Accepted manuscript version of 4.Gao, C., Wang, G., Santin, C., Doerr, S.H., Cong, J. & Zhao, H. (2021) Response of *Calamagrostis angustifolia* to burn frequency and seasonality in the Sanjiang Plain wetlands (Northeast China). *Journal of Environmental Management*, 300, 113759. (doi.org/10.1016/j.jenvman.2021.113759)

Response of *Calamagrostis angustifolia* to burn frequency and seasonality in the Sanjiang Plain wetlands (Northeast China)

Abstract

Fire is an important disturbance in many wetlands, which are key carbon reservoirs at both regional and global scales. However, the effects of fire on wetland vegetation biomass and plant carbon dynamics are poorly understood. We carried out a burn experiment in a *Calamagrostis angustifolia* wetland in Sanjiang Plain (Northeast China), which is widespread in China and frequently exposed to fire. Using a series of replicated experimental annual burns over a three-year period (spring and autumn burns carried out one, two or three times over three consecutive years), together with a control unburned treatment, we assessed the effect of burn seasonality and frequency on aboveground biomass, stem density, and carbon content of aboveground plant parts and ground litter. We found that burning promoted plant growth and hence plant biomass in burned sites compared to the unburned control, with this effect being greatest after three consecutive burn years. Autumn burns promoted higher stem density and more total aboveground biomass than spring burns after three consecutive burn years. Burning increased stem density significantly, especially in twice and thrice burned plots, with stem densities in September over 2000 N./m^2, which was much higher than in the control plots (987 ± 190 N./m^2). Autumn burns had a larger effect than spring burns on total plant biomass and litter accumulated (e.g. 1236±295 g/m^2 after thrice autumn burns compared 796.2±66.6 g/m^2 after thrice spring burns), except after two burn treatments. With time since burning, total biomass loads increased in spring-burned plots, while autumn-burned plots showed the opposite trend, declining towards values found at unburned plots in year three. Our results suggest that, at short fire return intervals, autumn burns lead to a more pronounced increase in aboveground biomass and carbon accumulation than spring burns; however, the effects of spring burns on biomass and carbon accumulation are longer lasting than those observed for autumn burns.

Keywords: fire, plant biomass, wetland, burn frequency, burn season.

Introduction

Fire, whether ignited naturally or by human activity, is an important ecological factor in many ecosystems and a primary disturbance mechanism affecting their structure, diversity and productivity (Battisti et al., 2016; Just et al., 2017). It also influences plant successional shifts in vegetation communities, and exerts substantial impacts on carbon and nitrogen cycling in a range of ecosystems, such as forests, grasslands, and wetlands (Butler et al., 2017; Lü et al., 2017; Wang et al., 2019). Each year fires burn 300–460 million hectares globally (~4% of the Earth's vegetated land surface), emitting 2200 Tg carbon (C) to the atmosphere, and producing 256 Tg of pyrogenic carbon (van der Werf et al., 2017; Jones et al., 2019). Fire effects on the carbon cycle are therefore substantial and their significance is increasing under ongoing climate and land cover changes (Flannigan et al., 2009; Turetsky et al., 2015; Santin et al., 2016; Walker et al., 2019). Fire effects on plant biomass and associated carbon storage are one of the key factors in understanding the interaction between fire and the carbon cycle, especially in ecosystems that act as globally important carbon stores (Ward et al., 2012; Bret-Harte et al., 2013).

Wetlands, which include peatlands and other biomass accumulating flooded environments, are globally important carbon reservoirs as they store more than 30% of the world's soil carbon. Many of them are naturally affected by fire (Yu et al., 2010; Marrs et al., 2018). In addition, accidental human-caused fires often impact these ecosystems (Zhang et al., 2019) and prescribed burning has become an increasingly used tool for managing and restoring wetlands (Middleton et al., 2006; White et al., 2008). This study focuses on the Sanjiang Plain in northeast China, one of the largest wetlands in the country (8100 km^2), with freshwater marshes being the predominant wetland type (Wang et al., 2011). This region has experienced intensive reclamation (i.e. drainage) and cultivation since the end of the 19th century. During this time, in addition to naturally ignited fire, burning has been frequently used as a land management tool to extend agricultural areas for supporting a rapidly growing human population (Gao et al., 2014; Gao et al., 2018). Also, burning of agricultural residues in the field after harvesting is widely used to accelerate turnover rates of nutrients in crops (Giardina et al., 2000). Historically, crop residues were collected and used for cooking and heating, but with rural families in China switching to cleaner fuels, more agricultural residues are burned in the fields (Li et al., 2007). This agricultural burning in farmlands often results in fires escaping and affecting nearby wetlands. Due to a combination of dry weather and the burning of agricultural areas by farmers in autumn and spring, burning of wetlands adjacent to crops usually occurs in both October and April in Northeast China (Zhao et al., 2017). *Calamagrostis angustifolia* (*C. angustifolia)* wetlands are one of the most widely distributed in China. *C. angustifolia* is an annual herbaceous grass of about 80 cm height that primarily grows at the edges of the wetlands, in areas that are mostly dry, making it especially vulnerable to the effects of fire spreading from surrounding agricultural areas.

The specific responses of vegetation after fire are partially conditioned by fire-driven changes in environmental conditions such as nutrient availability, soil temperature, surface albedo, and soil water content (Bret-Harte et al., 2013; Andrieux et al., 2018; Santin et al., 2018; Stirling et al., 2019). In wet meadows, fire during the early growing season has been seen to promote flowering of *Muhlenbergia capillaris*, *Paspalum monostachyum* and *Schizachyrium rhizomatum* in the following growing season (Main and Barry, 2002). Also, in salt marshes, it has been observed that annual prescribed burning decreases the accumulation of litter and increases biomass and stem densities of the wetland plant *Distichlis spicata* (Flores et al., 2011). In addition, it has been recently shown how fire can promote the growth of *Carex brevicuspis* in Chinese wetlands (Zhang et al., 2019). The effects of fire on plant growth are conditioned by many intrinsic and extrinsic factors, with the most important being fire regime characteristics such as burn frequency, burn season and time since fire. Even if *C. angustifolia* communities are widely distributed across China and are one of the wetland plant communities most frequently affected by fire, little is known about the impact of different burning scenarios on *C. angustifolia* communities.

