. However, whether the distribution of nitrogen and phosphorus are different after spring and autumn burning, and the effect of nitrogen and phosphorus changes on plant growth in the wetlands of the Sanjiang Plain, is still unclear.

To address these research gaps, we selected a site in the wetlands of the Sanjiang Plain and autumn burning was conducted in October 2007 and spring burning in April 2008, respectively. We conducted an inter-month survey (i.e., from May 2008 to September 2008) of this activity, comparing the changes in nitrogen and phosphorus contents in soil and plants, plant stem density, and biomass after different burning seasons. The objectives of this study were to distinguish the changes in soil nitrogen and phosphorus on an inter-month basis after spring and autumn burning, further explore plant growth by observing the changes in plant nitrogen and phosphorus contents at different burning sites.

height. Leaves, stems, and roots were separated, oven-dried to constant weight at 75 °C, and weighed separately for calculation of plant biomass and for nitrogen and phosphorus content analysis [28]. The carbon content of plant organs was determined using potassium dichromate plus thermal oxidation. A continuous flow analyser (SAN++CFA, Skalar) was used to determine the nitrogen content of the plant organs and the content of total, ammonium, and nitrate nitrogen in the soil. Soil microbial nitrogen and dissolved organic nitrogen were determined using the alkaline potassium persulfate oxidation method. Soil total phosphorus and plant phosphorus were determined using the molybdenum antimony blue colorimetric method.

2.3. Statistical Analysis

Considering the distribution of soil nutrient contents, the plant nutrient contents and plant growth observed in our experiments did not conform to the normal distribution very well; the chi-squared test was selected for the generalised linear mixed-effects model to analyse the effects of burning season on soil and plant nutrients. The generalised linear mixed-effects model in the package “lme4” in the R environment (Bates et al., 2014) was used to explore the consequent changes in soil nutrient contents (i.e., total nitrogen, NH_4^+ -N, NO_3^- -N, MBN, phosphorus, and N:P ratio), plant nutrient contents, and plant growth after spring burning and autumn burning. In order to reduce inter-month effects and errors from repeated sampling, burning season was set as a fixed-effect factor and months were treated as a random factor, and the significance level was 0.05.

3. Results

3.1. Effect of Burning on Soil Nitrogen and Phosphorus Contents

The increase in soil nitrogen and phosphorus levels after spring burning lasted only four months (i.e., until August), with nitrogen and phosphorus levels being 5.68 ± 0.67 g/kg and 0.05 ± 0.11 g/kg lower than at unburned sites, respectively (Figure 2a,e). Interestingly, early in the plant growth season, soil nitrogen and phosphorus contents in June were 1.61 ± 1.40 g/kg and 0.05 ± 0.08 g/kg higher at spring burning sites than at autumn burning sites, respectively (Figure 2a,e). In contrast, autumn burning caused a longer-lasting promotion of nitrogen and phosphorus than spring burning, with the contents remaining higher than those of the unburned sites until August (Figure 2a,e). The soil N:P ratio showed the same trend, with a temporary increase after burning in June and a gradual decrease over time (Figure 2f). At spring burning sites, the N:P ratio decreased more rapidly than at the autumn burning sites, with a significant difference in the upper soil layer (Figure 2f). In August, N:P ratios at spring and autumn burning sites were both lower than in the unburned plot, being 4.27 ± 0.73 and 2.06 ± 0.91 lower, respectively (Figure 2f), and the soil NH_4^+ -N and NO_3^- -N contents also increased briefly over time after burning (Figure 2b,c). Interestingly, the increase in NH_4^+ -N content was larger than that in NO_3^- -N and was significant at autumn burning sites, with NH_4^+ -N increasing by 16.95 ± 2.73 mg/kg and NO_3^- -N increasing by 0.09 ± 0.07 mg/kg in June (Figure 2b,c), and then, these contents showed a decreasing trend (Figure 2b,c). Consistent with the trend regarding nitrogen and phosphorus, soil NH_4^+ -N and NO_3^- -N contents decreased faster at spring burning sites than at autumn burning sites (Figure 2b,c). For example, in July, the NH_4^+ -N content at spring burning sites was 5.84 ± 4.89 mg/kg lower than that at unburned sites. However, the NH_4^+ -N content at the autumn burning sites was 7.53 ± 2.43 mg/kg lower than that at the unburned sites in August, with the promoting effect of autumn burning lasting at least one month longer than that of spring burning (Figure 2b). Interestingly, the promotion of MBN after spring burning occurred early in the plant growth season (i.e., in May and June), while the promotion of MBN after autumn burning occurred later in the season (i.e., in August and September), and the influence of both burning seasons on MBN content was significantly different (i.e., $p < 0.05$; Table 1).

