J. For. Res. (2020) 31(2):365–374
https://doi.org/10.1007/s11676-019-00946-5

ORIGINAL PAPER

Effects of climate and forest age on the ecosystem carbon exchange of afforestation

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Received: 25 October 2018 / Accepted: 12 March 2019 / Published online: 22 April 2019

Abstract Afforestation is believed to be an effective practice to reduce global warming by sequestering large amounts of carbon in plant biomass and soil. However, the factors that determine the rate of carbon sequestration with afforestation are still poorly understood. We analyzed ecosystem carbon exchange after afforestation based on eddy covariance measurements with the aim to identify factors responsible for the rate of carbon exchange following afforestation. The results indicated that afforestation in the tropical/subtropical and temperate climate zones had greater capacities for carbon sequestration than those in boreal zones. Net ecosystem production (NEP), gross primary production (GPP) and ecosystem respiration (RE) varied greatly with age groups over time. Specifically, NEP was initially less than zero in the < 10 year group and then increased to its peak in the 10–20 year group. Afforestation of varied previous land use types and planting of diverse tree species did not result in different carbon fluxes. The general linear model showed that climate zone and age of afforestation were the dominant factors influencing carbon sequestration. These factors jointly controlled 51%, 61% and 63% of the variation in NEP, GPP and RE, respectively. Compared to the strong regulation of climate on GPP and RE, NEP showed greater sensitivity to the age of afforestation. These results increase our understanding of the variation in ecosystem carbon exchange of afforestation and suggest that afforestation in subtropical and temperate areas after 20 years would yield greater carbon sink benefits than would afforestation of boreal regions.

Keywords Afforestation · Carbon sequestration · Eddy covariance · Climate · Age

Project funding: The work was supported by the National Natural Science Foundation of China (Nos. 31600347 and 41501381), National Key Research and Development Program of China (No. 2016YFA0600103), and International Partnership Program of Chinese Academy of Sciences (No. 121311KYSB20170004).

The online version is available at http://www.springerlink.com

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Introduction

Afforestation is defined as planting trees on land that was previously treeless for at least 50 years (Berthrong et al. 2009) and has been posited as an effective approach to sequester carbon (C) and mitigate global warming (Wright et al. 2000; Metz et al. 2007; Lal 2008). Globally, the area of afforestation has increased rapidly at a rate of 4 million hectares per year during recent decades (FAO 2017). By 2015, the global afforestation area reached 293 million hectares (FAO 2017). Understanding the magnitude of carbon sequestration and the related controlling factors of such extensive afforestation is of great importance for policy making in relation to global climate mitigation.

Afforestation greatly affects ecosystem C dynamics by altering land cover, C input and turnover, and thus impacts C sequestration and loss (Guo and Gifford 2002; Laganière et al. 2010; Li et al. 2012). It is believed that afforestation has a great potential to store C through plant biomass and soil C accumulation (Jandl et al. 2007). Plantations with perennial vegetations usually result in higher plant biomass and longer rotations. On the other hand, the presence of vegetations can ameliorate adverse microclimatic conditions and enhance physical structure of habitats, reduce erosion and nutrient leaching, and thus enhance C storage (Six et al. 2000). Changes in C storage are directly regulated by the balance of C input and output fluxes (Laganière et al. 2010). To maximize the C sink capacity of afforested areas, it is imperative to understand the mechanisms involved in controlling carbon fluxes after afforestation.

However, the effects of afforestation on C exchange and the related influencing factors remain unclear. Contrasting reports have suggested that afforestation produces a strong carbon sink (Wolf et al. 2011; Tong et al. 2012), is carbon neutral (Lohila et al. 2007; Don et al. 2009), or produces a strong carbon source (Cai et al. 2011). Wolf et al. (2011) reported that substantial amounts of C were sequestered by areas that underwent afforestation compared to adjacent pastures. In contrast, Cai et al. (2011) reported net release of 630 g C m^{-2} over 5 years from afforestation with hybrid poplar. These inconsistent results possibly result from the fact that the magnitude and direction of C exchange are affected by multiple factors, including climate, past land use type, tree species planted, and age of afforestation (Paul et al. 2002; Laganière et al. 2010). However, how these factors affect C exchange of afforestation are not well understood.

In the present study, we compiled a database of ecosystem C exchange based on the eddy covariance technique to address the questions of how fast C can be sequestered in afforested ecosystems and what factors affect this rate. A series of potential controlling factors that influence carbon exchange following afforestation were selected and analyzed, including climate zones, past land use types, tree species planted and age of afforestation. We hypothesized that carbon exchange would be affected by climate and age of afforestation.