To address this research gap, we examined the impact of burn season and frequency on aboveground biomass and necromass in *C. angustifolia*. We compare stem density, aboveground biomass, litter necromass and carbon content in different plant parts under different burn regimes. This field-based experiment lasted three years and three main potential controllers of the plant response to burning were analyzed: burn season (spring and autumn), burn frequency (from 1 to 3) and time since burning (from the first post-fire growing season (i.e. 2 or 8 months) to 2 years after burning). The objective of this study was to provide insights into the impact of fire on plant biomass and associated carbon stocks of *C. angustifolia* communities for burning scenarios that could occur either from naturally-ignited fire or escaped agricultural burns or could be applied as prescribed burning for localized fuel reduction prior to the agricultural burn seasons to prevent escaped agricultural burns from becoming intense, large-scale wetland wildfires.

2. Materials and Methods

2.1. Study site

The studied region (Sanjiang Plain, Northeast China) has a temperate climate, with an annual average temperature ranging from 1.9 to 3.9°C and rainfall from 500 to 650 mm. The low altitude, flat topography, and suitable climate conditions makes it one of the most extensive wetland regions in China (Wang et al., 2006). This area was historically a continuous wetland but it has been partially drained, fragmented and reduced in size due to its conversion for agriculture uses, which has led to increased burning in the remaining wetlands. The main wetland types are herbaceous wetlands near farmland and riparian wetlands along the rivers. Our study area (47°35′ N, 133°38′ E) was a graminoid marsh dominated, from the edge to the center, by *Calamagrostis angustifolia*, *Carex lasiocarpa*, *Carex pseudo-curaica*, *Carex meyeriana*, and *Carex appendiculata*. The *C. angustifolia* zone was, therefore, distributed near the edges and closest to the farmland. The water table in *C. angustifolia* communities is always lower than in the other wetland zones, and below ground all year except during the summer (Lou et al., 2017).

2.2. Experimental Design

In a wetland adjacent to farmland, nine sites within a homogenous area of *C. angustifolia* marsh were selected for the field experiment (Fig. 1). Local plant communities, soil moisture, and water table were similar for all sites. Each site comprised of an area of 150 m^2 (10 m × 15 m), with a gap of 5 m between sites. Three sites were subjected to autumn burns (A), another three to spring burns (S), and another three where left unburned as controls (C) (Fig. 1). Each site was further divided into three plots, each 10 m x 4 m, with a one-meter fire break between them. These plots were subjected to different burn frequencies over the three-year experimental period: burned once (O), twice (T) and thrice (H) (Fig. 1). The burn experiment started in autumn 2007 and was completed in spring 2010. A total of six burn campaigns were carried out, with autumn burns conducted in early October and spring burns in April. They were named AO (once in autumn; burned in Oct.

2007), AT (twice in autumn; burned in Oct. 2007 and 2008), AH (thrice in autumn; burned in Oct. 2007, 2008 and 2009), SO (once in spring; burned in April 2008), ST (twice in spring; burned in April 2008 and 2009), and SH (thrice in spring; burned in April 2008, 2009 and 2010). The selection of timing, i.e. autumn and spring, was because these are the times when crop residues are burned in the agricultural fields in this region, causing escaped fires in adjacent wetlands. Dry grasses were used for ignition. Burning was carried out under negligible wind, typically lasting ~30 min per plot. Fuels were sufficiently continuous to allow fires to be self-sustaining. In autumn, almost all aboveground grass material was consumed whereas, in spring burns, only the standing shoots and litter above the snow-ice coverage were burned, with the average thickness of snow/ice being ~5 cm above the soil surface. Burning did not directly affect the subsoil, and the snow/ice cover in spring limited any direct effects of burning on surface organic soils in spring, compared to autumn burns. Further details on the experimental design and the effects of these burns on soil organic carbon are given in (Zhao et al., 2012).

2.3. Sampling and chemical analysis

Vegetation assessment was done twice each year, at the beginning of the growing season (i.e. June 2008, 2009, 2010), and at its end (i.e. September 2008, 2009, and 2010). To estimate the number of stems in the plots, the aboveground plant components (i.e. leaves, stems) were clipped near the ground level and collected, together with ground litter (necromass), in three 0.3 m × 0.3 m quadrats per plot, and the stem numbers were counted after clipping. Afterwards, plant leaves and stems were separated, oven-dried at 75 °C to constant weight and weighed. After weighting, approximately 20 g of dry plant material was ground, and the carbon content in leaves, stems and ground litter was determined by the external heating potassium dichromate oxidation method (Wu and Tao, 1993). Total aboveground biomass and carbon loads (g/m^2) were then calculated with the respective biomass (i.e. the sum of stem and leaf biomass and litter necromass) and carbon data obtained. The average biomass per plant was calculated based on the stem density and aboveground biomass loads, and the carbon content in each plant was calculated based on the average biomass per plant and average carbon content.

To allow a more meaningful discussion of the plant parameters examined, soil sampling in

2010 was done to complement the soil samples taken at the sites in 2008 and 2009 and reported in Zhao et al., (2012). Six soil samples (0-15 cm depth) per treatment were taken in June and September 2010. These were analyzed for dissolved organic carbon (DOC), microbial biomass carbon (MBC), and soil organic carbon (SOC), following the methods of Zhao et al., (2012). In brief, DOC was measured as total organic carbon content in 100 ml solution, following extraction of DOC from 20 g oven-dry milled soils (soil fraction smaller than 2 mm) and determined with a TOC-V_{CPH} analyzer (Shimazdu, Japan). MBC was determined by the chloroform-fumigation extraction method, and SOC using the external heating potassium dichromate oxidation method.

2.4. Statistical analysis

A three-way analysis of variance (three-way ANOVA via SPSS 20.0 (SPSS, Inc.)) was used to evaluate whether different burn treatments were associated with significant differences in stem density (N./m^2), aboveground biomass in each plant part (stems, leaves) and ground litter (g/m^2), and their carbon stocks (g/m^2), and in the soil carbon pool (g/m^2) separately for DOC, MBC, and SOC. Burn season (spring or autumn), burn frequency (0, 1, 2, 3) and time since burning (unburned, first growing season after burning, one year since burning and two years since burning) were the factors tested. Significant differences are reported at the 0.05 probability level (i.e. $P<0.05$).