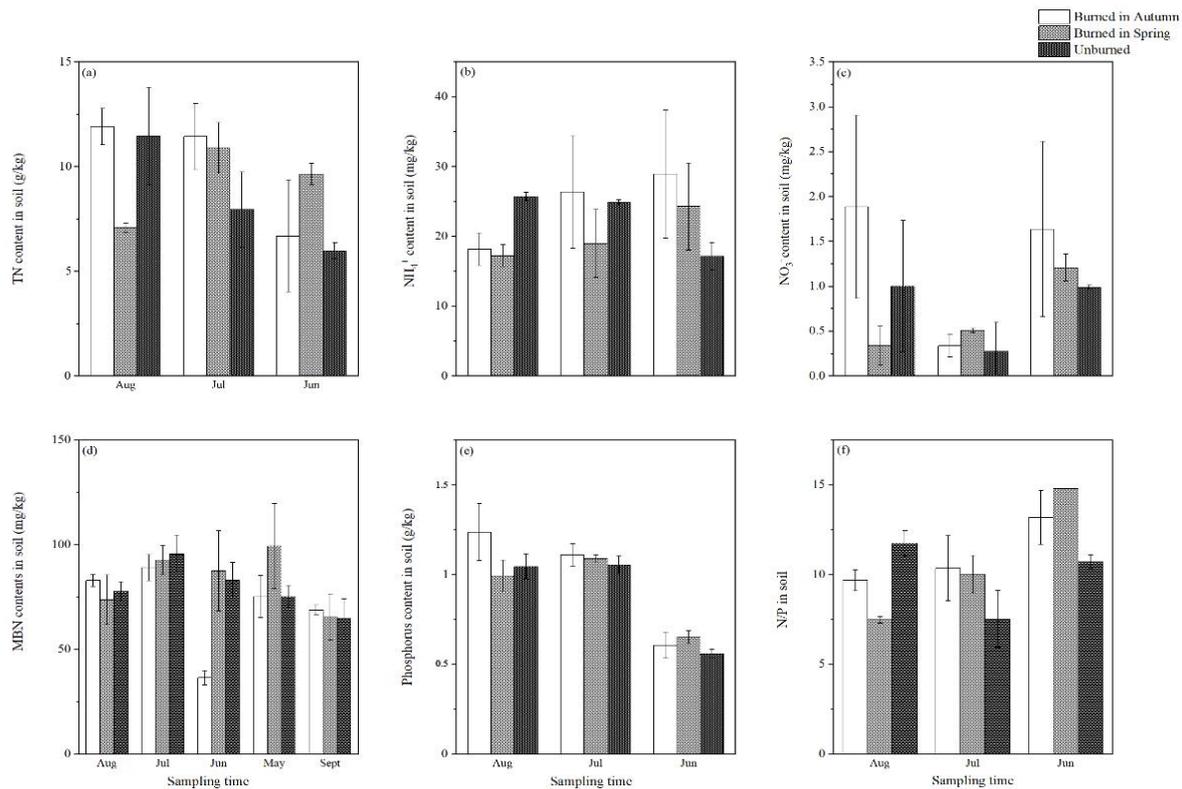


Figure 2. Average values (with standard error bars) for upper soil N content (a), NH_4^+ -N content (b), NO_3^- -N content (c), MBN content (d), P content (e), and N:P ratio (f) for samples taken from May to September 2008 for autumn burning, spring burning, and control groups.

Table 1. Generalised linear mixed-effects model analyses the effect of seasonal burning on soil nitrogen and phosphorus contents.