Materials and methods

Data collection

We compiled data relevant to ecosystem carbon exchange after afforestation from articles that were published before 2019. We performed the literature searches in the ISI Web of Science and China National Knowledge Infrastructure (CNKI) based on the keywords 'afforestation', 'afforest', 'carbon flux', 'carbon sequestration', and 'carbon exchange'. To increase the comparability of data, the following criteria were used to select publications: the carbon flux data should be uniformly measured by eddy covariance techniques (e.g., LI-7200, LI-7500); the ecosystem carbon fluxes following afforestation should be continuously observed for at least one full year. In addition, only sites with specified afforestation practices and clear afforestation time schedules were considered. The studies with ambiguous previous land uses or reforestation programs were excluded from this study. In total, 20 independent flux sites of afforestation were finally selected for our analysis (Table 1).

For each paper, the carbon exchange between ecosystems and the atmosphere, including gross primary production (GPP), ecosystem respiration (RE), and net ecosystem production (NEP) were compiled. In addition, we compiled detailed site information, including data source, site location, latitude, longitude, elevation, soil type, climate zone, mean annual temperature, mean annual precipitation, tree species, previous land use type, and year of afforestation. The dataset contained studies of afforestation ranging from tropical/subtropical and temperate to boreal zones. The planted tree species of afforestation were grouped into broadleaf, pine and spruce. Land use types prior to afforestation were farmland, pasture, and grassland. The years since afforestation were divided into four groups, viz. < 10, 10–20, 20–40, and $>$ 40 years. Detailed information for each study site is listed in Table 1.

Data analysis

The afforestation dataset was classified into different categories in terms of climate zone, age of afforestation, previous land use type and tree species planted. For each category, the mean and standard errors were calculated. One-way analysis of variance (ANOVA) was first used to compare mean carbon fluxes for each category (uncorrected effect). To account for confounding interactive influences among categories, we used analysis of covariance (ANCOVA) to investigate the net effect of one variable by excluding the variation of other variables (corrected effect). Specifically, to test the effect of climate zone (three levels) on carbon fluxes, climate zone was included as the fixed factor with age of afforestation, previous land use type (three levels) and tree species planted (three levels) as covariates. The similar method was followed to test the effects of age of afforestation, previous land use type and tree species planted, respectively. The effects of climate factors (mean annual temperature and

Table 1 Study site descriptions

Site name	Latitude (°N)	Longitude (°E)	Climate zones	Afforest time	Previous land use type	Tree species	Year of measurement	MAT (°C)	MAP (mm)	References
Sardinilla	9.32	− 79.63	Tropical	2001	Pasture	*Luehea seemanii, Cordia alliodora*	2008	25	2071	Wolf et al. (2011)
Qianyanzhou	26.73	115.01	Subtropical	1985	Grassland	*Masson pine*	2003–2012	18.4	1488	Huang et al. (2007), Tang et al. (2016)
Yueyang	26.73	115.01	Subtropical	2000	Grassland	*Populus deltoides*	2005–2007	17.85	1954	Han (2008)
Anqing	29.53	112.86	Subtropical	1989	Grassland	*Populus deltoides*	2005–2007	17.41	1671	Han (2008)
Xiaolangdi	35.02	112.63	Temperate	1976	Grassland	*Cork oak, black locust*	2006–2010	15	524	Tong et al. (2012)
WP39-ON	42.70	− 80.40	Temperate	1939	Grassland	*White pine*	2005–2008	8.8	944	Peichl et al. (2010, 2014)
WP74-ON	42.70	− 80.40	Temperate	1974	Grassland	*White pine*	2005–2008	8.8	944	Peichl et al. (2010, 2014)
WP89-ON	42.70	− 80.40	Temperate	1989	Farmland	*White pine*	2005–2007	9.1	918	Peichl et al. (2010, 2014)
WP02-ON	42.70	− 80.40	Temperate	2002	Farmland	*White pine*	2005–2008	8.8	944	Peichl et al. (2010, 2014)
Ontario	42.71	− 80.37	Temperate	1940	Farmland	*White pine*	2003	7.8	710	Arain and Coupe (2005)
Mehrstedt	51.28	10.66	Temperate	2003	Pasture	*Broadleaf, conifer*	2004–2006	8.5	522	Don et al. (2009)
Dooary-D9	52.95	− 7.25	Temperate	1993	Pasture	*Sitka spruce*	2002	9.95	899	Black et al. (2009)
Dooary-D14	52.95	− 7.25	Temperate	1988	Pasture	*Sitka spruce*	2002	9.95	899	Black et al. (2009)
Dooary-D30	52.95	− 7.27	Temperate	1972	Pasture	*Sitka spruce*	2002	9.95	899	Black et al. (2009)
Cullenagh-C45	52.95	− 7.27	Temperate	1957	Pasture	*Sitka spruce*	2002	9.95	899	Black et al. (2009)
Alberta	53.71	− 113.63	Boreal	2009	Farmland	*Hybrid Poplar*	2010–2011	3.38	405	Jassal et al. (2013)
Ashmont	54.35	− 111.52	Boreal	1973	Farmland	*Hybrid Poplar*	2005–2009	2	349	Cai et al. (2011)
Skogaryd	58.38	12.15	Boreal	1951	Farmland	*Norway spruce*	2008	8.7	1006	Meyer et al. (2013)
Alkkia	62.18	22.78	Boreal	2005	Farmland	*Scots pine*	2003	2.2	330	Lohila et al. (2007)
Vallanes	65.19	− 14.56	Boreal	1992	Pasture	*Siberian larch*	2004–2006	6.4	502	Bjarnadottir et al. (2009)