To isolate the effects of burn frequency and season on aboveground plant biomass parameters, data were divided into burned and unburned control plots groups for each year (i.e. once burned and control plots in 2008, twice burned and control plots in 2009, and thrice burned and control plots in 2010), with spring (S) and autumn (A) burn groups treated separately. To examine the effect of time since burning, the data obtained in 2010 were divided into control plot- and burned plot groups with different intervals (i.e. two years, one year, and the same growing season after spring burns), with spring (S) and autumn (A) burn groups treated separately. A two-way ANOVA analysis was then applied with the different treatments being grouped by Tukey's honestly significant differences (Tukey-HSD) test, respectively.

3. Results

3.1. Impact of burn frequency on stem density, biomass and carbon in aboveground plant parts and litter

Burn frequency had statistically significant effects on nearly all the plant variables measured, except stem density, for both June and September sampling (Table 1). Burning increased stem density in all cases in June, irrespective of burn frequency (Fig. 2a). However, the differences between the thrice burned plots and control plots were less pronounced than those between lower burn frequency (i.e. once or twice burned) plots and control plots (Fig. 2a, Fig. 3a). Especially in twice and thrice burned plots, stem densities, which ranged 1650-2300 N./m^2 in September, were much higher than those in the control plots (800-1000 N./m^2; Fig. 3a). Burning was associated with higher stem density, lower biomass per plant, and higher total biomass loads per plot in burned plots than those in unburned plots in absolute terms (Fig. 2b&c, Fig. 3b&c). For example, in September, plant biomass after burning twice was nearly double that in unburned plots (e.g. 647.7±82.0 g/m^2 in spring burned plots versus 292.2±92.0 g/m^2 in unburned plots; Fig. 3c). When comparing the biomass stored in stems vs. leaves,, for all plots most of the plant biomass was stored in the stems (50-75%), and burning decreased the proportion of total aboveground biomass stored in stems, especially in June which were 68.5±4.6% in unburned plots and 64.7±6.3% in burned plots (Fig. 2c&d). Regarding carbon, general trends were very similar to those observed for biomass, and the effects of burn frequency on plant carbon and plant biomass were also comparable (Fig. 2d-f, Fig. 3d-f).

3.2. Changes in aboveground plant parts and litter with time since burning

Based on a three-way ANOVA analysis, time since burning had significant effects on nearly all factors studied, except for stem density in June and September (Table 1). Stem density and total biomass loads for different lengths of time after burning in the final year of the experiment are shown in Fig. 4 and Fig. 5. In June, stem density increased with time since burning for the plots burned in (from 1852.0±60.0 to 2080.0±217.0 N. /m^2; Fig. 4a) but no significant changes were observed in September (around 1800 N. /m^2; Fig. 5a). At two years since burning, stem density in June for autumn-burned plots was 1172.0±348.0 N. /m^2, which was lower than that in unburned plots (1371.0±161.0 N. /m^2) (Fig. 4a). In June, a significant difference in biomass per plant between burned and unburned plots was found, especially between plots burned in 2008 (0.36±0.03g in spring and 0.40±0.08g in autumn burned plots) and unburned plots (0.30±0.02g) (Fig. 4b); however, in September, biomass per plant was not significantly different between unburned (0.62±0.15g) and burned (0.43-0.60g) plots (Fig. 5b).

3.3. Impact of burn season on aboveground plant parts and litter

Burn season had a significant effect on both stem density, plant litter necromass and biomass per plant in June, and no significant effect on these in September (Table 1). Interestingly, the interaction between burn season and each of the other two factors studied had significant effects on more biomass-related variables than the effects of burn season (Table 1). In September, plant biomass in autumn-burned plots was significantly higher than in spring-burned plots, except after two burn treatments, where plant biomass was similar irrespective of burn season (e.g. 643.8±243.0 g/m^2 in autumn-burned plots and 647.7±82.0 g/m^2 in spring-burned plots; Fig. 3c). With longer time since burning, stem density in September decreased, and the differences between burned and unburned plots were less evident. This trend was more pronounced after autumn than after spring burns (Fig. 5a). In contraposition to stem density, average biomass per plant increased with time since burning, with this trend being stronger in spring burned plots. In September, one year since burning, biomass per plant in spring-burned plots was higher than in autumn-burned plots (Fig. 5b). It is also noteworthy that total biomass loads increased with time since burning in spring-burned plots both in June and September, while biomass loads in the autumn-burned plots showed the opposite trend (Fig. 4c, Fig. 5c). With time since burning increasing, the stem density in June and September also showed contrasting patterns between spring burned plots and autumn burned plots (Fig. 4a, Fig. 5a).

4. Discussion

4.1. Impact of burning and burn frequency on aboveground biomass in subsequent growing seasons

Burn frequency was the most important factor that significantly influenced nearly all studied variables related to plant growth (Table 1), but, in general, most burn treatments resulted in an increase of aboveground biomass (Fig. 2 and Fig. 3). The fact that burning promotes plant growth has been reported in previous studies in other wetland environments. For example, in a northeastern Kansas wetland in the USA (*Spartina pectinata* community), aboveground biomass, inflorescence density and plant height were significantly higher in burned than unburned sites (Johnson and Knapp, 1993). In Gulf Coast wetlands of the USA, live aboveground biomass was also higher in burned than in unburned sites (Gabrey et al., 1999). In our study, burning increased both stem density and aboveground biomass of *C. angustifolia,* a perennial wetland plant that regrows mostly from belowground rhizomes. The growing season in our study region is relatively short (June-September) due to temperature limitations. Earlier emerging shoots and greater stem density were more commonly observed during field sampling at burned- than at unburned plots (Fig. 2a). Burning consumed the aboveground biomass as well as ground litter (especially in autumn burned plots), creating physical and biological openings in the wetland ecosystem. This may have allowed more direct sunlight warming up the soil surface, increasing diurnal temperature fluctuations, which have been shown to benefit plant germination (Ponzio et al., 2004). This may be especially important for increasing stem density, plant biomass and carbon accumulation in regions with relatively short growing seasons.

