Plant species richness prolongs the growing season of freely assembled riparian herbaceous communities under dry climatic conditions

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A B S T R A C T

According to two main and non-exclusive scenarios, plant diversity can influence the growing season of vegetation stands through: (i) functional complementarity among species and, (ii) functional selection of species from the regional pool. The objective of this study was to evaluate whether plant species richness prolongs the active photosynthetic period length (APPL) of freely assembled riparian herbaceous communities in agroecosystems of Eastern Canada. We selected a total of 44 herbaceous communities in riparian buffers of varying species richness but which were comparable in their soil characteristics and cumulative growing degree-days. Independent of abiotic factors, we observed a general positive relationship between species richness and the APPL of riparian herbaceous communities. In the first sampling year, the APPL of species-rich communities was, on average, 30 days longer than the APPL of species-poor communities. Species-rich communities were sheltering herbaceous species with delayed green offset dates in comparison to communities dominated by *Phalaris arundinacea*, a dominant species in these riparian buffers. This relationship was not observed in the second sampling year. We suggest that the presence of a significant and positive APPL–species richness relationship was related to exceptionally dry climatic conditions in the first sampling year. We estimated that, under certain conditions, restoring the species diversity of herbaceous riparian communities in intensively managed agroecosystems could account for a net carbon uptake gain of up to 900 kg C yr^{-1} ha^{-1} of riparian buffer.

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1. Introduction

Phenology is the study of periodic life cycle events, such as plant greening or flowering onset, and how these are driven by environmental factors (Lieth, 1974; Morisette et al., 2008). Over the last decades, studies of vegetation phenology have reported an extended growing season (e.g., Menzel and Fabian, 1999; Linderholm, 2006) and earlier flowering onset in several plant species (e.g., Abu-Asab et al., 2001; Ellwood et al., 2013). Consequentially, with longer growing periods it is, therefore, expected that carbon uptake should also increase. Accordingly, at the ecosystem level, Baldocchi (2008) observed that net carbon uptake in savannas increased by 3.7 g C m^{-2} for each additional growing day. Likewise, Richardson et al. (2013) reviewed the effect of the growing season length on interannual patterns of carbon

uptake and reported an increase in the range of 4–5 g C m^{-2} d^{-1} for grassland ecosystems.

While a link between growing season length and carbon uptake of plant communities seems evident, how community dynamics may relate to the growing season length has, to date, been understudied. Thus far, most phenological studies of vegetation have assumed that the growing season is primarily driven by abiotic factors. Moreover, vegetation growth has been studied either for a single community throughout time (e.g., Richardson et al., 2010) or different communities across space (e.g., Baldocchi, 2008), making it difficult to disentangle the role of species' functional characteristics.

At the level of plant communities, species richness and diversity are known to influence the seasonality and the timing of ecosystem functions such as plant biomass production (Al-Mufti et al., 1977; Ansquer et al., 2009). In synthesizing seven years of results in a large grassland biodiversity experiment, Allan et al. (2011) reported a strong positive relationship between plant species diversity (including measures of both species evenness and functional diversity) and the interannual production of

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aboveground biomass. In this study, the turnover in functionally complementary species rather than the presence of species with consistently high biomasses was identified as the key mechanism explaining the positive diversity–productivity relationship (Allan et al., 2011). However, the vast majority of published relationships between plant species diversity and ecosystem functions are derived from experimental (randomly assembled) communities, and so generalizing to freely assembled plant communities can always be questioned (Isbell et al., 2009; Tilman et al., 2012).

Independent of environmental factors, plant species diversity may influence the growing season of vegetation stands according to two principal, non–exclusive, developmental scenarios (e.g., Cardinale et al., 2007): functional selection (the selection effect) and functional complementarity (the complementarity effect). Plant communities sheltering species with extended growth periods may show a growing season at least as long as the dominant species' phenology (functional selection; Fig. 1a). Alternatively, communities composed of plants with complementary growth phenologies may display a longer growing season because of species turnover and replacement over time (functional complementarity; Fig. 1b). In both scenarios, reducing plant species diversity would reduce growing season length, unless monospecific communities are systematically dominated by plant species with extended growth phenologies.

In farmlands, riparian buffers are transition zones of vegetation established along drainage ditches, rivers, lakes and other wetlands to mitigate the impact of agricultural practices on aquatic ecosystems. Some ecosystem functions provided by riparian buffers include reducing the nutrient (Hickey and Doran, 2004), herbicide (Arora et al., 1996) and sediment loads (Yuan et al., 2009) to aquatic ecosystems, as well as regulating flooding events and riverbank erosion (Naiman and Décamps, 1997). Riparian buffers cover only a small fraction of the territory, and yet they represent areas of high primary productivity that are also used as dispersion corridors and refuges by many plant and animal species (Naiman and Décamps, 1997; Naiman et al., 1993).