	Chisq	p	Autumn Burned * Unburned		Spring Burned * Autumn Burned		Spring Burned * Unburned	
			z Value	p	z Value	p	z Value	p
Total nitrogen	3.08	0.21	−1.64	0.23	−1.32	0.38	0.30	0.95
NH_4^+ -N	2.82	0.24	−0.75	0.73	−1.68	0.21	−0.91	0.64
NO_3^- -N	6.31	<0.05	−2.35	<0.05	−1.90	0.14	0.44	0.90
MBN	6.00	<0.05	1.52	0.28	2.41	<0.05	0.78	0.72
Phosphorus	6.86	<0.05	−2.48	<0.05	−1.92	0.13	0.55	0.85
N:P	3.48	0.18	−1.87	0.15	−0.86	0.67	0.99	0.59

3.2. Effect of Burning on Plant Nitrogen and Phosphorus Contents

Nitrogen and phosphorus contents of all plant organs at autumn burning sites were lower than those at unburned sites during the whole growing season (Figure 3). In comparison, spring burning immediately increased plant nitrogen and phosphorus contents (Figure 3a,b). The increase in stem and leaf nitrogen contents after spring burning lasted for only two months (i.e., until June; Figure 3a,b). Later in the plant growth season (i.e., after July), the stem and leaf nitrogen contents at the spring burning sites were lower than those at unburned sites and decreased sharply (Figure 3a,b). For example, the leaf nitrogen content at spring burning sites in September was 3.59 ± 2.69 g/kg lower than in July. Plant leaf nitrogen content at the unburned sites in September was only 0.60 ± 3.72 g/kg lower than in July (Figure 3a). Interestingly, the root nitrogen content increased gradually as the plants grew and there was a significant difference between spring and autumn burning sites (i.e., $p < 0.01$; Table 2). At spring burning sites, the increase in root nitrogen content lasted until September, with the root nitrogen content being 2.07 ± 0.99 g/kg higher than that at unburned sites (Figure 3c). However, plant stem and leaf phosphorus contents at spring burning sites in May were only 0.21 ± 0.43 g/kg and 0.14 ± 0.11 g/kg higher than

those at unburned sites, respectively (Figure 3d,e), and spring burning also reduced the root phosphorus content, with the significant effects lasting for at least one growing season, until September (i.e., $p < 0.01$; Figure 3d–f; Table 2). Interestingly, the stem nitrogen and phosphorus contents both reached a maximum in May (Figure 3b,e), and the stem nitrogen content between spring and autumn burning sites showed a significant difference (i.e., $p < 0.01$; Table 2). For example, in May, plant stem nitrogen contents were, respectively, seven times higher at spring burning sites and four times higher at autumn burning sites than in July (Figure 3b), while the maximum root and leaf phosphorus contents both occurred in July. In particular, in July, the root phosphorus content was 1.21 ± 0.09 g/kg at spring burning sites, 1.37 ± 0.15 g/kg at autumn burning sites, and 1.82 ± 0.21 g/kg at unburned sites (Figure 3f).

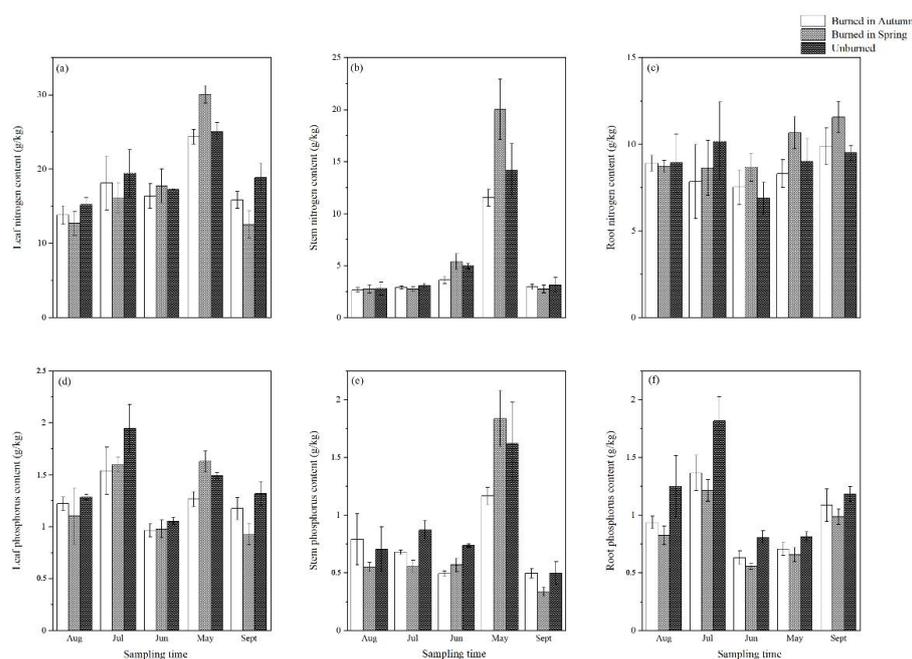


Figure 3. Average values (with standard error bars) for nitrogen content of plant leaves (a), stems (b), and roots (c), and phosphorus content of plant leaves (d), stems (e), and roots (f) for samples taken from May to September 2008 for autumn burning, spring burning, and control groups.