C. angustifolia allocated more stem and leaf biomass in burned plots- compared to unburned plots. Burning is also likely to have caused a higher turnover rate of nutrients with some of the nutrients remaining in ash after burning and becoming readily available to plants (Maass, 1995; Pereira et al., 2012; Pingree and DeLuca, 2018). Plant growth and biomass accumulation are enhanced under greater availability of light and nutrients. Conversely, plants from unburned areas with low nutrient resources exhibit proportionally lower biomass loads (Poorter et al., 2012). Burning does not only release nutrients from combusted biomass, it can also promote microbial activity (Medvedeff et al., 2015; Singh et al., 2017). In a parallel study focusing on soil C impacts within this burn experiment (Zhao et al., 2012), it was found that burning promotes significantly more DOC and MBC being available in June, and, therefore it may be enhancing microbial activity (Fig. S1, Table S1) (Zhao et al., 2012). Thus, we speculate that, a more beneficial microclimate, greater nutrient availability, and more active microbial metabolism in surface soils may be the main reasons for the increase in total aboveground biomass in burned plots.

Our findings suggest that, at least in the short term, *C. angustifolia* aboveground biomass benefits from fire, and this benefit seems to increase with fire frequency. Burning once and twice during the three-year study period had a similar enhancing effect on biomass, while burning every year over the three-year period led to significantly higher aboveground biomass than the other two burn frequencies (Fig. 3c). The post-fire responses are similar to those reported for other types of wetlands, such as *Spartina pectinata* wetland in the USA (Johnson and Knapp, 1995) and *Triarrhena lutarioriparia* wetland in China (Wang et al., 2019). This was most likely due to repeated burning not only removing more of the accumulated dry biomass and ground litter and the associated release of nutrients to surface soils, but also to the repeated promotion of microbial metabolism and rapid nutrient cycling from soils to plants (Cianciaruso et al., 2010).

4.2. Changes in plant characteristics with time since burning

Time since burning was also a factor that influenced nearly all plant parameters (Table 1). Two years after burning, aboveground biomass loads and stem density of the *C. angustifolia* communities were still higher than those in unburned areas at both sampling times, especially in September (Fig. 5). Plant type plays an important role during the recovery processes after fire. For example, in environments with woody plants, it can take decades to centuries for biomass to recover to pre-fire levels (Cleary et al., 2010). In contrast, where herbaceous plants dominate, including perennial ones such as *C. angustifolia* examined here, it is generally quicker for biomass to reach or even exceed pre-fire level, sometimes only one growing season. In this study, we found increased stem and leaf biomass during the first growing season after the fire. In addition, high aboveground biomass during the first growing season will lead to plant litter accumulation on the soil surface, which may result in increased nutrient supply for microbial metabolism and plant growth during the second growing season. With increasing time since burning, stem density and plant biomass in autumn burned plots decreased and approached those in unburned plots (Fig. 4). Potential reasons may have been the gradual reduction of both nutrients inputs and microbial activity in surface soils due to the lack of fire in this cool continental climate. A more rapid decline was reported from a sub-tropical wetland in Florida (USA), where microbial activity returned to those of unburned conditions after only one year (Medvedeff et al., 2013).

Due to the fact that nutrient availability influences the growth of stems more directly than leaves

(Poorter et al., 2012), the reduction on nutrients inputs with increasing time since burning may have led to individual stem biomass changing more than leaf biomass or litter necromass. In addition, the limited physical space in plots with high stem density may have been a major reason for reduced leaf growth in these plots. Thus, it seems that burning promotes stem growth more notably than leaf growth and, therefore, more biomass is allocated to the stems. With nutrient availability and soil microbial activity decreasing, the growth of stems biomass at burned plots with long-terms intervals also approached those at the unburned plots. This was especially evident two years since burning for plots burned in autumn, with aboveground biomass being similar to unburned plots.

4.3. Impact of fire season on plant aboveground biomass.

Research evaluating the impact of burn season on aboveground biomass in wetlands is very scarce. A previous study found that fire occurring early in the growing season promotes flowering of typical wetland plants in the following growing season (Main and Barry, 2002). These types of studies are much more extensive for other ecosystems (Sparks et al., 1998; James et al., 2018). For a short grass prairie ecosystem in the USA, burning during the growing season was found to be a more severe disturbance than burning during the dormant season (Brockway et al., 2002). Another recent study found that few differences in vegetation patterns (*Quercus spp.*) in Tennessee (USA) were directly influenced by burn season after a single burn, and several traits of plants in less intense autumn burns were similar to the more intense spring burns (Vander Yacht et al., 2017). We found similar results, with burn season having only significant effects on a few plant growth variables (Table 1). For example, stem densities were similar in different burn seasons in plots that were burned once or twice (Fig. 2, 3).

That noted, in this three-year study, repeated (3x) annual burning in autumn led to higher stem densities and total aboveground biomass loads than spring burns. Similar results were found in herbaceous communities in a mixed conifer forest in the western USA, where the effects of seasonal variation of burning became more marked after multiple burns (Knapp et al., 2009). The authors reported that greater fuel consumption and heat penetration into the soil may have killed more of the underground roots than the late spring/early summer burns, with *Pyrola picta Sm*. being reduced in frequency by late-season burns but not early-season burns. We also found elevated MBC and

DOC, and lower SOC in AH plots than those in SH plots in the 2010 June sampling (Fig. S1). In addition, when sampled in September, MBC was higher in AH plots than in SH plots (Fig. S1). This suggests that microbial metabolism in autumn burned plots was more active than in spring burned plots. In our study region, the average depth of the snow-ice cover during spring burns was ~5 cm above the soil surface, which prevented aboveground biomass from being completely consumed. The remaining unburned stubble and litter in spring burned plots might block some sunlight, resulting in the lower biomass growth observed. In contrast, the more complete consumption of biomass during autumn burns most likely improved physical conditions (e.g., less ground litter; increased sunlight) for re-sprouting (Lesica and Martin, 2003). Another difference between burn seasons was the time needed for recovery (i.e. aboveground biomass similar to that in unburned plots). Autumn burns also allow a longer period before the next growing season for plants and microbes to recover than spring burns (Knapp et al., 2007). Medvedeff et al. (2013), after burning a wetland in Florida (USA), found microbial activity decreased at first, and then increased markedly several months later. In the current study, after three burns, stem density and aboveground biomass in plots burned in autumn were still higher than in those burned in spring.

