



# How do disturbances and climate effects on carbon and water fluxes differ between multi-aged and even-aged coniferous forests?

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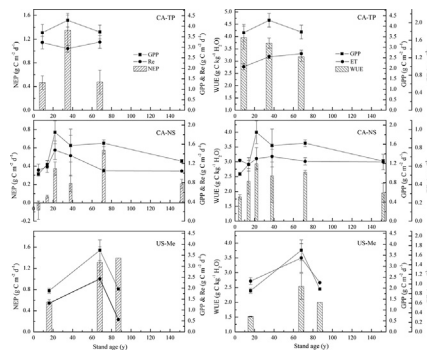
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## HIGHLIGHTS

- Recovery differences between multi- and even-aged forest chronosequences are revealed.
- Forest age determines the sign and magnitude of recovering carbon source-sink.
- Multi-aged forests sequester more CO<sub>2</sub> with time and maintained relatively higher WUE.
- Summer drought in boreal forest resulted in an increased NEP but not sustainable.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Disturbances and climatic changes significantly affect forest ecosystem productivity, water use efficiency (WUE) and carbon (C) flux dynamics. A deep understanding of terrestrial feedbacks to such effects and recovery mechanisms in forests across contrasting climatic regimes is essential to predict future regional/global C and water budgets, which are also closely related to the potential forest management decisions. However, the resilience of multi-aged and even-aged forests to disturbances has been debated for >60 years because of technical measurement constraints. Here we evaluated 62 site-years of eddy covariance measurements of net ecosystem production (NEP), evapotranspiration (ET), the estimates of gross primary productivity (GPP), ecosystem respiration ( $R_e$ ) and ecosystem-level WUE, as well as the relationships with environmental controls in three chronosequences of multi- and even-aged coniferous forests covering the Mediterranean, temperate and boreal regions. Age-specific dynamics in multi-year mean annual NEP and WUE revealed that forest age is a key variable that determines the sign and magnitude of recovering forest C source-sink strength from disturbances. However, the trends of annual NEP and WUE across successional stages between two stand structures differed substantially. The successional patterns of NEP exhibited an inverted-U trend with age at the two even-aged chronosequences, whereas NEP of the multi-aged chronosequence increased steadily through time. Meanwhile, site-level WUE of even-aged forests decreased gradually from young to mature, whereas an apparent increase occurred for the same forest age in multi-aged stands. Compared with even-aged forests, multi-aged forests sequestered more

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CO<sub>2</sub> with forest age and maintained a relatively higher WUE in the later succession periods. With regard to the available flux measurements in this study, these behaviors are independent of tree species, stand ages and climate conditions. We also found that distinctly different environmental factors controlled forest C and water fluxes under three climatic regimes. Typical weather events such as temperature anomalies or drying-wetting cycles severely affected forest functions. Particularly, a summer drought in the boreal forest resulted in an increased NEP owing to a considerable decrease in R<sub>e</sub>, but at the cost of greater water loss from deeper groundwater resources. These findings will provide important implications for forest management strategies to mitigate global climate change.

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## 1. Introduction

Terrestrial forests have been recognized as the most important carbon (C) sinks for mitigating regional and global climate change (Dixon, 1994; Pan et al., 2011). Considerable effort has been expended to study the carbon pools and fluxes of the world's tropical, temperate and boreal forests (Malhi et al., 1999; Tang et al., 2012). Despite large uncertainties in these estimates, forests in the middle-high latitudes of the Northern Hemisphere play a key role in the global carbon cycle, which also experienced apparent increases in carbon sequestration due to climate warming (Goodale et al., 2002; Piao et al., 2007; Thurner et al., 2014). However, evidence from ground observations and biogeochemical process models suggests that disturbance regimes and management practices affect the carbon balance of forests (Law et al., 2004; Amiro et al., 2010; Aguilos et al., 2014). Moreover, as a primary control of CO<sub>2</sub> exchange between terrestrial biosphere and atmosphere (Huxman et al., 2004; Wolf et al., 2013), water is receiving growing attention because future trends in water availability will severely alter the photosynthetic capacity of forests to mitigate anthropogenic CO<sub>2</sub> emissions (Sala et al., 2012; Biederman et al., 2016). Climate projections suggest a significant increase in the frequency and intensity of climate extremes, such as droughts, heatwaves, heavy precipitation events and storms (IPCC, 2011), which will profoundly affect ecological processes, such as ecosystem productivity and respiration, carbon allocation, light-use efficiency and water-use efficiency (Wolf et al., 2013; Schlesinger et al., 2015). Therefore, it is crucial to understand i) how forest disturbances affect ecosystem structure and functions including post-disturbance recovery of forest C sink strength and ii) how forest carbon dynamics respond and adapt to climate variability.

Forest structures result from a wide variety of disturbances including fire regimes, wind patterns, insect pests, and timber harvests such as selective thinning and plantation (Franklin et al., 2002; Kulakowski et al., 2011). Wildfire is one of the primary natural disturbances controlling forest age structure and species composition, shaping landscape diversity, and influencing energy flows and biogeochemical cycles (Sommers et al., 2014). Carbon emissions from wildfires in forests of the continental US are substantial, with recent estimates ranging from 13.4 Tg C/yr during 1990–1999 to 25.6 Tg C/yr for 1980–1989 (Goetz et al., 2012), whereas the average carbon sink from 1950 to 2010 is estimated at 206 Tg C/yr (Zhang et al., 2012). In the western of United States, Hicke et al. (2013) revealed that amounts of carbon in trees killed by fires and by beetle outbreaks are similar, whereas more recent analysis (Hicke et al., 2016) implied that the amount of biomass killed by fires is approximately half of that killed by beetles during 2003 to 2012. These reports emphasize that insect outbreaks can significantly affect forest carbon cycling. Clear-cutting removes the commercial stem wood but leaves residues on site, which results in a net carbon source for a long period (Palviainen et al., 2004; Chertov et al., 2009). The time of forest needs to shift from a carbon source to a carbon sink after severe disturbances can be defined as ecosystem carbon compensation point (Schulze et al., 1999), whereas the payback period represents when forest recaptures the amount of CO<sub>2</sub> emitted owing to the disturbance during the following recovery phase (Jonker et al., 2014). Approximately 7–20 years is required to reach the carbon

compensation point; a considerably longer time is needed for payback (Howard et al., 2004; Fredeen et al., 2007; Schulze et al., 2010; Coursolle et al., 2012; Dore et al., 2012). The range depends largely on whether the regeneration occurs naturally or following plantation, and optimal forest management can shorten this period (Peichl et al., 2010a; Aguilos et al., 2014; Paul-Limoges et al., 2015). The changing climate, especially extreme weather events such as frequent droughts during recent years, has severely altered biogeochemical and hydrological cycles, as well as the stability and productivity of forest ecosystems (Kolb et al., 2013; Reichstein et al., 2013; Mitchell et al., 2015). However, selective thinning has been found to reduce the adverse effects of these changes in some areas (D'Amato et al., 2013), and substantial afforestation can help offset the increasing atmospheric CO<sub>2</sub> concentration (Potter et al., 2007; Ostrom, 2014). But sometimes inappropriate afforestation such as tree species selection with large water requirements may cause severe consequences on the local/regional hydrological cycle despite that large carbon sequestration in a short period, which would be offset because of unsustainable water demand over multiple years (Monclus et al., 2006). Naudts et al. (2016) had suggested that two and a half centuries of European afforestation efforts have failed to mitigate climate warming.

Complicated disturbance histories are important drivers of forest dynamics, stand structural attributes and spatial heterogeneity; however, their potential effects remain poorly understood (Halpin and Lorimer, 2016). Forest recovery after high-severity wildfires usually regenerates toward even-aged stands, whereas a mixture of low- and high-severity fires may result in multiple regrowth processes through time, which yield multi-aged stands (Taylor and Skinner, 2003; Hessburg et al., 2007; Heyerdahl et al., 2012). The mixed-severity fires tend to regenerate forests with a mosaic of species and age classes (Halofsky et al., 2011). Within that mosaic, regeneration peaks in 3–5 years, and then there is a long tail of regeneration over the next ~15 years. Typically, managers immediately reseed forests after high-severity fires, which leads to a tighter age distribution, whereas managers tend to back-fill after moderate- and low-severity fires because ~50% of the original trees survive. Differences in the forest succession have resulted in a long debate about the relative productivity of different forest structures for alternative forest management in silviculture and forestry (Bourne, 1951; Smith and DeBald, 1978; Peng, 2000; Hanewinkel, 2002; O'Hara and Nagel, 2006; O'Hara and Ramage, 2013). Nearly all previous comparisons were based on differences in stem-volume production inferred from empirical growth models, stand growth simulations, or economic analyses. Moreover, both multi-aged and even-aged systems are highly variable in community structure, species composition and environmental conditions, which makes the indirect comparisons with accompanying assumptions rather difficult.

To evaluate whether multi-aged forests are more promising than even-aged systems for carbon sequestration and wood production after disturbances, it is necessary to examine the functional differences between these two stand structures. Currently, long-term measurements of carbon dioxide and water vapor fluxes based on the eddy covariance technique span across many forest types on Earth, providing us the feasibility to quantitatively and directly evaluate the potential impact of natural and human disturbances as well as extreme weather

events on forest carbon dynamics (Baldocchi, 2003; Law et al., 2004). However, a great number of biotic and abiotic factors jointly controlled the forest functional traits (Van Bodegom et al., 2012; Novick et al., 2015). Thus, it is inappropriate to infer the stand age-structure influence of forests from selected sites at different places (environmental heterogeneity) and tree species (differences in growth patterns, rates of photosynthesis, water use).