Table 2. Generalised linear mixed-effects model analyses the effect of seasonal burning on plant nitrogen and phosphorus contents.

	Chisq	p	Autumn Burned * Unburned		Spring Burned * Autumn Burned		Spring Burned * Unburned	
			z Value	p	z Value	p	z Value	p
Stem nitrogen	12.16	<0.01	1.51	0.29	3.49	<0.01	1.72	0.20
Leaf nitrogen	4.16	0.13	1.86	0.15	0.11	0.99	−1.76	0.19
Root nitrogen	10.29	<0.01	0.89	0.65	3.14	<0.01	2.02	0.11
Stem phosphorus	6.04	<0.05	2.43	<0.05	0.82	0.69	−1.67	0.22
Leaf phosphorus	15.63	<0.01	0.91	0.64	0.97	0.60	−0.01	1.00
Root phosphorus	66.77	<0.01	5.65	<0.01	−2.61	<0.05	−8.07	<0.01

3.3. Effect of Burning on Plant Growth and Carbon Content

The plant stem density and aboveground biomass increased significantly after burning (i.e., $p < 0.01$; Table 3). Interestingly, aboveground biomass was significantly different between autumn burning sites and spring burning sites (i.e., $p < 0.01$; Table 3). At autumn burning sites, the aboveground biomass was higher during the whole growing season than that at spring burning sites and reached a maximum in September, with 0.18 ± 0.17 kg/m² more than that at unburned sites (Figure 4b). In August, the aboveground biomass at spring burning sites reached a maximum, with 207.6 ± 104.2 g/m² more than that at unburned sites (Figure 4b). The increase in stem density and belowground biomass at spring burning

sites was larger than that at autumn burning sites, and reached a maximum in June, with $1156 \pm 422 \text{ N/m}^2$ and $5.53 \pm 3.29 \text{ kg/m}^2$ more than that at the unburned sites, respectively (Figure 4a,c). The maximum increase in stem density and belowground biomass at autumn burning sites occurred three months later (i.e., in September) than that at spring burning sites, being $1836 \pm 461 \text{ N/m}^2$ and $11.37 \pm 1.55 \text{ kg/m}^2$, respectively (Figure 4a,c). The stem carbon content after burning increased significantly and lasted for one growing season (i.e., $p < 0.05$; Table 3; Figure 4b,e). However, between spring and autumn burning, the effect on the plant stem carbon content was not significantly different (Table 3; Figure 4e). Overall, the plant stem carbon content was higher at spring burning sites than at autumn burning sites (Figure 4e). In July, the plant stem carbon content was $1.01 \pm 9.05 \text{ g/m}^2$ higher at spring burning sites than at autumn burning sites (Figure 4e). As the plants grew, their stem and leaf carbon contents varied significantly, with both rising to a maximum in July and then declining (Figure 4d,e). At autumn burning sites, the leaf carbon content was lower than that at the unburned sites during the whole growing season (Figure 4d). In contrast, the leaf carbon content increased after spring burning until June, being $4.86 \pm 5.61 \text{ g/m}^2$ higher at spring burning sites than at the unburned sites (Figure 4d).

Table 3. Generalised linear mixed-effects model outputs for the effects of seasonal burning on plant growth.

	Chisq	p	Autumn Burned * Unburned		Spring Burned * Autumn Burned		Spring Burned * Unburned	
			z Value	p	z Value	p	z Value	p
Stem density	24.83	<0.01	-3.09	<0.01	2.04	0.10	4.97	<0.01
Aboveground biomass	59.99	<0.01	-7.69	<0.01	-4.39	<0.01	3.62	<0.01
Belowground biomass	13.41	<0.01	-2.04	0.10	1.75	0.19	3.66	<0.01
Stem carbon	9.18	<0.05	-2.82	<0.05	-0.32	0.94	2.52	<0.05
Leaf carbon	1.21	0.55	3.62	<0.01	0.28	0.96	-3.37	<0.01
Root carbon	7.81	<0.05	-2.65	<0.05	-0.44	0.90	2.24	0.06