Regarding the combination of factors, the interaction between burn season and time since burning appears to be important for most of the plant growth variables studied. After a two-year interval, especially in the first month of the growing season, stem density and aboveground biomass in autumn-burned plots were similar to those in unburned plots, and markedly lower than those in spring-burned plots (Fig. 4). The longer time period between spring burns and the growing season of the following year might have led to most of the nutrients in the ash layer being lost rather than being available for microbial use and for promoting plant growth (Hotes et al., 2010; Wang et al., 2013). Accordingly, soil DOC and MBC contents in June were slightly increased after fire and then by year one post-fire, the increase was more pronounced after autumn burns than after spring burns (Zhao et al., 2012) (Fig. S2). This suggests that organic carbon and nutrients in ash had not yet moved into the soil during the first growing season after burning. In autumn burned areas, the ash was mixed with snow during the winter and the nutrients in ash might have been more easily released into soils during snow melt than during spring burns (Saarnio et al., 2018). The reason might be that the normally higher water table (wetter) in wetlands in the growing season inhibits the microbial metabolism and retards nutrient release from the ash (Ernfors et al., 2010; Straková et al., 2012). Thus, two years after burning, the difference in plant growth between autumn burns and spring burns may be largely influenced by nutrient release processes from ash to soils. Thus, overall, autumn burns seem to promote plant growth more in the first growing season, while spring burns appear to promote plant growth more than two years after burning.

5. Conclusion and management implications

Our results show that the three fire factors considered (fire frequency, fire season and time since fire) have significant effects on *C. angustifolia* growth in the wetlands examined here. Overall, repeated annual burning in both autumn and spring promotes plant growth in the following growing season. Stem density and aboveground biomass were always higher in burned than in unburned plots, and autumn burns promoted the growth of plants in the following growing season more than spring burns. However, the effect of spring burns on plant growth lasted longer than the effect of autumn burns, exceeding one year. Thus, unintentional burning from escaped fires or naturally-ignited fire, whether in spring or autumn, appears to have an overall positive, but declining effect on aboveground biomass in the first few years after fire. This, however, has to be set in a wider context, with fire promoting carbon mineralization rates in the soil as reported in our previous study (Zhao et al., 2012) and, also, in relation to any other effects burning might have on the environment that were not the focus of this study. For example, a study on floodplain wetlands in the wider region showed that bird species richness and abundance were lower on burned plots compared to unburned ones in the year of the burning, although not in the following year (Heim et al., 2019).

If fire is used as a management tool for fuel reduction to prevent agricultural burns from escaping into wetland areas, this study suggests that *C. angustifolia* recovers well after burning, irrespective of burn season and frequency at least for the three-year period studied here. Such fuel reduction burns, therefore, would have to be carried out just prior to the commencement of agricultural burns given the rapid and enhanced biomass recovery rate in the growing season. This would be especially relevant for autumn burns, which resulted in nearly a doubling of plant biomass in the subsequent growing season.

Acknowledgments

The authors thank Prof. Beth Middleton of U.S. Geological Survey for constructive comments on an earlier version of this manuscript, Yuxia Zhang, Haiyang Zhao, and Shaoqing Zhang for sample analyses, and Yang Wang for help with the experimental burning. Assistance of the Sanjiang Mire Wetland Experimental Station, Chinese Academy of Sciences is also gratefully acknowledged. Financial support was provided by the National Natural Science Foundation of China (No. 41771504, 42171103，42101108, 41911530188), and the National Key R&D Plan of China (No. 2017YFC0212303), the Youth Innovation Promotion Association CAS (No. 2020235). This study also benefitted from discussion facilitated by Royal Society UK-China cost share grant IEC\NSFC\181002.

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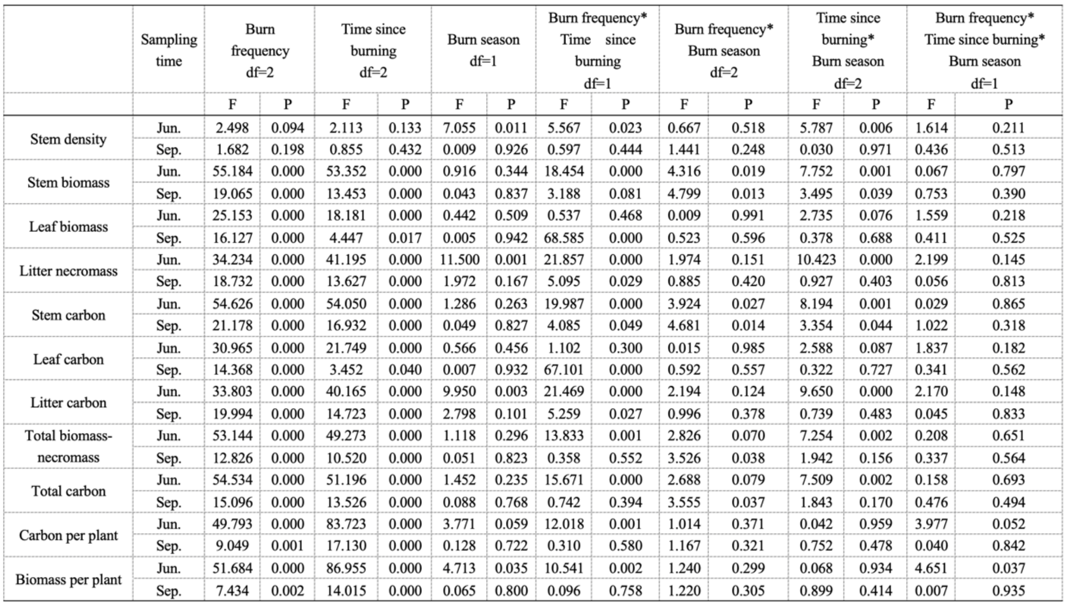
Table 1. Three-way ANOVA outputs for vegetation variables (i.e. stem density, stem biomass, leaf biomass, litter necromass, stem carbon, leaf carbon, litter carbon, total aboveground biomass-necromass, total carbon in aboveground plant parts, average biomass per plant, and average carbon per plant) at the two sampling times (i.e. the first month of the growing season (June), and the last month of growing season (September)). Burn frequency, time since burning, and burn season were considered as three independent variables.