Compared with spatially sparse observations, flux measurements taken at forest chronosequences can provide more detailed information on succession stages after disturbance, and the recovery processes of carbon and water fluxes under the same environmental conditions. Gross primary production (GPP), ecosystem respiration ( $R_e$ ), net ecosystem production (NEP), evapotranspiration (ET) and water-use efficiency (WUE) are the main processes relevant to terrestrial carbon and water cycles. At the ecosystem level, NEP is the difference between GPP by plant photosynthesis and carbon loss through  $R_e$ , while GPP and water consumption ET are strongly coupled by WUE. To date, many studies have analyzed the age-dependent recovery of carbon sequestration in ponderosa pine forests, temperate white pine plantations and boreal stands (McMillan et al., 2008; Thomas et al., 2009; Peichl et al., 2014), but few attempts have been made to compare the recovering processes from complicated disturbances among different forest age-structures. Therefore, this study aimed i) to reveal the recovery differences of the C sink strength during forest succession between multi- and even-aged coniferous forest chronosequences that experienced various disturbance history; ii) to examine whether the multi-aged system is a promising way for alternative forest management compared to the even-aged system, and iii) to evaluate the environmental controls on forest carbon and water fluxes in boreal, temperate and Mediterranean zones.

## 2. Materials and methods

### 2.1. Site descriptions

This study was based on carbon and water flux observations in three chronosequences of multi-aged and even-aged coniferous forests under different climate and disturbance regimes. In total, data from 14 flux sites across various tree species, climate regions and recovery stages after stand-replacing fire or clear-cutting were used (Table 1). One of the two even-aged forest chronosequences included three white pine stands (CA-TP) in southern Ontario, Canada, while the other one consisted of six black spruce dominated sites (CA-NS) in northern Manitoba, Canada. The most notable distinction between these two chronosequences is the mechanism of regeneration. CA-TP stands are plantations on cleared oak-savannah land/former agricultural fields, whereas CA-NS stands are natural secondary forests suffering from severe wildfires. The multi-aged ponderosa pine chronosequence (US-Me) encompassed three sites located in the semi-arid region of central Oregon, USA, which generally experienced complicated disturbance histories and stand dynamics. In addition, data from two even-aged ponderosa pine sites (US-Me3 and US-Me6) in the neighboring region were used to further distinguish the differences in carbon sequestration potential and water-use efficiency between the multi-aged and even-aged forest stand structures.

Climatic conditions at the three forest chronosequences cover the Mediterranean, temperate and boreal zones of North America, which are similar for individual chronosequence because of the close proximity of their respective sites. The even-aged CA-TP sites are an age-sequence (young, intermediate and mature) of three white pine (*Pinus strobus* L.) afforestation stands which are part of the Turkey Point Flux Station located on the north shore of Lake Erie. The region has a temperate climate with multi-year mean annual temperature of 8.1 °C and annual precipitation of 1036 mm mainly from May to September (Peichl et al., 2014). The two older forests were planted in 1939 (CA-TP4) and 1974 (CA-TP3) on cleared oak-savannah land,

whereas the younger stand was established on former agricultural lands in 2002 (CA-TP1) (Peichl and Arain, 2006). All three sites have generally similar soil conditions with little organic matter, low-to-moderate water holding capacity, and sandy to loamy sand soil texture.

The chronosequence of CA-NS stands are representative growth stages of secondary succession after large stand-replacing fires. These sites are located in the Boreal Ecosystem–Atmosphere Study Northern Study Area (Sellers et al., 1997). All stands are even-aged and resulted from stand-killing wildfires that occurred in ~1850, ~1930, 1964, 1981, 1989 and 1998 (Goulden et al., 2006; McMillan et al., 2008; Goulden et al., 2011). The youngest CA-NS7 is dominated by black spruce (*Picea mariana* Mill.) saplings ~0.2 m tall with a thick understory of herbaceous and ruderal species. The CA-NS6 site comprises small black spruce, jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.). Most fire-killed black spruce trees fell from 2000 to 2005. The medium-aged stand (CA-NS3) is dominated by black spruce trees (~54%), whereas the other tree species including jack pine (~28%) and aspen (15%) are experiencing significant mortality and thinning. The older stands (CA-NS2 and CA-NS1) are closed-canopy black spruce forests with a well-developed moss layer, comprising sphagnum (*Sphagnum* spp.) and feather moss (*Hylocomium splendens*). For Manitoba, the multi-year mean annual temperature and precipitation are  $-3.2$  °C and 536 mm, respectively. The terrain of this region is generally flat, with soils developed from glacial Lake Agassiz sediments with underlying permafrost.

Multi-aged forests usually have two or more age classes as the result of partial natural and anthropogenic disturbances. The ponderosa pine (*Pinus ponderosa* Doug. Ex P. Laws.) sites—US-Me are part of the Terrestrial Ecosystems Research & Regional Analysis project with different disturbance classes. The young pine stand (US-Me5) regenerated naturally following logging in 1978. Both the dominant deciduous understory species—antelope bitterbrush and the sole coniferous overstory species—ponderosa pine reach the maximum leaf area during later summer months (Irvine et al., 2004). Following a stand replacement disturbance in the early 20th century, the US-Me2 forest was allowed to regenerate naturally, resulting in a maximum stand age of 97 years recorded in 2012 (Thomas et al., 2009). It comprises almost exclusively ponderosa pine, with a few scattered incense cedar (*Calocedrus decurrens* (Torr.) Florin). The old US-Me4 pine site consists of ~48% mixed age (~87 years), ~27% old growth (~156 years) and ~25% young aged (~54 years) stands (Vickers et al., 2012). The old-growth component has remained unchanged since the 1748 fire that caused a 100% stand replacement; in 1854, a fire led to a 50% stand replacement and then, the youngest trees are the result of a 50% replacement fire in 1944. To understand the influence of changes in forest age structure on the land-surface exchanges of carbon and water with the atmosphere, two even-aged young ponderosa pine forests were also included for comparison with the multi-aged ponderosa stands. The US-Me3 site is a 3-m-tall stand with seasonal grass understory which was clear-cut and replanted by the US Forest Service in 1987 (Vickers et al., 2012), while the US-Me6 stand is dominated by an ~23-year old ponderosa pine plantation with an average height of 5.2 m after a severe fire during the late 1990s (Ruehr et al., 2012). The climate of this region is Mediterranean with hot dry summers, and cool wet springs and winters, with precipitation mainly falling as rain and occasionally as snow. The long-term annual mean precipitation is 460 mm, with monthly minimum and maximum temperatures ranges of  $-5.5$  °C– $10.5$  °C during winter and  $2.5$  °C– $27.8$  °C during summer.

### 2.2. Data acquisition and processing

Continuous measurements of ecosystem  $\text{CO}_2$ , water vapor, and energy exchanges relying on the eddy covariance technique, have generated ecosystem-scale latent heat flux (LE), net ecosystem exchange (NEE), and the estimates of GPP and  $R_e$  derived from the measured NEE at half-hour, daily, weekly, and monthly time scales. Meanwhile, the

**Table 1**  
Main characteristics of the three series of multi-aged and even-aged coniferous forest sites in this study.

Disturbance type	Climate	Site name	Latitude (°)	Longitude (°)	Elevation (m)	MAT (°C)	MAP (mm)	Dominant species	Age category	Stand age (yr)	Canopy height (m)	Available data	Reference
Even-aged plantation after clear-cutting	Warm summer Temperate	CA-TP1	42.6609	−80.5595	265	8.9	1098	White pine	Young	~8	~3.6	2009–2013	Peichl et al. (2014)
		CA-TP3	42.7068	−80.3483	184	9.1	1100	White pine	Intermediate	~34	~13.5	2009–2013	Peichl et al. (2010a)
		CA-TP4	42.7098	−80.3574	184	8.6	1090	White pine	Mature	~63	~22.5	2003–2013	Peichl and Arain (2006); Peichl et al. (2010b)
Even-aged secondary forest after stand-replacing fire	Continental Boreal	CA-NS7	56.6358	−99.9483	297	−2.1	310	Black spruce	Seedling	~4	~0.2	2003–2005	Goulden et al. (2006)
		CA-NS6	55.9167	−98.9644	244	−1.8	237	Black spruce	Young	~13	~1.5	2002–2005	McMillan et al. (2008)
		CA-NS5	55.8631	−98.4850	254	−2.5	211	Black spruce		~21	~4.5	2002–2005	Goulden et al. (2011)
		CA-NS3	55.9117	−98.3822	258	−3.4	280	Black spruce	Intermediate	~38	~5.5	2002–2005	McMillan et al. (2008)
		CA-NS2	55.9058	−98.5247	257	0.9	256	Black spruce	Mature	~72	~14	2002–2003	Goulden et al. (2006)
		CA-NS1	55.8792	−98.4839	253	1.2	240	Black spruce	Old-growth	~152	~17.2	2003–2005	Goulden et al. (2011)
Multi-aged secondary forest after several disturbances	Dry summer Mediterranean	US-Me5	44.4372	−121.5668	1188	7.6	400	Ponderosa pine	Young	~16; 22 (max.)	~4.3	2001–2002	Irvine et al. (2004)
		US-Me2	44.4523	−121.5572	1255	7.3	580	Ponderosa pine	Intermediate	~64; 97 (max.) ~156 (old-age);	~22	2002–2012	Thomas et al. (2009)
		US-Me4	44.4992	−121.6224	922	8.3	641	Ponderosa pine	Mature	~87 (mixed-age); ~54 (youngest)	~32.6	2000	Vickers et al. (2012)
Even-aged plantation after clear-cutting/severe fire		US-Me3	44.3154	−121.6078	1005	8.5	423	Ponderosa pine	Young	~17	~3.1	2004–2008	Vickers et al. (2012)
		US-Me6	44.3232	−121.6043	977	7.5	460	Ponderosa pine		~23	~5.2	2013–2014	Ruehr et al. (2012)

Note: Three even-aged white pine flux towers are located in Ontario, Canada and six even-aged black spruce flux sites are placed in Manitoba, Canada. Three multi-aged ponderosa pine flux towers are in Oregon, USA and additional two even-aged US-Me3 and US-Me6 sites are used for comparison. Mean annual temperature (MAT) and precipitation (MAP) are the average values during the measurement periods. "max." refers to the maximum stand age.

relevant environmental variables including solar radiation ( $R_g$ ), air temperature ( $T_a$ ), soil temperature/moisture ( $T_s$ /SWC), relative humidity (used to calculate vapor pressure deficit–VPD) and natural precipitation ( $P$ ) are measured by a suite of standard meteorological instruments (Peichl and Arain, 2006; McMillan et al., 2008; Vickers et al., 2012).