The objective of this study was to evaluate whether plant species richness prolongs the active photosynthetic period length (APPL) of freely assembled riparian herbaceous communities, independent of other environmental factors. If functional complementarity among plant species regulates the relationship, we predict that the APPL of riparian herbaceous communities should correlate positively with beta diversity (species turnover) but not alpha diversity (mean species number). If functional selection is the leading scenario, we predict that the APPL of herbaceous communities should correlate positively with alpha diversity but not beta diversity. A third possibility is that the two scenarios are at play; that is the APPL correlates positively with both alpha and beta diversity.

2. Methods

2.1. Experimental design

The study was conducted in the floodplain of the St-Lawrence River near Berthierville, Québec (Canada) and is composed of two sampling years, 2012 and 2013. The floodplain is flooded annually in spring and dominated by agricultural activities. This region is characterized by a growing season varying in length from 100 to 201 days (110 to 125 days without freezing events) and annual precipitation ranges from 825 to 975 mm (Gouvernement du Québec, 2002).

In 2011, we conducted a stratified selection of 13 riparian herbaceous buffers along a gradient of varying plant species richness. All riparian buffers were at least 4 m wide and located next to cultivated fields. In each riparian buffer, we selected two herbaceous communities for a total of 26 communities (Table 1).

In 2012 and at peak production (July 18–20), we harvested the aboveground biomass of half of the communities to stimulate species turnover (beta diversity) and further comparison of our results with those from biodiversity experiments of managed (harvested) grasslands (Fig. 2).

2.2. Biotic and abiotic environmental factors

On July 18–20, 2012, we assessed the aboveground dry biomass of all communities. To not interfere with our measures of the growing season, we clipped aerial plant tissues at 5 cm above the ground in one small 25×25 cm quadrat. We collected one biomass sample per community. We oven dried the samples at 72 °C for 48 h to obtain estimates of dry biomass (Table 1).

In each riparian buffer we measured the ground water depth using a piezometer. Each piezometer consisted of one 150 cm long plastic pipe perforated with 0.2 cm diameter holes at fixed intervals. We buried the piezometers in the soil at depths ranging from 80 to 114 cm depending on the substrate (Faulkner et al., 1989). Every two weeks throughout the growing season we monitored the ground water depth by measuring the water line depth on a wooden stick. Depth measures were corrected to account for the volume of water displaced by the wooden stick. We then averaged ground water depths across the growing season (Table 1).

To determine clay content of each riparian buffer we pooled three soil cores taken from the first 0–10 cm layer. We analyzed the soil granulometry using the standard method of the Centre d'expertise en analyse environnementale du Québec (2010). We oven dried the soil samples at 105 °C for 24 h (VWR model 1330, West Chester, PA) and sieved (2 mm) them to remove coarser particles. We digested the soil organic matter with 20 ml of hydrogen peroxide 30% and dried the samples at 105 °C for an
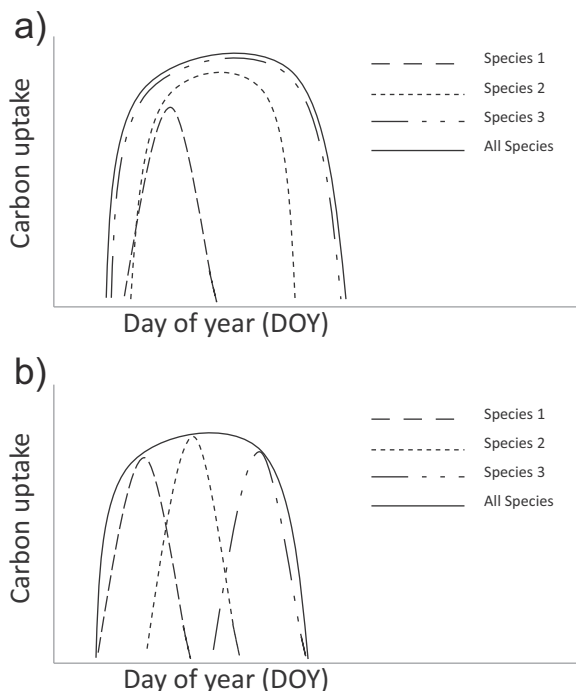
Fig. 1. Schematic representation (a) functional selection and (b) functional complementarity scenarios to the active photosynthetic period (APPL) of herbaceous communities. The APPL of each individual species in the community (all species) is represented by a different curve.