	Sampling time	Burn frequency df=2		Time since burning df=2		Burn season df=1		Burn frequency* Time since burning df=1		Burn frequency* Burn season df=2		Time since burning* Burn season df=2		Burn frequency* Time since burning* Burn season df=1	
		F	P	F	P	F	P	F	P	F	P	F	P	F	P
Stem density	Jun.	2.498	0.094	2.113	0.133	7.055	0.011	5.567	0.023	0.667	0.518	5.787	0.006	1.614	0.211
	Sep.	1.682	0.198	0.855	0.432	0.009	0.926	0.597	0.444	1.441	0.248	0.030	0.971	0.436	0.513
Stem biomass	Jun.	55.184	0.000	53.352	0.000	0.916	0.344	18.454	0.000	4.316	0.019	7.752	0.001	0.067	0.797
	Sep.	19.065	0.000	13.453	0.000	0.043	0.837	3.188	0.081	4.799	0.013	3.495	0.039	0.753	0.390
Leaf biomass	Jun.	25.153	0.000	18.181	0.000	0.442	0.509	0.537	0.468	0.009	0.991	2.735	0.076	1.559	0.218
	Sep.	16.127	0.000	4.447	0.017	0.005	0.942	68.585	0.000	0.523	0.596	0.378	0.688	0.411	0.525
Litter necromass	Jun.	34.234	0.000	41.195	0.000	11.500	0.001	21.857	0.000	1.974	0.151	10.423	0.000	2.199	0.145
	Sep.	18.732	0.000	13.627	0.000	1.972	0.167	5.095	0.029	0.885	0.420	0.927	0.403	0.056	0.813
Stem carbon	Jun.	54.626	0.000	54.050	0.000	1.286	0.263	19.987	0.000	3.924	0.027	8.194	0.001	0.029	0.865
	Sep.	21.178	0.000	16.932	0.000	0.049	0.827	4.085	0.049	4.681	0.014	3.354	0.044	1.022	0.318
Leaf carbon	Jun.	30.965	0.000	21.749	0.000	0.566	0.456	1.102	0.300	0.015	0.985	2.588	0.087	1.837	0.182
	Sep.	14.368	0.000	3.452	0.040	0.007	0.932	67.101	0.000	0.592	0.557	0.322	0.727	0.341	0.562
Litter carbon	Jun.	33.803	0.000	40.165	0.000	9.950	0.003	21.469	0.000	2.194	0.124	9.650	0.000	2.170	0.148
	Sep.	19.994	0.000	14.723	0.000	2.798	0.101	5.259	0.027	0.996	0.378	0.739	0.483	0.045	0.833
Total biomass-necromass	Jun.	53.144	0.000	49.273	0.000	1.118	0.296	13.833	0.001	2.826	0.070	7.254	0.002	0.208	0.651
	Sep.	12.826	0.000	10.520	0.000	0.051	0.823	0.358	0.552	3.526	0.038	1.942	0.156	0.337	0.564
Total carbon	Jun.	54.534	0.000	51.196	0.000	1.452	0.235	15.671	0.000	2.688	0.079	7.509	0.002	0.158	0.693
	Sep.	15.096	0.000	13.526	0.000	0.088	0.768	0.742	0.394	3.555	0.037	1.843	0.170	0.476	0.494
Carbon per plant	Jun.	49.793	0.000	83.723	0.000	3.771	0.059	12.018	0.001	1.014	0.371	0.042	0.959	3.977	0.052
	Sep.	9.049	0.001	17.130	0.000	0.128	0.722	0.310	0.580	1.167	0.321	0.752	0.478	0.040	0.842
Biomass per plant	Jun.	51.684	0.000	86.955	0.000	4.713	0.035	10.541	0.002	1.240	0.299	0.068	0.934	4.651	0.037
	Sep.	7.434	0.002	14.015	0.000	0.065	0.800	0.096	0.758	1.220	0.305	0.899	0.414	0.007	0.935

Figure Captions

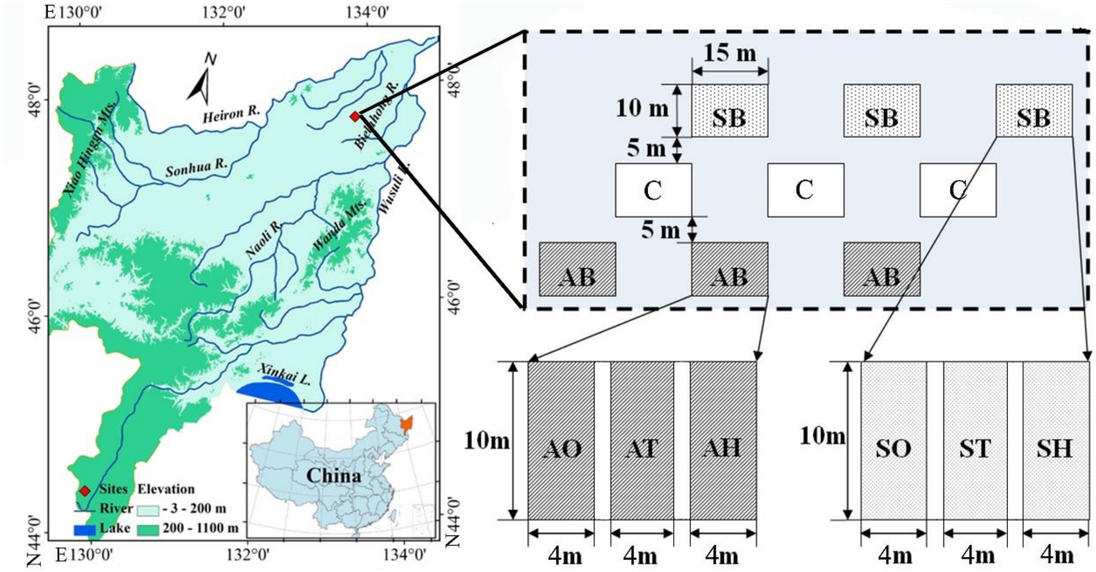
Figure 1. Location of the study area and experimental design. Each of the 9 sites was divided in three plots. Burn treatments in the sites (one per site) are: AB: autumn burns; SB: spring burns; C: unburned controls. Plot treatments within each site (three per site) are: AO: burned once in October 2007; AT: burned twice, in October 2007 and October 2008; AH: burned three times, in October 2007, October 2008, and October 2009; SO: burned once in April 2008; ST: burned twice in April 2008 and April 2009; SH: burned thrice in April 2008, April 2009 and April 2010. Sampling commenced in the year following the first burn (2008) and was done in June and September during 2008-2010.