This study used 14 even-aged and multi-aged coniferous forest sites with a total of 62 site-year dataset (Table 1). Each site has a tower instrumented for eddy covariance flux and meteorological measurements. Flux measurement systems are comprised of three-axis sonic anemometers measuring wind speed, wind direction and virtual temperature, and infrared gas analyzers measuring water vapor and  $CO_2$  concentrations. A wide range of different software programs (EddyRe developed by the University of Edinburgh, UK) are used for real-time and post-processing analysis (Goulden et al., 2006; Peichl et al., 2010a). Data collection and regular calibrations of tower-based flux measurements followed the description by Ruehr et al. (2012). The data are quality-checked, and data gaps due to system failure or data rejection are gap-filled using standardized methods (Falge et al., 2001; Papale et al., 2006) to obtain complete and standardized data sets. The measured NEE data were partitioned into two main components GPP and  $R_e$  by nonlinear regressions with air/soil temperature (Desai et al., 2008). In this study, the night-time based flux-partitioning algorithm proposed by Reichstein et al. (2005) was applied for separation. This method derives a short-term temperature response of  $R_e$  from eddy covariance data based on the Lloyd and Taylor (1994) regression model and then applies this relationship to the extrapolation from night-time to daytime  $R_e$ . Eventually, this algorithm yields less biased estimates of GPP and  $R_e$ . The good performance of this partitioning methodology was also validated by Stoy et al. (2006). Meanwhile, the missing values can be gap-filled because of the covariance between flux measurements and meteorological driving factors. To maintain consistency across multiple sites, we used the daily integrated level 2 flux measurements and the associated meteorological data downloaded from the AmeriFlux Site and Data Exploration System (<http://ameriflux.ornl.gov/>).

NEE is defined as the measured  $CO_2$  flux between the biosphere and the atmosphere when using the eddy-covariance method. A negative NEE value indicates net C uptake; by contrast, a negative net ecosystem production (NEP) value indicates C loss from the ecosystem (Turner et al., 2011). In this study, the positive NEP values represent carbon sink. NEP can be quantified as the difference of GPP and  $R_e$ .

$$NEP = GPP - R_e \quad (1)$$

At ecosystem level, forest WUE is generally defined as (Hu et al., 2008; Beer et al., 2009; Niu et al., 2011):

$$WUE = GPP/ET \quad (2)$$

where ET is evapotranspiration ( $mm\ d^{-1}$ ). We used the daily WUE ( $g\ C\ kg^{-1}\ H_2O$ ) to reflect the seasonal dynamics of even-aged and multi-aged stand responses to disturbances and climate variability. Considering only days with active photosynthetic activity during the growing season, we applied a filter to exclude daily GPP and ET values when mean daily latent heat flux ( $LE$ )  $< 20\ W/m^2$ , global radiation ( $R_g$ )  $< 150\ W/m^2$  and mean  $T_a < 0\ ^\circ C$  (Kuglitsch et al., 2008). ET was inferred from the observed LE as:

$$ET = LE/\lambda \quad (3)$$

where  $\lambda$  is the amount of energy required to evaporate per unit mass of liquid water to vapor (approximately  $2,454,000\ J/kg$ ) (Alavi et al., 2006; Tang et al., 2015). Meanwhile, annual mean WUE can be characterized as the slope of linear regression between daily GPP and daily ET during one site-year, which represents the general capacity of a particular ecosystem (Wolf et al., 2013; Huang et al., 2015).

### 2.3. Research framework

To determine the difference between the capacity of multi-aged and even-aged forests to sequester atmospheric  $CO_2$  during forest regeneration, we collected and analyzed 55 site-year flux and climate data from two even-aged chronosequences of white pine and black spruce, and one multi-aged ponderosa pine chorosequence. Despite the growing availability of flux measurements, additional data were not obtained for chronosequences of multi- and even-aged forest sites with similar characteristics regarding tree species, age structure, climate regions and disturbance histories. Here, we therefore limited our analysis to the general age-dependent trends in ecosystem C and water fluxes between two stand structures. By employing two additional even-aged ponderosa pine sites in the adjacent region (US-Me3 and US-Me6), the biogeochemical processes including ecosystem GPP,  $R_e$ , NEP, ET and WUE were compared with multi-aged US-Me5 under the same conditions. Together with the age-dependent trend analysis, functional differences between multi- and even-aged forests were inferred throughout the successional stages. Finally, we evaluated the effects of environmental controls on forest C and water fluxes across climate zones. Fig. 1 briefly described the framework of this study. The main statistical analyses including multi-year mean annual GPP,  $R_e$ , NEP, ET and WUE values as well as the correlations between them and the associated climate factors were completed with IBM SPSS Statistics 19. Pearson correlation analysis was performed to detect the dominant environmental factors that determine the variability in NEP and WUE.

## 3. Results

### 3.1. Age-related variations in land-atmosphere carbon and water fluxes during succession

The age-specific patterns in multi-year mean annual carbon and water fluxes from the two even-aged (CA-TP and CA-NS) and one multi-aged (US-Me) coniferous forest chronosequence sites exhibited large changes in magnitude (Fig. 2 and Table 2). In general, GPP underwent a rapid increase in the early successional stages, followed by a gradual decrease in the later succession periods. However, the time of maximum GPP for three clusters differed apparently. GPP of the even-aged forests reached peak earlier than that of multi-aged US-Me sites.  $R_e$  generally covaried consistently with the dynamics of GPP, but was also affected by the disturbance history particularly during the early recovery. For the young secondary forests (CA-NS) after stand-replacing fire, compared with limited GPP by plant photosynthesis, larger  $R_e$  at CA-NS7 can be ascribed to severe heterotrophic respiration derived from decayed woody debris. The successional patterns of annual NEP exhibited an inverted-U trend at the even-aged CA-TP and CA-NS sites, whereas NEP increased steadily throughout the succession stages for US-Me chronosequence. It implied that forest structure with multiple age-classes can persist a strong carbon uptake even when the forest is mature. Although GPP decreased considerably during this period, ecosystem  $R_e$  also had a large reduction. It is noteworthy that NEP shifted from a carbon source ( $-0.08 \pm 0.10\ g\ C\ m^{-2}\ d^{-1}$ ) at ~5-year-old CA-NS7 to a weak carbon sink ( $0.07 \pm 0.02\ g\ C\ m^{-2}\ d^{-1}$ ) at ~14-year-old CA-NS6 site, and the fire-disturbed forest needs a long time to recover the carbon sequestration potential prior to the disturbance. This study indicated the role from carbon source to sink occurred in about 10 years for black spruce ecosystem. In addition, Fig. 2 showed that forest age is a key ecosystem state variable in determining the sign and magnitude of the carbon and water budgets.

ET increased gradually with stand age and stayed relatively constant during the later succession stages for even-aged forests, whereas the peak ET of multi-aged US-Me sites lagged, followed by a sharp decrease. In the early regeneration periods of CA-NS forest chronosequence, relative larger ET at CA-NS7 than CA-NS6 can be explained by soil evaporation and plant transpiration that jointly determine ET but the function of