MAT mean annual temperature, *MAP* mean annual precipitation

precipitation) on carbon sequestration of afforestation were analyzed by regression analysis with the residual regressed on age of afforestation. A general linear model (GLM) was built to further identify the individual and interactive effects of temperature, precipitation and age of afforestation. All statistical analyses were performed using SPSS 16.0 software (SPSS Inc., USA).

Results

Carbon exchange variation of afforestation by climate zone

After afforestation, ecosystems acted as carbon sinks in different climate zones (Fig. 1). However, the rate of carbon sequestration varied by climate zone. In boreal zones, afforestation resulted in near-zero NEP (34 ± 119 g C m^{-2} a^{-1}). Afforestation in tropical/subtropical zones exhibited strong carbon uptake with average NEP of over 400 g C m^{-2} a^{-1}. This was followed by temperate zones, where mean NEP was 314 ± 78 g C m^{-2} a^{-1} (Fig. 1a). After eliminating the effects of tree species, land use type, and age, NEP, GPP and RE still differed significantly by climate zone ($p = 0.07$, 0.005, 0.002 for NEP, GPP and RE respectively). GPP and RE consistently ranked in decreasing order as tropical/subtropical > temperate > boreal (Fig. 1b, c). NEP of afforestation was higher in tropical/subtropical and temperate zones than that in boreal zones (Fig. 1a).

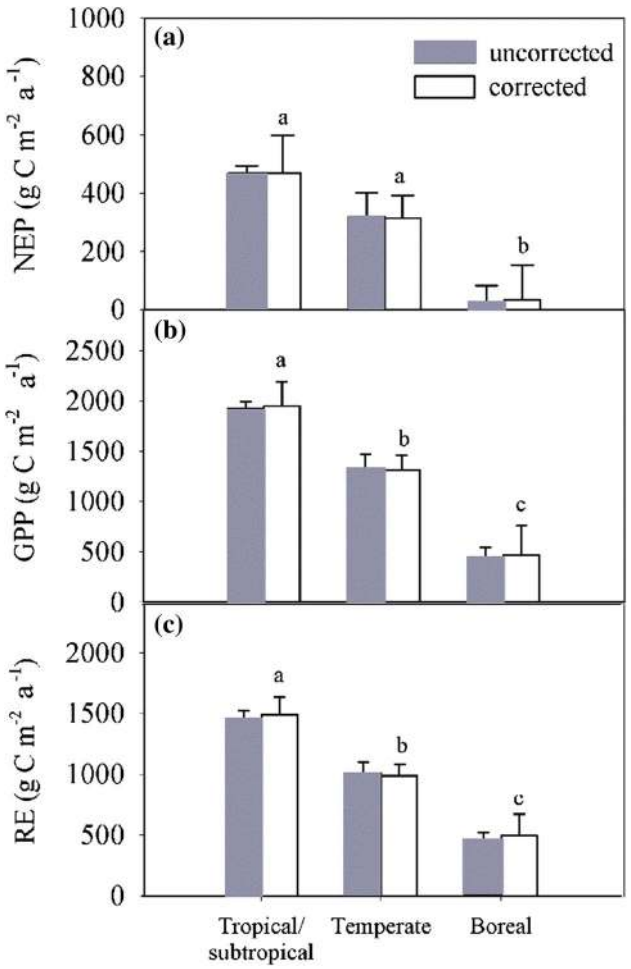

Fig. 1 Carbon exchange of afforestation in different climate zones. **a** NEP, net ecosystem production; **b** GPP, gross primary production; **c** RE, ecosystem respiration. The error bars represent standard errors. Tropical/subtropical, n = 4; Temperate, n = 11; Boreal, n = 5. Different letters above the bars indicate significant differences at the level of $p < 0.05$ for GPP and RE, and $p < 0.1$ for NEP