Figure 2. Average values (with standard error bars) for stem density (a), biomass per plant (b), total plant biomass-necromass (c), stem biomass (d), leaf biomass (e), and ground litter necromass (f) at control and burned plots, for samples taken in June 2008, 2009 and 2010. Burn frequency in burned plots was once for 2008 (burned in 2007), twice for 2009 (burned in 2007 and 2008), and thrice for 2010 (burned in 2007, 2008 and 2009), respectively. Carbon contents are shown in grey shaded columns in figures b to f. Different lowercase letters (a-b) indicate significant differences (Tukey-HSD test) among burn frequencies and different uppercase letters (A-B) indicate significant differences (Tukey-HSD test) between burn seasons. C: unburned control plots, S: spring-burned plots, A: autumn-burned plots.

Figure 3. Average values (with standard error bars) for stem density (a), biomass per plant (b), total plant biomass-necromass (c), stem biomass (d), leaf biomass (e), and ground litter necromass (f) at control and burned plots, for samples taken in September 2008, 2009 and 2010. Burn frequency in burned plots were once for 2008 (burned in 2007), twice for 2009 (burned in 2007 and 2008), and thrice for 2010 (burned in 2007, 2008 and 2009), respectively. Carbon contents are shown in grey shaded columns in figures b to f. Different lowercase letters (a-b) indicate significant differences (Tukey-HSD test) among burn frequencies and different uppercase letters (A-B) indicate significant differences (Tukey-HSD test) between burn seasons. C: unburned control plots, S: spring-burned plots, A: autumn-burned plots.

Figure 4. Average values (with standard error bars) for stem density (a), biomass per plant (b), total plant biomass-necromass (c), stem biomass (d), leaf biomass (e), and ground litter necromass (f) at control plots (i.e. the longest time since burning) and burned plots (i.e. burned in 2008 (two years since burning); burned in 2008 and 2009 (one year since burning); burned in 2008, 2009, and 2010) sampled in June 2010. Carbon contents are shown in grey shaded columns in figures b to f. Different lowercase letters (a-b) indicate significant differences (Tukey-HSD test) among burn frequencies and different uppercase letters (A-B) indicate significant differences (Tukey-HSD test) between burn seasons. C: unburned control plots, S: spring-burned plots, A: autumn-burned plots.

Figure 5. Average values (with standard error bars) for stem density (a), biomass per plant (b), total plant biomass-necromass (c), stem biomass (d), leaf biomass (e), and plant litter necromass (f) at control plots (i.e. the longest time since burning) and burned plots (i.e. burned in 2008 (two years since burning); burned in 2008 and 2009 (one year since burning); burned in 2008, 2009, and 2010) sampled in September 2010. Carbon contents are shown in grey shaded columns in figures b to f. Different lowercase letters (a-b) indicate significant differences (Tukey-HSD test) among burn frequencies and different uppercase letters (A-B) indicate significant differences (Tukey-HSD test) between burn seasons. C: unburned control plots, S: spring-burned plots, A: autumn-burned plots.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China
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- 3 - 200 m
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Figure 1

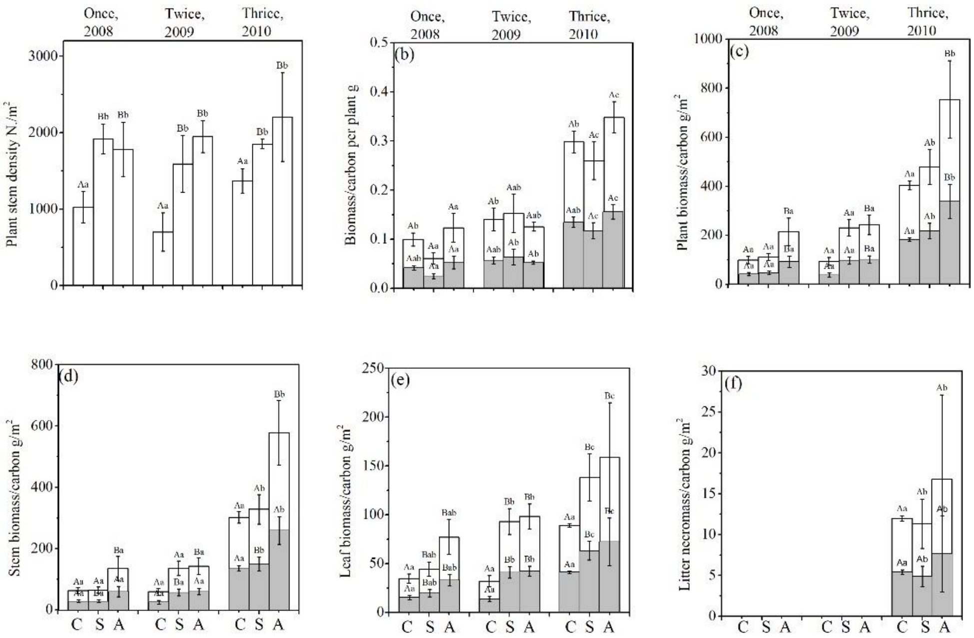
Once, 2008
Twice, 2009
Thrice, 2010
Plant stem density N./m^2
(b)
Biomass/carbon per plant g
(c)
Plant biomass/carbon g/m^2
(d)
Stem biomass/carbon g/m^2
(e)
Leaf biomass/carbon g/m^2
(f)
Litter necromass/carbon g/m^2
C S A
C S A
C S A

Figure 2

Accepted manuscript version of 4.Gao, C., Wang, G., Santin, C., Doerr, S.H., Cong, J. & Zhao, H. (2021) Response of *Calamagrostis angustifolia* to burn frequency and seasonality in the Sanjiang Plain wetlands (Northeast China). *Journal of Environmental Management*, 300, 113759. (doi.org/10.1016/j.jenvman.2021.113759)