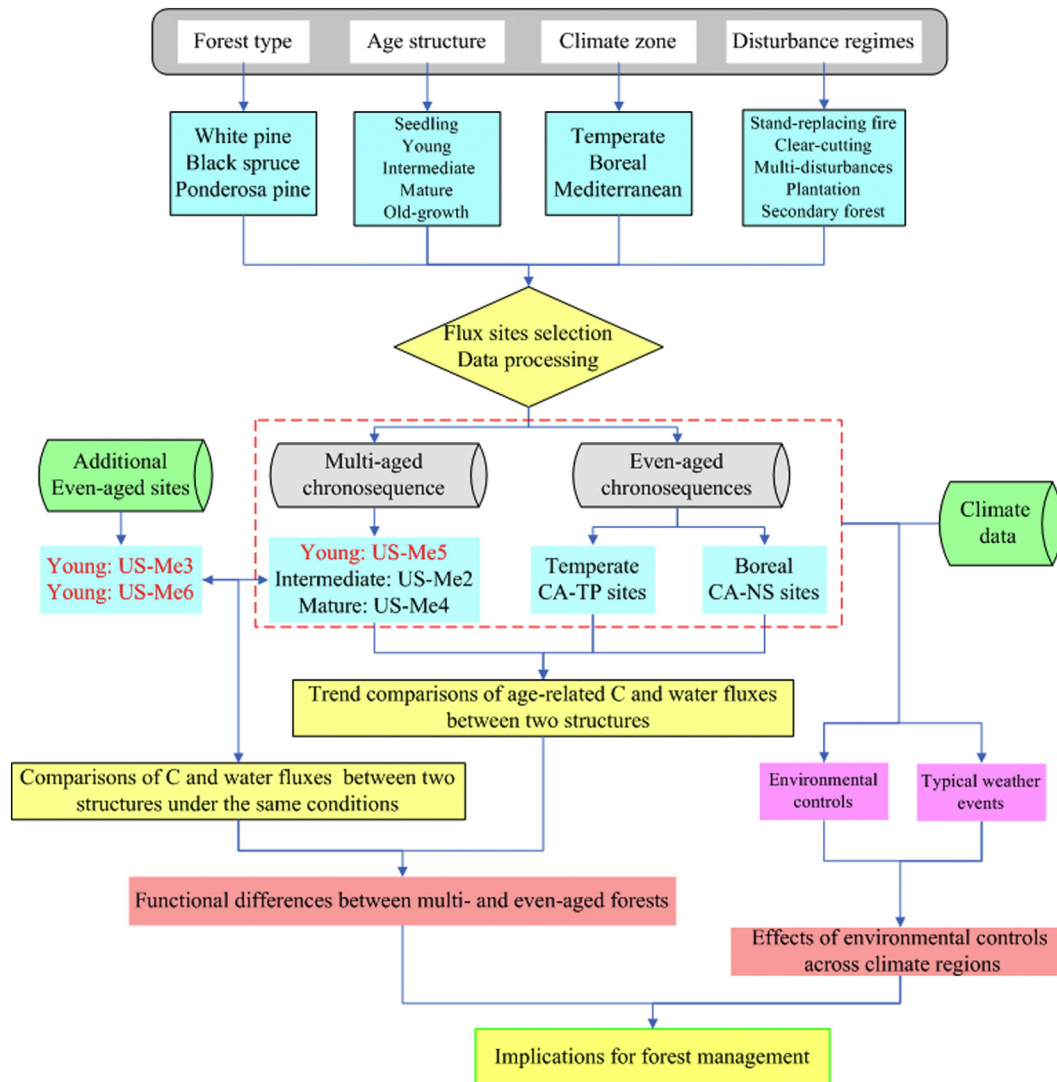


Fig. 1. Overview of the research framework.

soil decreased later. As a proxy of carbon uptake per unit of water consumption, ecosystem WUE indicated that processes controlling water loss in stands of different ages will result in dissimilar rates of carbon exchange. Site-level WUE computed from GPP and ET at the even-aged forest sites decreased gradually from young to mature developmental stages whereas WUE of multi-aged US-Me sites increased apparently during the same forest ages. Plantation after land clearing at CA-TP sites caused WUE to peak ~10 years earlier than at the secondary CA-NS forests suffering from stand-replacing fire. The behavior may be associated with the wood decay of fire-killed tree trunks, roots and branches that hinder the growth of secondary forests at the seedling stage of CA-NS chronosequence, accompanying by amounts of water consumption during decomposition processes.

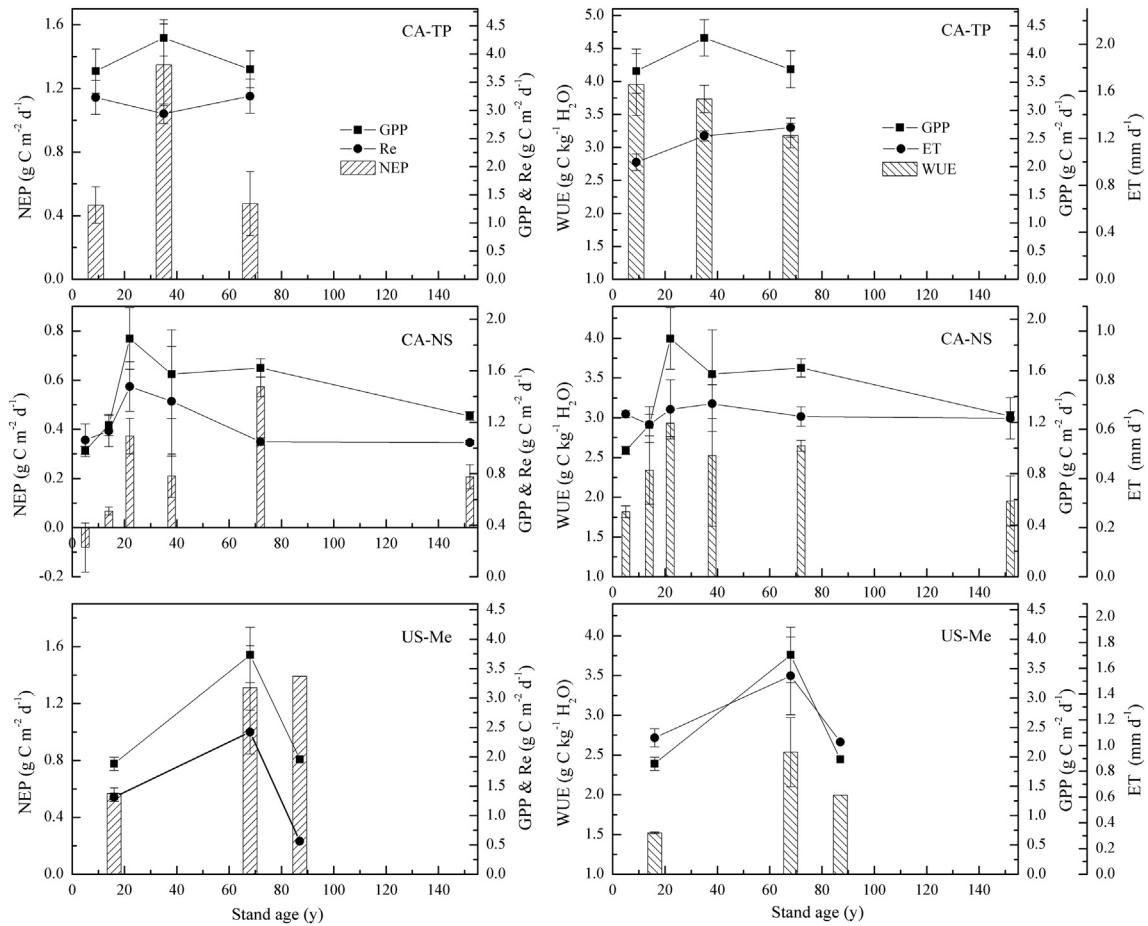
### 3.2. Functional differences between multi-aged and even-aged coniferous forests

The possible interferences from different tree species and stand ages should be excluded when comparing functional effects between multi-aged and even-aged forests. Fig. 3 presented the differences in interannual NEP and WUE among white pine (CA-TP), black spruce (CA-NS) and ponderosa pine (US-Me) with changes in stand age at three coniferous forest chronosequences. This comparison revealed that the functional traits at different stages of forest regeneration differed

apparently for the same dominant tree species. Statistical results of both NEP and WUE at these coniferous forest sites were also exhibited in Table 2. Furthermore, large variations existed in NEP and WUE at each flux site, which can be ascribed to the influence of interannual climate variability.

In addition, we selected CA-TP4, CA-NS2 and US-Me2 sites with similar stand ages for further analysis. Fig. 4 illustrated distinct differences in multi-year mean annual NEP and WUE among the white pine, black spruce and ponderosa pine ecosystems (Table 2), despite all these sites being coniferous forests. Mean NEP of CA-TP4 and CA-NS2 sites were  $0.48 \pm 0.20 \text{ g C m}^{-2} \text{ d}^{-1}$  and  $0.57 \pm 0.04 \text{ g C m}^{-2} \text{ d}^{-1}$ , which were significantly lower than US-Me2 site ( $1.31 \pm 0.29 \text{ g C m}^{-2} \text{ d}^{-1}$ ). These results revealed that ponderosa pine has the strongest carbon uptake capacity among the three tree species. However, the patterns in ecosystem WUE were contrary. Compared with the other tree species, white pine forests had the highest water-use efficiency ( $3.18 \pm 0.18 \text{ g C kg}^{-1} \text{ H}_2\text{O}$ ), whereas the WUE of black spruce and ponderosa pine were approximately equal.

However, such analyses did not account for the effect of climate regions. Actually, a series of internal and external conditions including forest type, tree species, stand age and climatic factors (spatial proximity) need to be considered for functional comparisons and alternative forest management. In this study, two even-aged (US-Me3 and US-Me6) and one multi-aged (US-Me5) ponderosa pine sites generated an optimized



**Fig. 2.** Age-specific dynamics in multi-year mean annual carbon and water fluxes as well as ecosystem water-use efficiency from chronosequences in two even-aged (CA-TP and CA-NS) and one multi-aged (US-Me) coniferous forest chronosequence. GPP,  $R_e$  and NEP represent gross primary production, ecosystem respiration and net ecosystem production, respectively; ET and WUE are ecosystem-level evapotranspiration and water-use efficiency, respectively. The sites used are listed in Table 1. Error bars represent one standard error during the measurement period of each site.

combination owing to data constraints. As shown in Fig. 5, NEP of the multi-aged US-Me5 site ( $0.57 \pm 0.04 \text{ g C m}^{-2} \text{ d}^{-1}$ ) was markedly greater than that of both even-aged forest sites. However, the large discrepancy in NEP of US-Me3 ( $0.34 \pm 0.15 \text{ g C m}^{-2} \text{ d}^{-1}$ ) and US-Me6 ( $0.20 \pm 0.05 \text{ g C m}^{-2} \text{ d}^{-1}$ ) can be partly explained by the different disturbance histories occurred in the two stands. Larger ecosystem  $R_e$  offsets

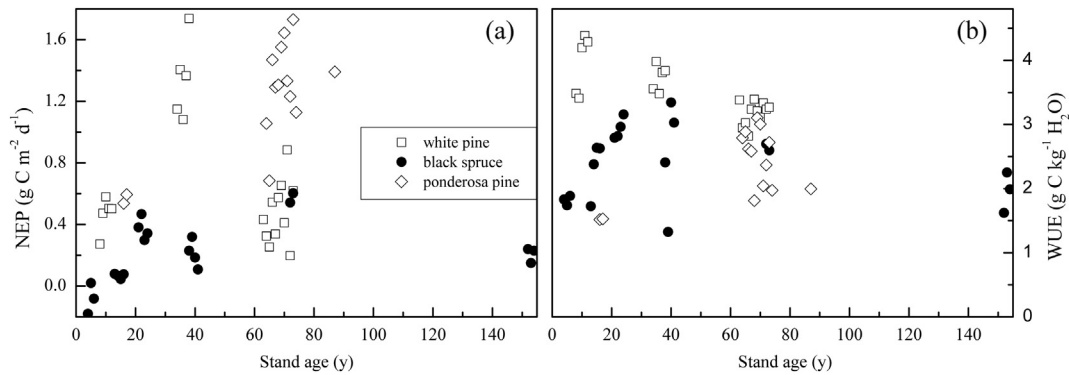
more GPP during the post-fire recovery in ponderosa pine forest (US-Me6). On the contrary, WUE of the multi-aged forest was slightly lower than that of even-aged sites (~17.7%), which was mainly ascribed to the relatively higher ET component in the multi-aged stands. Given that these findings are only based on the young ponderosa pine forest, direct extrapolation to other succession stages may be inappropriate.