Carbon exchange variation by land use type prior to afforestation

Previous land use type did not affect rates of carbon sequestration (Fig. 2). Afforestation of grassland yielded marginally higher NEP, GPP and RE than did farmland or pasture. But after eliminating the effects of climate, tree species, and age of afforestation, grassland, farmland and pasture were similar in terms of NEP, GPP, and RE (ANCOVA) (Fig. 2).

Carbon exchange variation by afforestation tree species

The species of tree used in afforestation did not affect carbon fluxes (Fig. 3). NEP declined from spruce stands (341 ± 120 g C m^{-2} a^{-1}) to pine (267 ± 92 g C m^{-2} - a^{-1}) to broadleaf trees (219 ± 111 g C m^{-2} a^{-1}), but means were not statistically different (ANCOVA, $p > 0.05$) (Fig. 3a). Similar GPP and RE were obtained between the different tree species (ANCOVA, $p > 0.05$; Fig. 3b, c).

Carbon exchange variation by age of afforestation

Carbon fluxes varied by age of afforestation (ANCOVA, $p < 0.05$). NEP and GPP varied by age group and exhibited different dynamic patterns over time (Fig. 4). NEP was initially low at < 10 years after afforestation, peaked at 10–20 years and then decreased with increasing age of afforestation (Fig. 4a). GPP tended to increase during the initial stage, peaked at 10–20 years, and then decreased at 20–40 years. There was a slight increase in GPP at > 40 years after afforestation (Fig. 4b). The variation of RE with age of afforestation was not as significant as that of GPP, but RE followed a similar dynamic pattern. RE increased gradually at the early stage of < 20 years and then decreased at 20–40 years. Also, there was a relative increase in RE at > 40 years after afforestation (Fig. 4c).

The effects of climate factors and age on carbon exchange of afforestation

Mean annual temperature and precipitation influenced carbon flux after afforestation (Fig. 5). After detrending the effects of age of afforestation, NEP increased significantly with mean annual temperature ($R^2 = 0.27$, $p < 0.001$) and

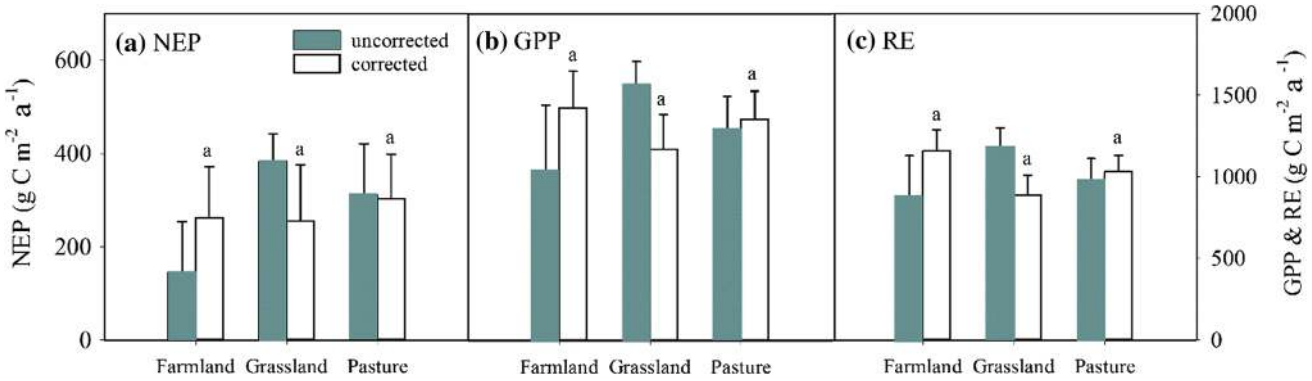

Fig. 2 Carbon exchange in different previous land use types of afforestation. **a** NEP, net ecosystem production; **b** GPP, gross primary production; **c** RE, ecosystem respiration. The error bars represent standard errors. Farmland, n = 7; Grassland, n = 6; Pasture, n = 7. Different letters above the bars indicate significant differences at the level of $p < 0.05$