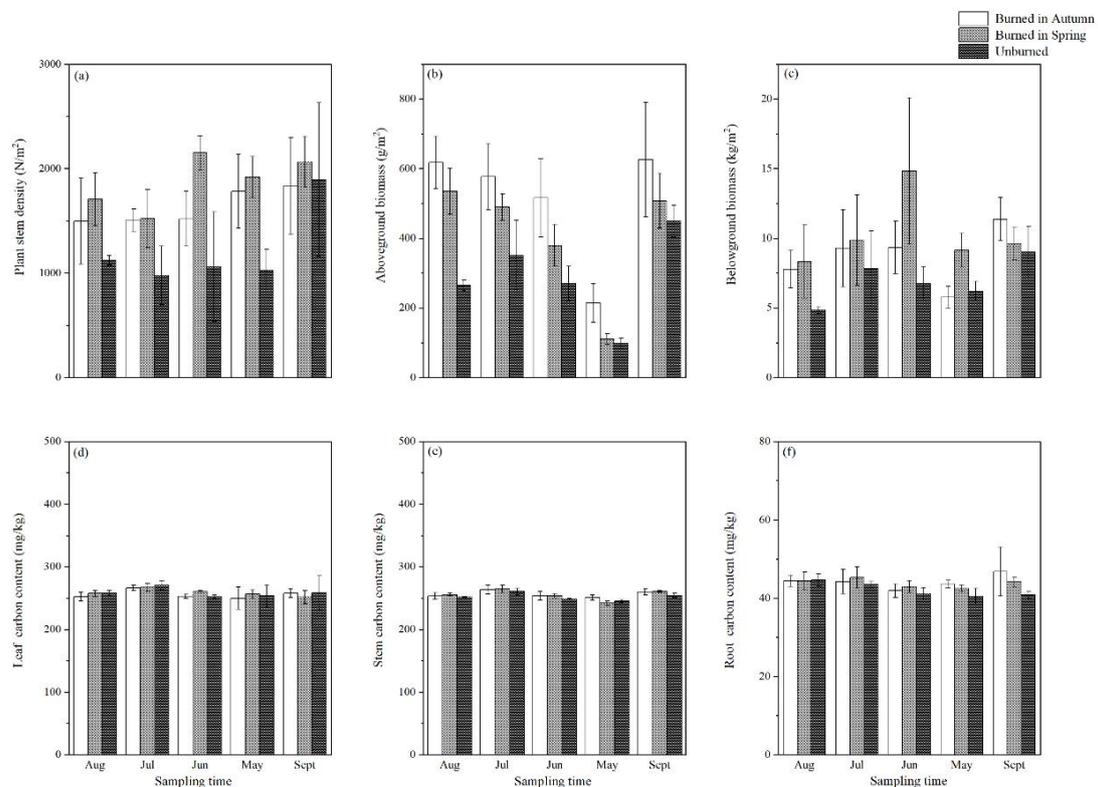


Figure 4. Average values (with standard error bars) for stem density (a), aboveground biomass (b), belowground biomass (c), and the carbon content of plant leaves (d), stems (e), and roots (f) for samples taken from May to September 2008 for autumn burning, spring burning, and control groups.

4. Discussion

4.1. The Effect of Burning on Soil Nitrogen and Phosphorus Contents

Burning increased the soil nitrogen and phosphorus contents, and the increase lasted for at least 3 months (Figure 2a,e). Burning converts aboveground biomass, such as plants and litter, into ash [33], which immediately increases the upper soil nitrogen and phosphorus contents [34]. Burning also accelerates the decomposition of belowground humus [23], which promotes the slow release of nitrogen and phosphorus into soil. In Venezuelan grasslands, the solar radiation that reached the ground after burning was different from that of the unburned grasslands, which increased the humidity of the air and topsoil and promoted the death and decay of the belowground plant tissue [35]. In our study, the soil N:P > 14 occurred in June (Figure 2f), which means that the nutrient limitation pattern changed from nitrogen-limited to nitrogen and phosphorus co-limitation ($14 < \text{N:P} < 16$). Nitrogen is volatile; burning causes part of the soil nitrogen to be volatilised as gas and another part to be converted into NH_4^+ -N and NO_3^- -N. Additionally, plant growth increases the demand for soil phosphorus, and low phosphorus inputs and inorganic phosphorus tend to combine with cations to form compounds deposited in the soil, reducing the availability of phosphorus, which increases the phosphorus limitation [36]. However, as the plants grew, the nutrient limitation pattern in our study gradually changed from nitrogen and phosphorus co-limitation to being nitrogen-limited in July, with this occurring below the unburned sites in August (Figure 2f). Plant utilisation, volatilisation via burning, and water or wind erosion accelerate the loss of nitrogen. Phosphorus requires a high temperature for volatility; thus, the losses of phosphorus were lower than those of nitrogen.