**Table 2**

Statistical results of multi-year mean annual GPP,  $R_e$ , NEP, ET and WUE for all coniferous forest sites in this study.

Sites	GPP ( $\text{g C m}^{-2} \text{ d}^{-1}$ )		$R_e$ ( $\text{g C m}^{-2} \text{ d}^{-1}$ )		NEP ( $\text{g C m}^{-2} \text{ d}^{-1}$ )		ET ( $\text{mm d}^{-1}$ )		WUE ( $\text{g C kg}^{-1} \text{ H}_2\text{O}$ )	
	$\bar{\mu}$	$\sigma$	$\bar{\mu}$	$\sigma$	$\bar{\mu}$	$\sigma$	$\bar{\mu}$	$\sigma$	$\bar{\mu}$	$\sigma$
CA-TP1	3.70	0.39	3.23	0.30	0.47	0.12	1.00	0.07	3.95	0.47
CA-TP3	4.29	0.32	2.94	0.17	1.35	0.26	1.22	0.04	3.73	0.21
CA-TP4	3.73	0.33	3.25	0.30	0.48	0.20	1.29	0.08	3.18	0.18
CA-NS7	0.98	0.03	1.06	0.13	-0.08	0.10	0.66	0.01	1.82	0.07
CA-NS6	1.18	0.08	1.13	0.12	0.07	0.02	0.62	0.07	2.34	0.43
CA-NS5	1.85	0.24	1.48	0.19	0.37	0.07	0.68	0.12	2.93	0.17
CA-NS3	1.57	0.34	1.36	0.42	0.21	0.09	0.70	0.11	2.53	0.81
CA-NS2	1.62	0.07	1.05	0.03	0.57	0.04	0.65	0.04	2.65	0.07
CA-NS1	1.25	0.03	1.04	0.02	0.21	0.05	0.64	0.08	1.95	0.32
US-Me5	1.88	0.11	1.31	0.07	0.57	0.04	1.06	0.07	1.52	0.02
US-Me2	3.73	0.45	2.42	0.37	1.31	0.29	1.54	0.30	2.54	0.43
US-Me4	1.96	-	0.57	-	1.39	-	1.03	-	2.01	-
US-Me3	1.89	0.14	1.54	0.16	0.34	0.15	1.01	0.07	1.77	0.23
US-Me6	2.08	0.02	1.88	0.04	0.20	0.05	1.02	0.03	1.94	0.12

Note:  $\bar{\mu}$  and  $\sigma$  are the mean value and standard error, respectively. Positive and negative values of NEP represent carbon sink and source, respectively. “-” means data loss.



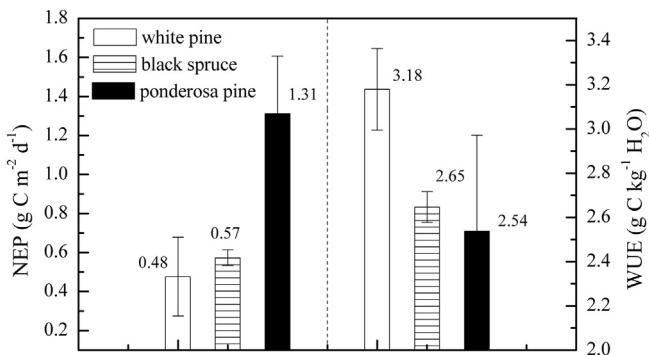
**Fig. 3.** Comparisons of interannual NEP (a) and WUE (b) of white pine (CA-TP), black spruce (CA-NS) and ponderosa pine (US-Me) with changes in stand age at the two even-aged and one multi-aged coniferous forest chronosequences. The stand age of each flux site is in Table 1.

Despite limited data availability, by means of the trend analysis between the two stand structures in Fig. 2, we conclude that multi-aged forest ecosystem can sequester more CO<sub>2</sub> with forest regeneration and maintain a relatively higher WUE in the later succession periods compared with even-aged stands, which showed a decreasing trend in WUE.

### 3.3. Environmental controls on carbon and water exchanges across climate zones

Three chronosequences of coniferous forest sites spanned the Mediterranean, temperate and boreal climate zones. Both NEP and WUE in temperate CA-TP forests were significantly and positively correlated with annual rainfall (Table 3). Moreover, a significant negative relationship was found between  $T_a$  and NEP rather than ecosystem WUE. In contrast, significantly positive relationships between NEP and  $R_g/T_a$  in boreal CA-NS sites existed, which indicated the distinct differences in the water-limited/temperature-limited forest ecosystems. However, annual P was found to be significantly negatively correlated with the interannual dynamics of NEP and WUE in Mediterranean forests (US-Me).  $T_a$  also exhibited a marginally significant negative correlation. The effects of climatic characteristics with hot, dry summers and mild, wet winters in Mediterranean zone on plant phenological stages likely resulted in these negative correlations.

This study also explored the effects of typical annual precipitation on the carbon and water fluxes of coniferous forests. Fig. 6 illustrates the responses of forest C and water exchanges to different annual P but similar  $T_a$  events in the Mediterranean US-Me2 site which possessed a long record of flux measurements. Annual mean  $T_a$  in 2006 and 2007, and 2008 and 2010 were approximately 7.5 °C and 7.0 °C, respectively. Both events indicated that larger NEP and WUE occurred in the year with less annual precipitation. However, several differences still existed.



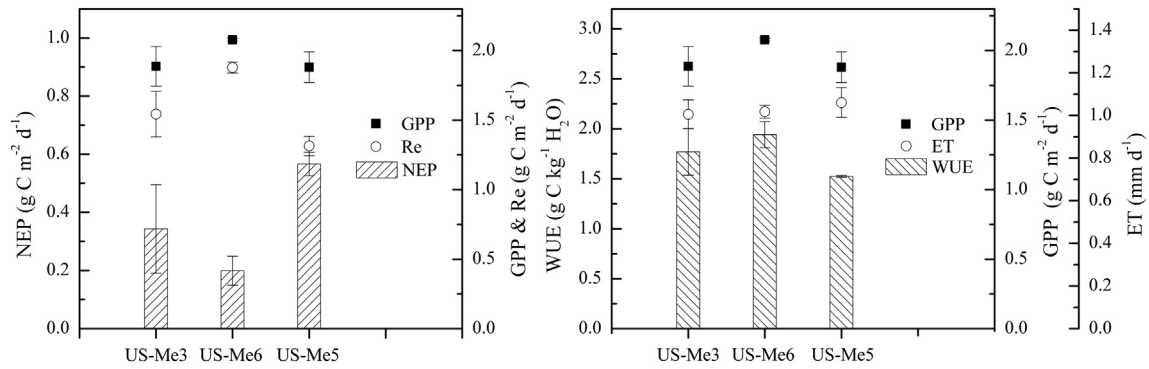
**Fig. 4.** Differences in multi-year mean annual NEP and WUE of white pine, black spruce and ponderosa pine at the similar stand age (~70 years) for CA-TP4, CA-NS2 and US-Me2, respectively. Error bars represent one standard error.

From wet year (2006) to dry year (2007), an apparent increase in GPP but a small increase in  $R_e$  resulted in a relatively large NEP, whereas GPP, together with slightly decreasing ET, gave rise to a sharp growth in WUE. Fig. 6b also demonstrated this pattern on daily time scale. However, from dry year–2008 to wet year–2010, the relatively strong NEP in 2008 was mainly resulted from a significant increase in ecosystem  $R_e$  during the period of 2010. GPP in 2008 and 2010 were estimated at 3.95 and 3.88 g C m<sup>-2</sup> d<sup>-1</sup>, respectively. Larger ET corresponded with more rainfall, which led to the large decrease in ecosystem WUE in 2010.

Despite that water availability is the dominant environmental factor that constrains the carbon sequestration in temperate coniferous forest (Table 3), the effects of annual mean temperature variability on ecosystem C and water fluxes still need further consideration, particularly under more intense, more frequent and longer-lasting heat waves observed in recent years. Fig. 7 compared the potential environmental influences on daily dynamics in GPP,  $R_e$ , ET, and annual NEP and WUE at the temperate CA-TP4 site caused by the large differences in annual mean temperature in 2009 and 2012 with 7.72 °C and 10.33 °C, respectively. In contrast to multi-year mean annual  $T_a$  of 8.6 °C, the weather in 2012 was apparently hotter whereas annual precipitations in 2009 and 2012 were very close (995 mm vs 1000 mm). Along with the larger increase in spring  $T_a$  of 2012, daily GPP,  $R_e$  and ET also increased substantially. However, as a whole, the higher temperature in 2012 did not improve the carbon fixation of the temperate forest site with only a slighter increase in GPP but much more flux enhancement in ecosystem  $R_e$ . NEP decreased from 0.65 g C m<sup>-2</sup> d<sup>-1</sup> in 2009 to 0.20 g C m<sup>-2</sup> d<sup>-1</sup> in 2012, while ecosystem WUE between the two years were similar at approximately 3.22 g C kg<sup>-1</sup> H<sub>2</sub>O.