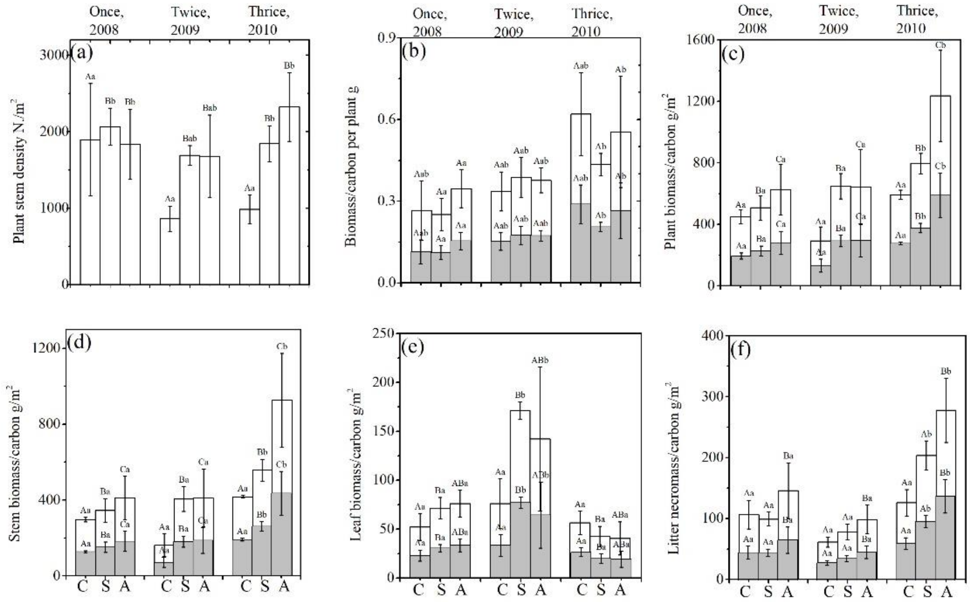

Figure 3

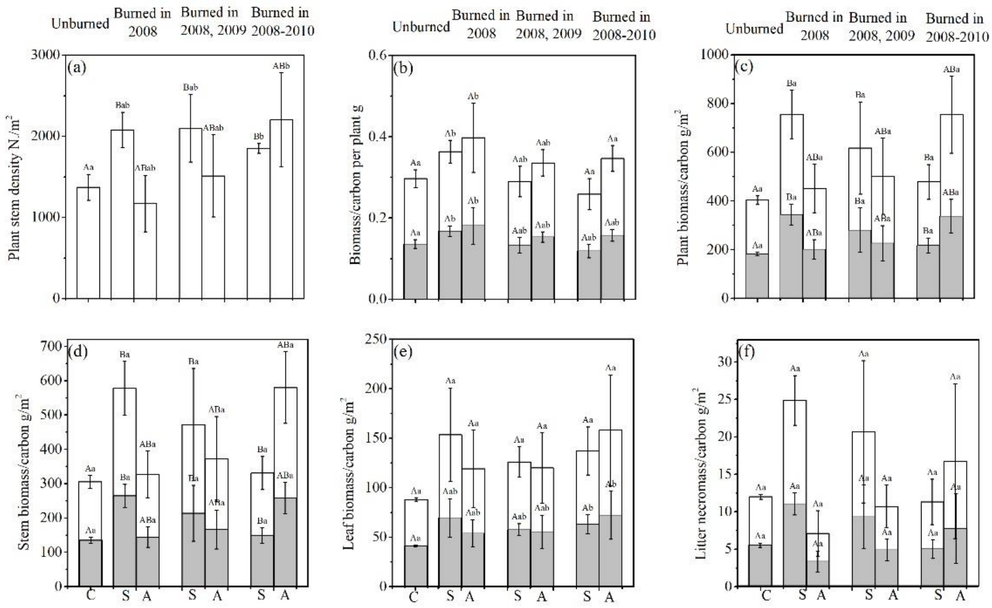
Unburned
Burned in 2008
Burned in 2008, 2009
Burned in 2008-2010
(a)
Plant stem density N./m^2
(b)
Biomass/carbon per plant g
(c)
Plant biomass/carbon g/m^2
(d)
Stem biomass/carbon g/m^2
(e)
Leaf biomass/carbon g/m^2
(f)
Litter necromass/carbon g/m^2
C
S
A
S
A
S
A

Figure 4

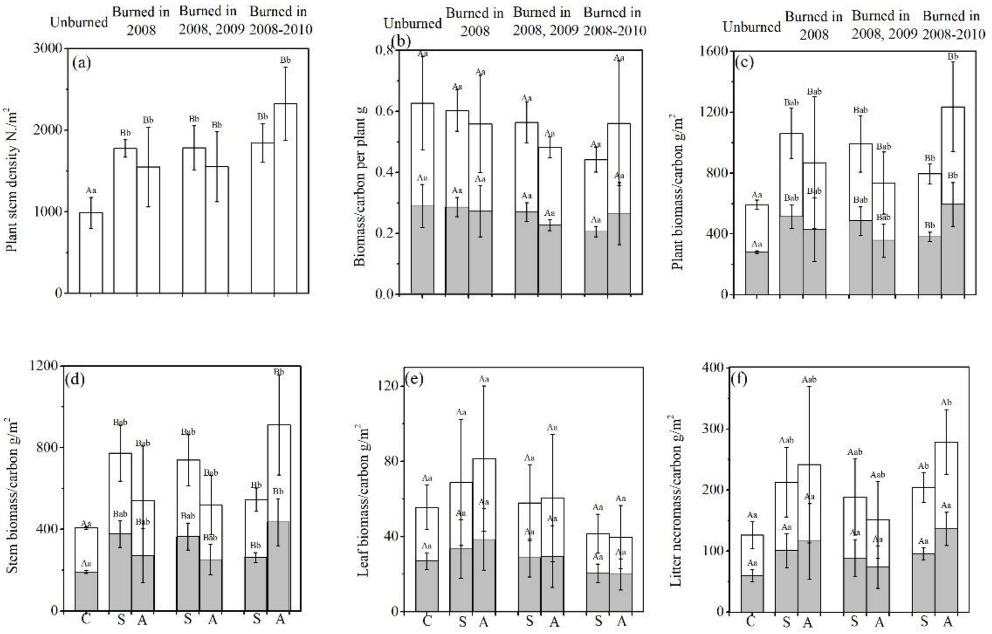
Unburned
Burned in 2008
Burned in 2008, 2009
Burned in 2008-2010
(a)
Plant stem density N./m^2
0
1000
2000
3000
Aa
Bb
Bb
Bb
Bb
Bb
Bb
(b)
Biomass/carbon per plant g
0.0
0.2
0.4
0.6
0.8
Aa
(c)
Plant biomass/carbon g/m^2
0
400
800
1200
1600
Aa
Bab
Bb
(d)
Stem biomass/carbon g/m^2
0
400
800
1200
Aa
Bab
Bb
(e)
Leaf biomass/carbon g/m^2
0
40
80
120
Aa
(f)
Litter necromass/carbon g/m^2
0
100
200
300
400
Aa
Aab
Ab
C
S
A
S
A
S
A

Figure 5