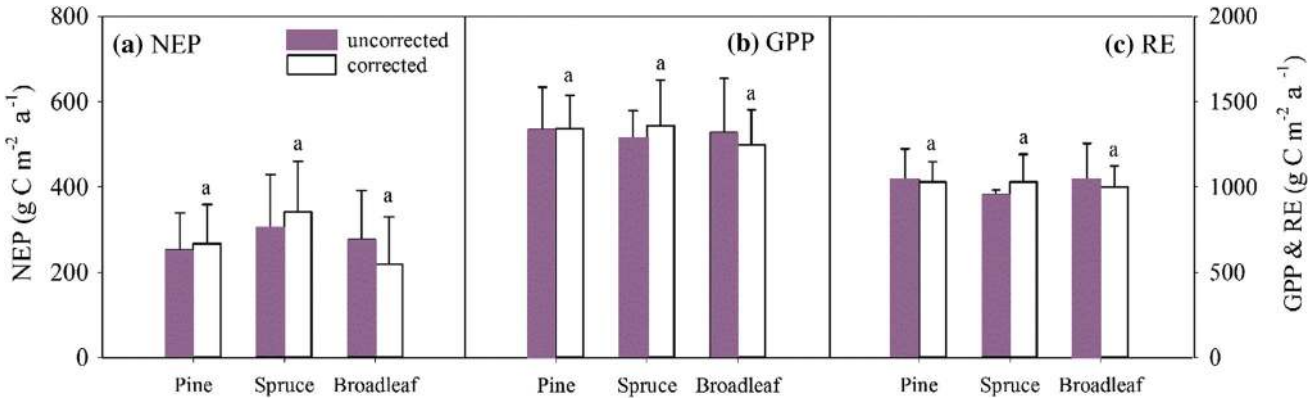

Fig. 3 Carbon sequestration with different afforested tree species. **a** NEP, net ecosystem production; **b** GPP, gross primary production; **c** RE, ecosystem respiration. The error bars represent standard errors. Pine, n = 8; Spruce, n = 5; Broadleaf, n = 7. Different letters above the bars indicate significant differences at the level of $p < 0.05$

mean annual precipitation ($R^2 = 0.31$, $p < 0.001$) (Fig. 5a, d). GPP and RE both showed linear increases with temperature (Fig. 5b, c) and precipitation (Fig. 5e, f).

Given the dominant influences of climate factors and age of afforestation, we used the developed general linear model to quantify individual and interactive effects of these factors. The results showed that climate factors, age of afforestation and their interactive effects jointly accounted for 51%, 61% and 63% of the post-afforestation variation in NEP, GPP and RE, respectively (Fig. 6). Variations of GPP and RE were primarily influenced by temperature, while NEP was more sensitive to the change of age of afforestation, which individually explained 20% of the variation in NEP (Fig. 6).

Discussion

Climate

Climate can affect carbon sequestration through processes associated with vegetation production and biological respiration. At the global scale, plant productivity and metabolic rates vary with climate (Beer et al. 2010; Bond-Lamberty and Thomson 2010). Across climate zones from tropical, temperate to boreal, there is a gradually decreasing trend in ecosystem production, respiration and net carbon sequestration (Luyssaert et al. 2007; Fernández-Martínez et al. 2014). Our results demonstrated that post-afforestation carbon exchange followed the same pattern found in natural ecosystems. NEP, GPP and RE followed the consistent decreasing order of tropical/subtropical > temperate > boreal. This suggests that afforestation in subtropical and temperate zones have greater carbon sink capacities than do boreal zones.

Climate zones are characterized by a combination of mean annual temperature and precipitation, which are