Temperature has received much emphasis as a kinetic driver of vegetation activity, but droughts especially during the growing seasons can exert substantial influences on plant carbon uptake and water use. However, how NEE and its components GPP and  $R_e$  responded to such events remained poorly understood. Fig. 8 showed the daily patterns of GPP,  $R_e$ , ET and NEE of the boreal forest site (CA-NS3) under normal precipitation (363 mm in 2002) and during an extremely dry summer (only 30 mm in 2003). Compared to the other sites of this chronosequence with moderate reduction in precipitation, almost no rainfall fell throughout the growing period of 2003, which severely altered the seasonal dynamics of carbon and water fluxes. GPP increased quickly in the early period followed by a deep trough during the peak growth, whereas  $R_e$  maintained a low value to the end of the drought event. Both GPP and  $R_e$  covaried with the plant growth during the normal precipitation year and reached peak in the summertime. However, seasonal patterns of ET did not exhibit distinct differences between the two years. The boreal forest in the dry year 2003 even sequestered slightly more CO<sub>2</sub> (0.32 g C m<sup>-2</sup> d<sup>-1</sup>) compared to 2002 (0.23 g C m<sup>-2</sup> d<sup>-1</sup>), which may be ascribed to suppressed ecosystem  $R_e$  under summer water deficit. GPP is also highly depressed (Fig. 8),





**Fig. 5.** Comparison of multi-year mean annual carbon and water fluxes as well as ecosystem WUE for two even-aged (US-Me3 and US-Me6) and one multi-aged (US-Me5) forest sites with the same tree species (ponderosa pine), environmental conditions and similar stand age. Error bars represent one standard error.

but probably less than  $R_e$ , which leads to larger negative NEE values. However, this endurance may be not sustainable particularly during a prolonged drought, ecosystem WUE decreased sharply from  $2.41 \text{ g C kg}^{-1} \text{ H}_2\text{O}$  in normal year–2002 to  $1.32 \text{ g C kg}^{-1} \text{ H}_2\text{O}$  during drought year–2003.

#### 4. Discussion and conclusions

##### 4.1. Effects of forest age on functional recovery

Forest age, which is affected by stand-replacing ecosystem disturbances (such as wildfires, insect pests and harvesting), plays a distinguishing role in determining the magnitude of carbon fluxes in terrestrial forest ecosystems (Pregitzer and Euskirchen, 2004). A primary objective of the present work is to investigate the effect of stand age on forest C fluxes in multi-aged and even-aged forests. Currently, flux tower measurements of carbon dioxide, water vapor, and energy exchanges relying on the eddy covariance technique have become the major method for evaluating the recovery processes of forest ecosystem carbon dynamics after disturbances over a long time (Goulden et al., 2006; Dore et al., 2012). An alternative approach is biometric-based estimation, which calculates NEP from ecological inventories of various carbon components, including net primary production of plants and heterotrophic respiration from soil and woody debris (Curtis et al., 2002; Peichl et al., 2010b; Yashiro et al., 2010). The main difference between the two methods is that the former measured  $\text{CO}_2$  flux in hourly or half hourly increments and the latter in yearly time scales. Plenty of studies are also based on the biometric NEP estimates to assess the functional recovery during forest succession and can provide evidence for the present study. To understand how ecosystem production change during recovery after a stand-replacing crown fire, Goulden et al. (2011) compared the year-round eddy covariance measurements ( $\text{NEP}_{\text{EC}}$ ) with biometry and biomass harvests minus decomposition estimated from soil and woody debris respiration ( $\text{NEP}_{\text{B}}$ ) along a chronosequence of boreal forest stands that were 1, 6, 15, 23, 40, 74, and 154 years old, and found the agreement between the measures of

NEP was quite reasonable. Bond-Lamberty et al. (2004) measured the NEP of a boreal forest chronosequence comprised of seven black spruce-dominated sites over the forest age from 3 to 151 years after stand-replacing fire, and implied that the youngest stands were moderate C sources (approximately  $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ ), the middle-aged stands were relatively strong sinks ( $100\text{--}300 \text{ g C m}^{-2} \text{ yr}^{-1}$ ), and the oldest stands were about neutral with respect to the atmosphere. The NEP curve is similar to the CA-NS chronosequence in Fig. 2. Meanwhile, NEP of the over-mature boreal even-aged stands is about zero or negative as reported by other studies (Magnani et al., 2007; Taylor et al., 2014). Taylor et al. (2007) quantified the carbon storage against stand age of seven temperate even-aged red spruce dominated stands across different chronological stages of development, and pointed out that the red spruce stand at  $\sim 33$  years old after harvest accumulated carbon dioxide the fastest ( $2.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ ). The even-aged white pine plantation CA-TP3 site at similar stand age (Fig. 2) also exhibited the strongest carbon sequestration capacity among the forest chronosequence.

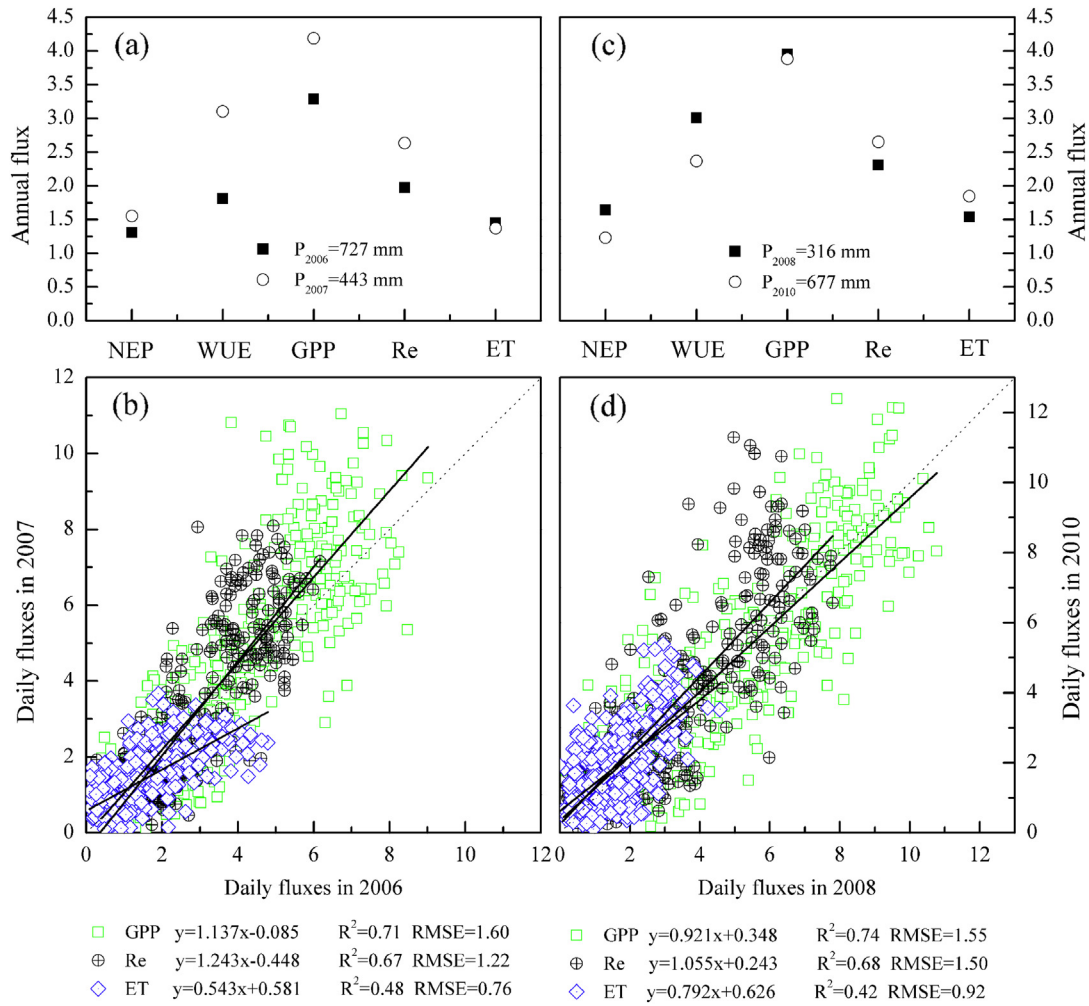
By means of flux measurements of three multi-aged Mediterranean ponderosa pine chronosequence, this study discovered an increasing trend in NEP of US-Me sites across the succession stages. On a series of ponderosa pine stands ranging from 9 to 106 years in central Oregon, USA, Law et al. (2003) used biological measurements to examine the NEP variation at 9 stands with stand age, which was lowest in the initiation stands (9–23 years), moderate in young stands (56–89 years), and highest in mature stands (95–106 years). The study also indicated that the complex structure of the multi-aged forest may lead to greater net carbon uptake than expected from models based on homogenous stands. Knohl et al. (2003) revealed that a large carbon sink existed in an uneven-aged managed 250-year-old deciduous forest in Central Germany, which provided significant implications for forest management practice about biological sinks within the context of the Kyoto Protocol. An eddy-flux tower installed in a > 300-year-old hemlock-hardwood forest also observed a small carbon sink during two years of measurements (Desai et al., 2005). Similarly, the eddy-flux estimates of NEE for the 16-month period at the 500-year-old Wind River old-