It was only in June that soil nitrogen and phosphorus contents at spring burning sites were higher than those at autumn burning sites (Figure 2a,e). Autumn burning occurred six months earlier than spring burning, during which time a part of the soil nitrogen was lost through volatilisation. However, with the process of melting snow and ice in spring, some of the soil nutrients were lost, and the increase in soil nitrogen and phosphorus after spring burning lasted for only two months (i.e., June and July; Figure 2a,e). As the plants grew, the increase in soil nitrogen and phosphorus contents after autumn burning was gradually larger than those after spring burning and lasted at least until September (Figure 2a,e). In autumn, the soil surface bears much litter. Therefore, the slow decomposition of ash and the high intensity of autumn burning promoted nutrient release more consistently than spring burning and resulted in the soil nitrogen limitation being less at autumn burning sites than at spring burning sites. The nitrogen and phosphorus co-limitation at spring burning sites lasted only until June (Figure 2e). One potential reason for this is that, compared to autumn, the snowmelt in spring accelerates the loss of nitrogen through water erosion. In addition, the high burning intensity in autumn results in a greater release of phosphorus than in spring. Thus, the N:P ratio after spring burning declined more than that after autumn burning. Therefore, planned autumn burning of wetlands is necessary to mitigate wetland nitrogen and phosphorus limitations and increase soil nitrogen and phosphorus contents.

In this study, burning also immediately promoted the effectiveness of soil nitrogen, which increased the contents of NH_4^+ -N and NO_3^- -N (Figure 2b,c). The increase in NH_4^+ -N content was larger than that in NO_3^- -N, indicating that burning was conducive to nitrogen mineralisation (Figure 2b,c). First, burning immediately increased the soil MBN content and promoted the microbial mineralisation of soil nitrogen. Subsequently, the increased availability of soil phosphorus after burning promoted soil nitrogen mineralisation, thus promoting the accumulation of soil NH_4^+ -N. However, the increase in available nitrogen after burning was temporary. The soil NH_4^+ -N and NO_3^- -N contents decreased, beginning in August and occurring below the unburned sites (Figure 2b,c). As plants grow, the use of NH_4^+ -N and NO_3^- -N increases and wind or water erosion accelerates the loss of soil NH_4^+ -N and NO_3^- -N [19,21]. Interestingly, in our study, soil NO_3^- -N was reduced more slowly than NH_4^+ -N (Figure 2b,c). Burning decomposes humus in the soil while increasing soil voids and creating aerobic conditions conducive to nitrogen nitrification. The increase in NH_4^+ -N and NO_3^- -N after spring burning was only evident in June and July, respectively,

and was lower than that at autumn burning sites in the plant growth season (Figure 2b,c). In addition, the NO_3^- -N content at autumn burning sites increased significantly until August (i.e., $p < 0.05$; Table 1; Figure 2b,c). As the plants grew, the loss of NH_4^+ -N and NO_3^- -N was faster after spring burning than after autumn burning (Figure 2b,c). After spring burning, the plants are in the early stages of growth and absorb a great deal of nutrients. With the hydrology of the spring snowmelt, NH_4^+ -N and NO_3^- -N are rapidly lost. The increase in effective nitrogen and phosphorus in the soil after autumn burning provides nutrients for wetland plant growth for a longer period than spring burning, which is important for the wetland ecosystem.