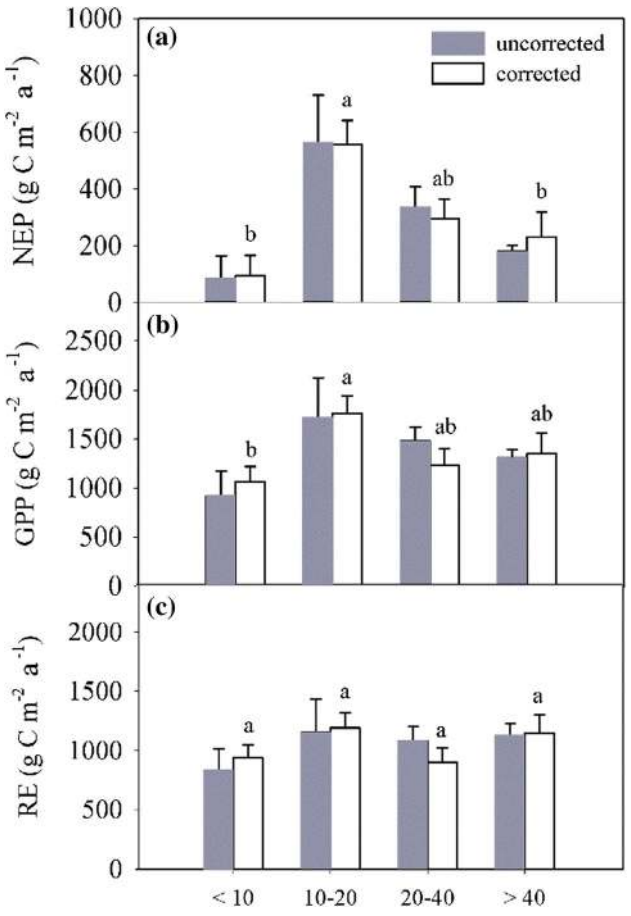

Fig. 4 Carbon exchange in different ages of afforestation. **a** NEP, net ecosystem production; **b** GPP, gross primary production; **c** RE, ecosystem respiration. The error bars represent standard errors. Age of afforestation < 10, n = 6; 10–20, n = 4; 20–40, n = 6; > 40, n = 4. Different letters above the bars indicate significant differences at the level of $p < 0.05$

factors affecting carbon exchange processes. Our results showed that NEP, GPP and RE of afforested lands all significantly increased with increasing mean annual temperature and precipitation (Fig. 5). This result adequately explains the increasing trend of carbon fluxes from cold and arid to warm and humid climate zones. Warmer temperature and greater precipitation effectively prolong the growing season length, enhance the photosynthetic capacity and microbial activity, and thus promote plant growth and respiration (Kato and Tang 2008; Chen et al. 2013). Our results also indicated that the positive climate effects were more predominant on GPP and RE than on NEP. This result confirms reports on natural ecosystems (Law et al. 2002; Chen et al. 2013). Owing to the net balance between GPP and RE, the direct regulation of climate on NEP is likely weakened by the parallel responses of production and respiration. In contrast, NEP is more sensitive to biotic factors, such as the age of afforestation, as reported by others (Law et al. 2002; Thornton et al. 2002) and documented here.

Previous land use type

Previous types of land use might affect the rate of plant and soil carbon sequestration due to the altered vegetation and soil conditions. For example, grasslands tend to accumulate soil C at faster rates than agricultural sites (Silver et al. 2000; Kukal and Bawa 2014; Liu et al. 2018). Generally, cultivated or pasture lands are characterized by low soil nutrient levels because of a depletion of organic matter inputs by human activities (Kukal and Bawa 2014; Liu et al. 2018). In contrast, natural grasslands continuously maintain vegetation cover on the soil, and can have high rates of accumulation and turnover that add organic matter from below ground to the soil (Li et al. 2012). Our results indicated that afforestation of grassland yielded higher plant production and ecosystem respiration than did afforestation of farmland or pasture. However, after factoring out the effects of climate, age and tree species, there was no significant difference in either production or respiration among grassland, farmland and pasture. This to some extent demonstrates the dominant influences of climate and age on the variation in post-afforestation carbon exchange.

Tree species planted

The planted tree species probably influence the rate of carbon exchange by their different leaf traits, photosynthetic capacities, and litterfall qualities. Many studies have documented that C sequestration in soil is strongly influenced by the species of trees planted on afforestation sites (Paul et al. 2002; Berthrong et al. 2009; Laganière et al. 2010; Li et al. 2012). Broadleaf trees tend to increase soil C sequestration while coniferous trees either have no effect or reduce soil C sequestration (Paul et al. 2002; Laganière et al. 2010). Our results showed that ecosystem carbon sequestration did not vary by tree species. This result was supported by a meta-analysis that revealed no significant differences in carbon fluxes between coniferous and broadleaf forests (Fernández-Martínez et al. 2014). Although needle-leaves generally have lower photosynthetic efficiencies and decomposition rates than broadleaves (Lusk et al. 2003), needleleaved forests have approximately 2.8 times more foliar biomass than broadleaved forests (Fernández-Martínez et al. 2014). The offsets between metabolic rate and leaf quantity probably contribute to the comparability of ecosystem carbon sequestration between coniferous and broadleaf forests.