**Table 3**

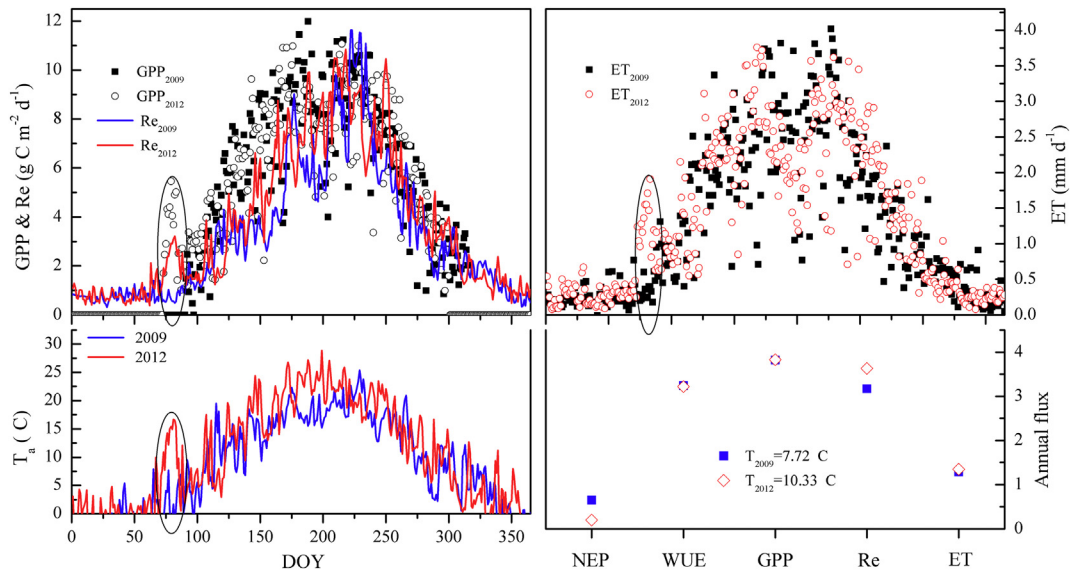
Pearson correlation analysis between interannual net ecosystem production (NEP) and ecosystem water-use efficiency (WUE) with the associated environmental factors at the two even-aged (CA-TP and CA-NS) and one multi-aged (US-Me) coniferous forest series.

Climate zone	Process	$T_a$	P	VPD	$T_s$	SWC	$R_g$
CA-TP (Temperate)	NEP	−0.674*	0.697*	−0.747*	−0.574	0.337	−0.097
	WUE	−0.297	0.754*	−0.162	−0.443	0.692	−0.289
CA-NS (Boreal)	NEP	0.717*	−0.430	0.563	0.162	—	0.795*
	WUE	0.385	0.480	0.638	−0.551	—	−0.605
US-Me (Mediterranean)	NEP	−0.515	−0.871**	−0.220	−0.016	−0.715*	0.539
	WUE	−0.348	−0.856**	−0.042	0.285	−0.486	0.135

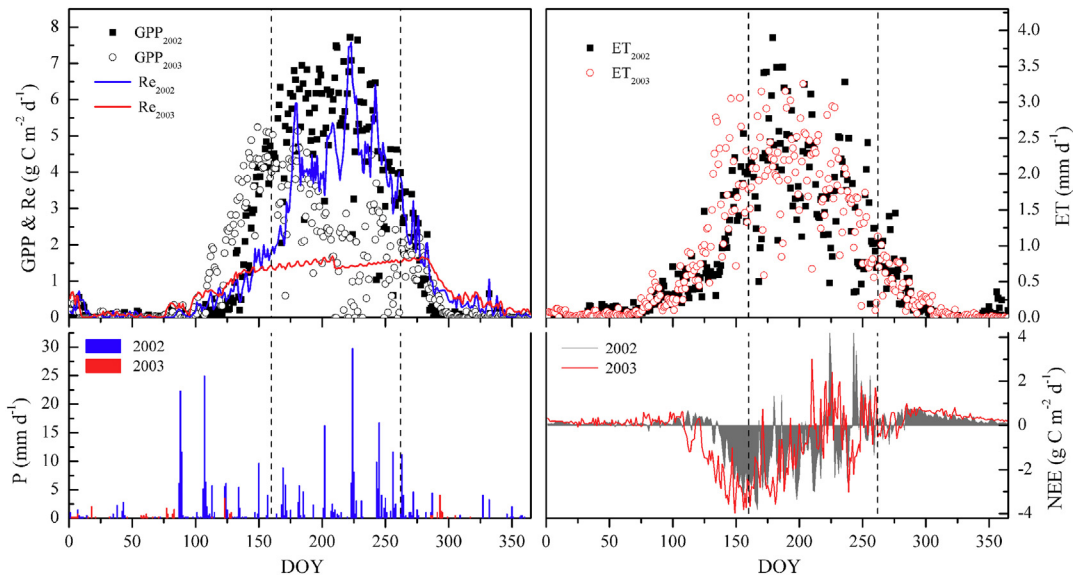
Note:  $T_a$  means air temperature; P represents annual precipitation; VPD is vapor pressure deficit;  $T_s$  refers to soil temperature; SWC is soil water content;  $R_g$  is solar radiation. \*\* and \* represent significant relationships at 0.01 or 0.05 level, respectively. “—” means data unavailable.



**Fig. 6.** Effects on the carbon and water fluxes as well as ecosystem water-use efficiency from different natural precipitations but similar temperature at the Mediterranean US-Me2 forest site. Annual mean temperatures of 2006 and 2007, as well as 2008 and 2010 are 7.5 °C and 7.0 °C, respectively. Fluxes in (a) and (c) are annual mean NEP, WUE, GPP,  $R_e$  and ET while (b) and (d) are the associated daily values. The dashed lines in (b) and (d) are 1:1 line. The unit of GPP,  $R_e$  and NEP is  $g\ C\ m^{-2}\ d^{-1}$ . The units of ET and WUE are  $mm\ d^{-1}$  and  $g\ C\ kg^{-1}\ H_2O$ , respectively.  $R^2$  and RMSE are the coefficient of determination and the root mean square error of regression, respectively.



**Fig. 7.** Environmental influence on ecosystem C and water fluxes at the temperate CA-TP4 forest site under different temperature ( $T_a$ ) with similar natural precipitation (995 mm in 2009 and 1000 mm in 2012) conditions. Annual mean temperature in 2009 and 2012 were 7.72 °C and 10.33 °C, respectively.



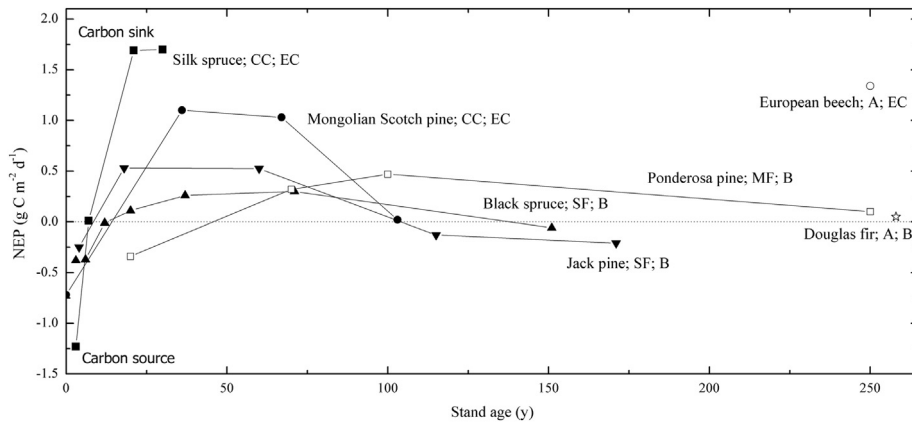
**Fig. 8.** Daily GPP,  $R_e$ , ET and NEE of the continental boreal CA-NS3 site under normal precipitation (363 mm in 2002) and extremely dry summer (only 30 mm in 2003). The dashed lines confine the period of summer drought across DOY 160–262.

growth forest showed a net carbon gain within the error derived independently from inventory data by Harmon et al. (2004). Based on amount of literature and databases for forest carbon-flux estimates, Luysaert et al. (2008) expected that old-growth forests on Earth sequester about  $1.3 \pm 0.5$  Gt of carbon per year. But it is noteworthy that NEP of the over-aged multi-aged forest (~500 years old) will also decrease gradually and become neutral (Harmon et al., 2004). All these analyses can indirectly validate our finding on the long-term trends of multi- and even-aged stands during forest succession (Fig. 9). Therefore, appropriate management practices (such as rotation length) are necessary to maintain a series of healthy age classes of trees spanning from young, moderate to mature. In addition, age effects account for 92% of the total variability in the NEP of five chronosequences collected as part of the CARBOEUROPE project, which spanned from boreal coniferous to temperate broadleaf forests (Magnani et al., 2007). This study also indicated that in order to evaluate the effects of wildfire/clear-cutting disturbances on forest structural changes and carbon dynamics, the stand-age effects must be included in the general purpose of large-scale biogeochemical models. Therefore, reliable assessments of regional forest carbon dynamics require detailed spatial information on forest age structure for a better understanding of the

interactions among forest age, disturbance history, and forest carbon fluxes.