4.2. The Effect of Burning on Plant Nitrogen and Phosphorus Contents

Our research indicated that the changes in nitrogen and phosphorus contents in various plant organs were different on an inter-month basis after burning (Figure 3). Early in the plant growth season, nitrogen and phosphorus contents in stems and leaves at burning sites were higher than those at unburned sites (Figure 3). One possibility is that the soil and plants are linked inextricably in wetland ecosystems [37], and the immediate increase in soil-available nitrogen and phosphorus after burning is quickly absorbed by plants [38–40], and then, this stimulates plant photosynthesis and growth. The same conclusion was reached in a study of dune herbs by Anderson R C et al. (1997) [41]. Additionally, leaf nitrogen and phosphorus are involved in plant respiration and photosynthesis, and stems are responsible for transporting and storing nutrients for plant growth [42]. Burning stimulates plant production resilience mechanisms that transfer nutrients from roots to leaves and stems [8]. In the leaf, plants augment the number of chloroplasts and the respiration rate by increasing the nitrogen and phosphorus contents, and in the stem, they increase the plant's stress resistance by storing these contents in large amounts. A similar explanation was proposed by Minden V et al. in their desert plant studies, stating that a stronger nitrogen retention in leaves is a response to salt stress [43]. However, in our study, the increase in plant nutrients after burning was temporary. As plants grew, the nitrogen and phosphorus reached their maximum contents in stems in May and in leaves in July, respectively, and then declined sharply to below the content levels of the unburned sites (Figure 3). Soil nitrogen and phosphorus are lost with wind and hydrology and absorbed by plants, which results in a reduced amount of nitrogen and phosphorus that can be stored by plants. Additionally, as plants grow, the leaf and stem nutrient contents gradually decrease after July [44,45]. As plants senesce, the nutrient content of aboveground organs is gradually transferred to and stored in belowground roots for subsequent growth. The changes in root nutrient contents in our study confirmed the view that these contents increase steadily as plants grow (Figure 3). However, burning reduced the root phosphorus content and these results lasted for at least one growing season (Figure 3f). First, burning increases soil organic acid secretion and soil acidification, leading to the loss of available soil phosphorus [46]. Subsequently, as plants grow, the residual inorganic phosphorus that they have not absorbed gradually combines with other soil ions and is converted into forms of phosphorus that are difficult for them to absorb [47]. The content of plant root phosphorus also decreased after burning in the Great Xing'an Mountains [48].

Autumn burning reduced the plant nitrogen and phosphorus contents in these sites compared to the unburned sites, and the effects lasted for at least one growing season (Figure 3). Autumn burning occurred six months before the plants grew and the soil nitrogen and phosphorus contents were sufficient for plant growth compared to those at the unburned sites. Thus, plants did not require stored nutrients to adapt to burning. The stem nitrogen and phosphorus contents were significantly different between spring and autumn burning sites (i.e., $p < 0.01$; Table 2). Spring burning increased the stem and leaf nitrogen and phosphorus contents, but the effect was temporary (Figure 3). The nitrogen contents at spring burning sites were only larger in stems in May and in leaves in June than those at the unburned sites, and the increase in stem and leaf phosphorus contents lasted for only one month (i.e., until May; Figure 3). With the advent of plant maturity (i.e., in July),

the storage of nitrogen and phosphorus in stems and leaves after spring burning was less than that after autumn burning. Spring burning occurs in the early stage of plant growth and has an immediate stimulating effect on plants, causing stems and leaves to absorb large amounts of nitrogen and phosphorus to compete for growth. Later in the growing season, large amounts of soil nitrogen and phosphorus are lost due to the snow and ice melting, gradually reducing the nutrients available for plant uptake. Meanwhile, as the plants mature, the nitrogen and phosphorus in stems and leaves are gradually transferred to storage in the roots. This explanation has been confirmed by our experiment on the changes in nitrogen content in plant roots, which increased, then decreased, and then increased as the plants grew. However, the root phosphorus in spring burning plots was significantly less than that at autumn burning sites during the whole growing season (i.e., $p < 0.05$; Table 2). Therefore, planned burning during autumn is less damaging to plants than during spring.