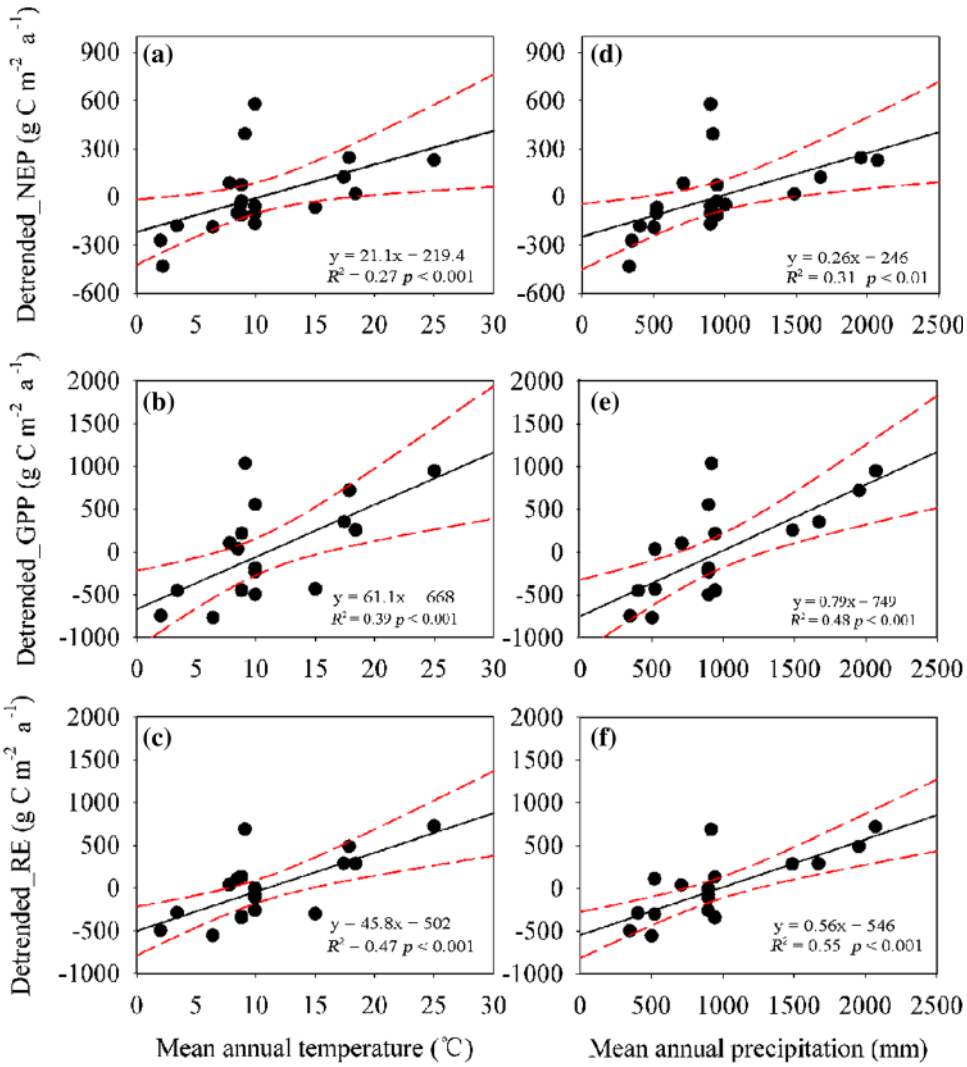

Fig. 5 Relationships between carbon fluxes (NEP, GPP, RE) and mean annual temperature (**a**–**c**) and mean annual precipitation (**d**–**f**). The red dashed lines indicate the 95% confidence intervals of the regressions

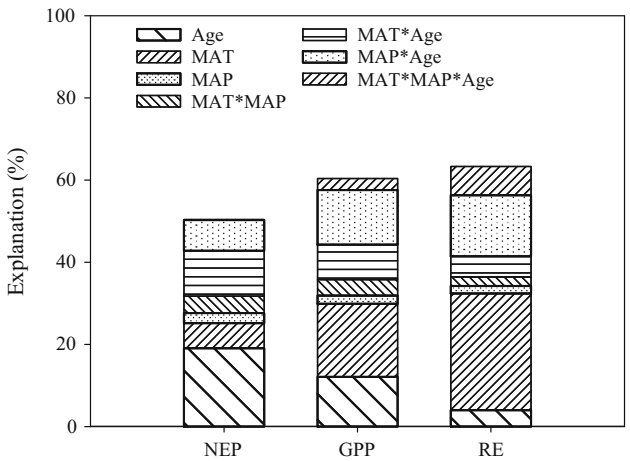

Fig. 6 Interactive effects of climate factors and age on carbon fluxes of afforestation. *MAT* mean annual temperature, *MAP* mean annual precipitation, *NEP* net ecosystem production, *GPP* gross primary production, *RE* ecosystem respiration