4.2. Influence of tree species on forest carbon and water fluxes

Numerous biotic (community structure, plant composition, stand age, etc.) and abiotic (environmental conditions such as light, nutrient, temperature and water availability) factors affect the recovery of forest carbon flux after diverse disturbances (Desai, 2010). Plant functional types (PFTs) bridge the gap between plant physiology and ecosystem processes, thus providing a powerful tool in global change biology (Diaz and Cabido, 1997; Bonan et al., 2002). Currently, several comparative studies and biogeochemical models are developed in accordance with PFTs such as evergreen broadleaf forest, deciduous broadleaf forest, evergreen needleleaf forest, deciduous needleleaf forest and mixed forest. Tang et al. (2014) investigated the latitudinal trend in WUE of terrestrial ecosystems across different PFTs with FLUXNET data, and found that evergreen forests generally had higher WUE than deciduous ecosystems at similar latitudes (Kuglitsch et al., 2008; Tian et al., 2010). Zhang et al. (2014) found that WUE of each biome varied greatly, average annual WUE decreased from needleleaf forests, to



**Fig. 9.** Comparative analysis of age-related NEP in forest chronosequences following disturbance. Four even-aged stands comprise silk spruce, Mongolian Scotch pine, black spruce and jack pine. The data are extracted from Magnani et al. (2007), Bond-Lamberty et al. (2004) and Taylor et al. (2014). Three multi-aged stands include ponderosa pine, European beech and Douglas fir, where the data are from Law et al. (2003), Knohl et al. (2003) and Harmon et al. (2004). Given the limited magnitude of the x-axis, the true tree age of the Douglas fir stand is approximately 500 years old. CC, clear-cutting disturbance; SF, stand-replacing fire; MF, multiple fires; A, abandoned. EC, NEP based on eddy covariance technique; B, biometric estimates of NEP.

broadleaf forests, to cropland, to grassland and to shrubs. Novick et al. (2015) revealed that evergreen pine forest can assimilate CO<sub>2</sub> year-round representing an important carbon uptake advantage while deciduous forests were dormant. In addition, global dynamic vegetation models use the PFT definition to explain important structural and functional variables controlling land-surface energy, carbon, nutrient and water budgets (Wullschlegel et al., 2014). Nevertheless, ecologists question whether current PFT scheme is sufficient for modelling ecological processes and may miss important feedbacks without accounting for species-driven differences (Van Bodegom et al., 2012). Currently it remains a challenge to acquire the spatial distribution of tree species in large scale. However, this study indicated distinct differences in multi-year mean annual NEP and WUE among white pine, black spruce and ponderosa pine stands, despite these sites being coniferous forests at a similar stand age (Fig. 4 and Table 2). Compared to white pine and black spruce, ponderosa pine forest exhibited the strongest carbon sequestration potential with about 1.31 g C m<sup>-2</sup> d<sup>-1</sup>. It was 2–3 times the NEP of the other two tree species. Such effects may be related to differences in plant photosynthesis and litter decomposability among tree species. Therefore, the global analyses of carbon and water fluxes cannot neglect the differences in plant functional traits.

Today, Earth-system models use extremely reduced descriptions of functional diversity to simulate ecological processes. Disaggregation of the information lumped into a small number of global PFTs is required to understand how ecosystem carbon storage and climate sensitivity will evolve into the future, which requires more systematically collected knowledge of plant traits (Schimel et al., 2015). Specific properties of tree species associated with photosynthesis, carbon-water interactions, decomposability and other processes are the basis of the elementary succession mechanism (Yan et al., 2014; Pedro et al., 2015). Therefore, it is vital to identify the dominant control coming from the tree species themselves. Meanwhile, multi-species forests are thought to increase ecosystem resistance for a broad range of climate events, including wet or dry, moderate or extreme, and brief or prolonged, which can stabilize ecosystem productivity, and productivity-dependent ecosystem services (Thompson et al., 2009; Gamfeldt et al., 2013). Therefore, tree species together with community composition regulate global carbon and energy cycling, biophysics and climate feedbacks. Within the context of functional biogeography, further investigation of the extent at which species can explain the variability in ecosystem function is needed (Marquard et al., 2009; Paquette and Messier, 2011).

#### 4.3. Potential effects of extreme weather events on forest function

Changing climate is exerting considerable influence on the hydrological and biogeochemical processes in the world's forests (Mitchell et al., 2015). Therefore, we must improve our understanding of climate change–terrestrial feedbacks to increase the ability to manage forests in the face of extreme weather events. This knowledge is also needed to improve the parameterization of such changes in Earth system models for future predictions of ecosystem WUE and flux dynamics. Similar to age-related water-use dynamics across three temperate conifer forest plantations investigated by Skubel et al. (2015), the younger secondary forests (CA-NS) may be best suited to maximize growth and carbon uptake efficiency under increasing precipitation in boreal regions (Fig. 2). However, the response of NEP to a changing climate is not straightforward. NEP is an aggregate of biophysical processes such as GPP and R<sub>e</sub>, which transport CO<sub>2</sub> in opposite directions. High temperature may stimulate R<sub>e</sub> and GPP to a certain threshold (Desai, 2010; Goulden et al., 2011). In water-limited ecosystems, increases in SWC may also increase GPP (Guo et al., 2015) and R<sub>e</sub> (Riveros-Iregui et al., 2012). However, even though photosynthetic and respiratory CO<sub>2</sub> fluxes respond similarly to temperature and water availability, the magnitudes and sensitivities can differ (Ruehr et al., 2012; Biederman et al., 2016). Larger NEP in the year with less annual precipitation (Fig. 6) may be correlated with more frequent precipitation events hindering

photosynthetic GPP in the Mediterranean climate. Although this study revealed that larger NEP and WUE happened in the year with less annual precipitation but similar T<sub>a</sub> from two events (2006 vs 2007, and 2008 vs 2010), it needs to be noted that similar annual mean T<sub>a</sub> did not represent the consistency in temperature variability on short time scales. The complicated interactions between climate change and mass cycles resulted in distinct feedbacks in forests across different climatic zones, such as water-limited, light-limited and temperature-limited (Poorter and Rose, 2005; Lindner et al., 2010).

Increased frequency and intensity of drought events is among the prospects that we are facing due to climate change. How ecosystems respond to and cope with extreme droughts will be crucial in the terrestrial feedback to climate change. Ecosystem responses to drought, however, are highly variable in time and space (Kolb et al., 2013; Wolf et al., 2013). Our knowledge of these responses remains limited, in part because research on the effects of extreme droughts began only relatively recently. Given the strong link between carbon and water cycles, the effects of droughts on NEP have been investigated recently at site-level and national scales (Xiao et al., 2009; Schlesinger et al., 2015), which depends on the relative responses of annual GPP and annual R<sub>e</sub> to drought. Therefore, the response to droughts of annual NEP along with GPP and R<sub>e</sub> might change spatially and temporally with the severity, continuation and timing of droughts (Mitchell et al., 2015). Plenty of studies revealed that drought led to reduced GPP and NEP (Wu et al., 2011; Logan and Brunsell, 2015). GPP is mainly affected by droughts in growing seasons, while R<sub>e</sub> might be affected by droughts throughout all seasons. At the early stage of drought, GPP is impacted only marginally, thanks to the absorption of water from deep soil layers by plants, which maintains a normal photosynthesis rate (Fig. 8). However, R<sub>e</sub> might be significantly affected since soil organic carbon is usually concentrated in upper soil layers. Both GPP and R<sub>e</sub> decreased throughout the drought, with the latter exhibiting greater reduction. Consequently, NEP would not decrease or even increase in this study. The subsequent sharp decrease in GPP might be due to increasing water stress (Fig. 8). In spite that NEP increased from 0.23 g C m<sup>-2</sup> d<sup>-1</sup> to 0.32 g C m<sup>-2</sup> d<sup>-1</sup> during the drought year, ecosystem WUE had an apparent reduction from 2.41 g C kg<sup>-1</sup> H<sub>2</sub>O to 1.32 g C kg<sup>-1</sup> H<sub>2</sub>O. Approximately equal ET during the two years indicated that the increase in NEP came at the cost of significantly increased water loss from deeper groundwater, which could be detrimental in conjunction with predicted climate change.

#### 4.4. Implications for forest management from disturbance regimes

Forest ecosystems can contribute toward reducing future atmospheric CO<sub>2</sub> concentrations. An understanding of natural disturbance regimes and adaptations of forest to them is a prerequisite for forest management. Structural diversity is the primary difference between multi-aged and even-aged forests. These structures actually exist on a continuum of structural diversity from even-aged at one extreme and the most complex multi-aged on the other (O'Hara and Nagel, 2006; Turner et al., 2009). The differences in forest functions between two structures are small and difficult to quantify on the ecosystem level because of the limited technical means of measurements, which has resulted in a historical controversy over relative ecosystem productivity of multi-aged and even-aged stands pending for >60 years (Bourne, 1951; Smith and DeBald, 1978; Hanewinkel, 2002; O'Hara and Nagel, 2006). Previous methods mainly included empirical or ecological process-based growth and yield simulations (Peng, 2000; D'Amato et al., 2010), which were commonly hampered because maintaining these two stand structures required two disparate management approaches. It also brought about plenty of uncertainties without considering the interactions among community characteristics and effects of environment differences. However, the resilience may be higher in multi-aged stands because complicated age structure can impart a greater ability to quickly recover to a pre-disturbance state (Goulden

et al., 2006; Halpin and Lorimer, 2016). By investigating EC data from three young ponderosa pine sites (two even-aged vs one multi-aged) in the neighboring regions, this study identified a higher carbon sequestration potential but relatively smaller WUE in the multi-aged stands in comparison with the even-aged sites (Fig. 5). Nevertheless, trend analysis over the entire forest succession indicated that multi-aged management system was a promising approach for the recovery of ecosystem functions in the post-disturbance environment. It is noted that these findings in the present study still need more reliable validation for large-scale applications.

The challenges of multi-aged forest management are to establish and maintain a series of tree age classes that maximize the resilience of the stand (Lundstrom et al., 2011; O'Hara and Ramage, 2013). Moreover, management practices may modify the allocation of growing space to stand components, by varying species composition or by varying the length of the cutting cycle to meet particular goals (Thomas and Waring, 2015). Afforestation and forest management are recognized as key strategies in mitigating climate change by the Paris agreement of the United Nations Framework Convention on Climate Change (Ostrom, 2014). The establishment of large-scale plantations are ongoing in China (772,000 km<sup>2</sup>), the United States (254,000 km<sup>2</sup>), and the Russian Federation (170,000 km<sup>2</sup>) (Meyfroidt and Lambin, 2011). However, any climate framework that includes land management as a pathway for climate mitigation should not only account for land-cover changes, but also should equally address changes in forest management such as species changes, because not all forest management strategies contribute to climate change mitigation (Alkama and Cescatti, 2016). Therefore, the search for the best forest management strategy that cools the climate and meanwhile sustains wood production as well as other ecosystem services remains a central goal.

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