4.3. Differences in the Effects of Burning on Plant Growth

Plant growth is a visual indicator of the degree of environmental disturbance. Burning significantly increased the plant stem density and these results lasted for at least one growing season (i.e., $p < 0.01$; Table 3; Figure 4). The removal of litter through burning increases the area of bare ground, which increases the surface solar radiation and temperature of the soil [49,50], and the diurnal soil temperature difference promotes seed germination. Previous research has shown that seeds from burned plants of *S. bracteolate* had higher germinability than seeds from unburned plants [51]. In our study, burning resulted in the maximum plant stem density at spring burning sites three months earlier than at autumn burning sites (Figure 4). In Soberania National Park, the increase in soil nutrients after burning intensified the competition between seeds and accelerated the production of *Saccharum* seeds [52]. The changes in plant carbon content could reflect plant adaptation to soil nutrient changes after being burned. Burning increased the plant carbon content, and the promotion of plant growth lasted for at least one growing season (Figure 4). Early in the growing season, plants generate resilience mechanisms through the augmented leaf area and thickness to increase photosynthesis and respiration [8]. The increase in soil nitrogen and phosphorus contents provided sufficient nutrients for plant photosynthesis and respiration, which promoted the growth of stems and leaves. Once the stem densities stabilised, the plants began to grow rapidly after 2 months (i.e., between June and July), leading to the elongation of the stem and the storage of nutrients therein in response to burning [52]. Meanwhile, the aboveground biomass increased consistently after burning, with these results lasting for at least one growing season (Figure 4b). In the early stages of plant growth, the aboveground biomass in burning plots significantly increased to nearly twice as much as that at the unburned sites and reached a maximum in August (i.e., $p < 0.01$; Table 3; Figure 4b). Burning resulted in the invasive spread of other species [52], increasing the plant community richness and aboveground biomass. Nutrient conditions at burning sites also promoted plant root growth, thereby increasing the root carbon content [48,53,54]. Thus, burning also increased the belowground biomass in one season of plant growth. As the plants matured (i.e., after July), the carbon content of their aboveground organs gradually decreased and was transferred to and stored in the belowground root.

The plant stem density was greater at spring burning sites than at autumn burning sites during the whole season of plant growth (Figure 4a), and the plant stem density maximum at spring burning sites was approximately twice that at unburned sites and appeared three months earlier than at autumn burning sites (Figure 4a). Spring burning began at the pre-emergence stage, which reduced the ground litter and increased the soil temperature to promote seed germination. In addition, spring is the season when the snow melts, and the burning intensity is less than during autumn burning, causing less damage to the soil and plants. *S. bracteolate* burned at low temperatures produced seeds that were larger and three times more numerous than those of unburned plants [51]. Spring burning also increased the plant carbon content compared to autumn burning

(Figure 4). The increase in the leaf carbon content at spring burning sites lasted for only two months (i.e., May and June), and the increase in the stem and root carbon content lasted for one growing season (Figure 4). Plants were in the germination stage after spring burning. The timely supply of nutrients after spring burning can enable plants to adapt to burning by augmenting the area and thickness of leaves, thereby increasing the absorption of sunlight. As plants grow, they gradually store nutrients in their stems and roots to ensure survival. Compared with autumn burning, spring burning is lower in intensity and causes less damage to roots, which increases the belowground biomass. In contrast, in our study, autumn burning increased the aboveground biomass significantly than spring burning (i.e., $p < 0.01$; Table 3). Autumn burning increases the spread of invasive species seeds with the wind, and after a full winter of dormancy, seeds of invasive species contain ample nutrient stores. Additionally, during the growth season after burning, the height of dominant plants is limited, which provides more space for invasive plants. Thus, the emergence of a rich plant community after autumn burning resulted in a higher aboveground biomass compared to after spring burning, promoting successional processes in wetland plant communities.

5. Conclusions

Spring burning immediately increased the nitrogen and phosphorus cycling in both plants and soil, but these effects only lasted until July. At autumn burning sites, the large amounts of decomposing ash increased the soil nitrogen and phosphorus contents until August. In addition, autumn burning was less damaging to plants than spring burning, and significantly increased the aboveground biomass. Spring burning only increased the plant nitrogen content until June and increased the stem and leaf phosphorus contents until July, and compared to autumn burning, spring burning significantly reduced the root phosphorus content. Meanwhile, spring burning increased the competition between plants, and the resulting stem density and belowground biomass were significantly larger than those observed after autumn burning. Thus, conducting autumn burning before the commencement of agricultural burning not only reduces combustible accumulation and prevents unplanned fires but also provides suitable management approaches to promote nitrogen and phosphorus cycling and plant growth in wetlands. The data on nitrogen and phosphorus in soil and plants obtained during our experiment may provide a basis for predictions regarding wetland carbon storage capacity, as nitrogen and phosphorus are important impact indicators of carbon. The increase in plant biomass after burning also further increased the carbon fixation capacity of the wetland and contributed to mitigating the greenhouse effect.

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