Age of afforestation

Age of afforestation has a significant influence on carbon exchange in afforested land. Our results showed that age of afforestation together with climate zone jointly accounted for 51% of the variation in NEP, of which 20% was attributable to age of afforestation alone (Fig. 6). NEP varied by age group (Fig. 4). At the initial stage of afforestation (< 10 years), NEP approached zero, indicating that ecosystems are generally weak carbon sources or are carbon neutral during the early stages of afforestation. NEP gradually increased and peaked during 10–20 years after afforestation, and subsequently declined. This temporal pattern of post-afforestation NEP was consistent with patterns documented for natural and secondary succession (Pregitzer and Euskirchen 2004; Goulden et al. 2011). Chronological studies indicate that forest NEP is initially negative after a disturbance; the ecosystem transitions from a carbon source to a sink at 10–20 years, peaks during the

middle stage of 20–50 years, and then declines at older stages (Pregitzer and Euskirchen 2004; Amiro et al. 2006; Goulden et al. 2011). Our results indicated that relative to natural and secondary succession, afforestation showed a quicker transition from a carbon source to a sink and exhibited an earlier peak. This quick recovery reflects the rapid growth of planted trees and acceleration of growth by human management of afforested lands (Berthrong et al. 2009).

How NEP varies with age of afforestation directly depends on the dynamic patterns of GPP and RE. Our results showed that after afforestation, GPP tended to gradually increase to its highest value at 10–20 years and then decreased. Variation in RE paralleled that of GPP. At the early stage of afforestation, ecosystems acted as weak carbon sources because GPP was constrained by the low foliar biomass, while large residuals in the ground and soil decompose rapidly under the influence of land preparation. With the rapid expansion of leaves, GPP rapidly increases and reaches its peak at the medium stage of 10–20 years. After the canopy is fully closed, GPP gradually declines with stand age (Peichl et al. 2010; Coursolle et al. 2012). Our results also demonstrated that there were slight increases in GPP and RE at the late stage of > 40 years after afforestation. These increases were attributed in part to the expanded community of understory shrubs and herbs and increased fine root turnover and root metabolism at the late stage as reported by Goulden et al. (2011). We found that afforested stands showed their most rapid carbon sequestration at 10–20 years, which suggests that management practices such as timber harvest should be carried out after 20–30 years to obtain the greatest carbon sequestration benefits.

Uncertainties

As is common in literature reviews, uncertainties might have been introduced to results due to differing observation approaches, data analysis methods, and other factors. To reduce the errors caused by varied approaches, we only assessed carbon exchange as reported based on the eddy covariance technique. Based on eddy measurement, the carbon sequestration of afforestation was estimated to be 468 ± 130, 314 ± 78, and 34 ± 119 g C m^{-2} a^{1} in tropical/subtropical, temperate and boreal zones respectively. This result is consistent with the reports of carbon budget inventories which documented average rates of uptake for afforestation in tropical, temperate and boreal zones as 400–800, 150–450, and 40–120 g C m^{-2} a^{-1}, respectively (IPCC 2000; Liu et al. 2016). However, we note that there are large variations in estimates associated with both methods, especially in tropical and boreal zones. Carbon sequestration showed high sensitivity to land use in tropical and boreal zones where there were few reported measurements (Wolf et al. 2011). In future studies, more comparative measurements in tropical and boreal areas are needed for a greater understanding of carbon balance after afforestation.

Conclusions

Ecosystem carbon sequestration after afforestation greatly varied among different climate zones, while it was weakly influenced by previous land use and tree species. Climate zone and age of afforestation were the dominant factors influencing carbon sequestration, and jointly accounted for 51–63% of the variation in NEP, GPP and RE. Compared to the dominant effect of climate on GPP and RE, NEP was more sensitive to age of afforestation. These results add to our knowledge of the variation in ecosystem carbon exchange after afforestation. To more accurately assess the carbon balance it will be necessary to conduct more studies, especially in climate-sensitive and labile areas such as tropical and boreal zones.

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