Effects of tree size heterogeneity on carbon sink in old forests

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ABSTRACT

Old-growth forests are carbon sinks as supported by increasing evidence in recent years. However, finding a resolution of the contradiction between the carbon sink function and neutral hypothesis at the community and individual scales is still a challenge. Tree size heterogeneity may offer an alternative answer. To determine this point, we studied subalpine (above an altitude of 3000 m) primeval *Abies fabri* forests located in the western part of China by comparing theoretical predictions and actual results. In theory, we first derived a model of the general carbon use efficiency (CUE) based on an individual scale, which allowed us to obtain the stand CUE by incorporating the carbon budget of all individuals. Afterwards, we quantified the effects of the gradual disturbance on the mortality of individuals with different sizes and predicted that the size of most individuals will trend to be medium (relative to the largest with the state of carbon neutral), meaning that the CUE of old stands has a high probability of tending to be a certain value (e.g. 0.4). In practice, the CUEs of old and middle-aged communities (0.405 and 0.602) calculated by the model were exceedingly close to the actual (0.401 and 0.597), indicating the effectiveness of the model. Further model-based analyses were performed, showing that the CUE of two old communities at different altitudes during the period from 2005 to 2015 were around 0.40, which are different from the reduced CUE from 0.64 to 0.60 in the middle-aged community. Meanwhile, in old forests, heterogeneous individuals dominated by medium-sized individual trend to be stable. Our findings indicated that with the increases in gradual disturbance events, a stable distribution of medium-sized individuals is an important cause for the carbon sink of old stands, and most of the carbon uptake by trees may further be stored in the soil. In addition, our model implied that environmental factors may change the forest carbon sink capacity by affecting the individual's potential maximum biomass.

1. Introduction

The hypothesis that the carbon sequestration capacity of old forests is negligible is based on two simple rules regarding individual growth: (i) The age-related decline in stand primary net productivity (NPP) (Ryan et al., 1997) potentially reduces the capacity for forests to become sinks for carbon (Hurtt et al., 2002); (ii) This trend cumulates in stabilized natural forests in which the maximum biomass is maintained by all photosynthates. Spontaneously, changes in productivity with age in complex, multi-aged, multi-species natural forests can be modelled simply as scaled-up versions of individual trees or even-aged stands (Carey et al., 2010). Accordingly, on community (i.e. all living trees, population to community level) and ecosystem (including dead wood and soil) scales, old forests are unlikely to exhibit strong carbon sinks. The presence of significant carbon sinks in old-growth forests at two scales, however, has recently been supported by more evidence (Piao

et al., 2005, 2009a; Ciais et al., 2008; Luyssaert et al., 2008; Tan et al., 2011), which may suggest that many individuals do not reach carbon balance. In fact, this simplified scale-up treatment may ignore some important dynamic details in community, such as tree competition, death, and recruitment, and these changes have a substantial effect on the forest carbon budget, especially for old forests. For example, long-term recruitment and late-successional species may have significant effects on the whole stand productivity (Carey et al., 2010). In this process, carbon accumulation declines substantially as forests mature and stocks approach their maximum carrying capacity, and thus younger stands play a major role in carbon accumulation (Gray et al., 2016). Obviously, it is not difficult to speculate that the dynamic balance between stand new growth (younger trees) and death loss (old trees) should still contribute to carbon sink by exporting carbon into other pools (deadwood, soil), although this balance is also considered carbon neutral at the community scale. Anyway, individual

heterogeneity should receive more attention. Given that tree age do not significantly relate to the mean live above-ground biomass (Mcgarvey et al., 2015), it is critical to consider the effect different size exert on old-community carbon dynamics.

While it is difficult to measure the specific carbon budget of different individuals due to the huge individual heterogeneity, carbon use efficiency (CUE) without any specific characteristic, defined as the ratio between net primary productivity (NPP) and gross primary productivity (GPP), may offer a new angle and cut-in point to integrate the carbon dynamics of different individuals. Likewise, a wide range of CUE values at the community level regardless of constant (0.5) (Dewar et al., 1998) or variation (0.2–0.8) (Litton et al., 2007) may not support that old forests are carbon-neutral (CUE = 0), although old-growth forests may have lower CUE than younger and secondary forests (Litton et al., 2007). Interestingly, a decline in individual CUE with tree age or size was also reported (Mäkelä and Valentine, 2001) and that the negligible relative growth rate (RGR) can lead to values of CUE that are close to 0. After all, tree (or organism) size cannot indefinitely grow, and the height and size of trees may not achieve more than 130 m and 2000 m^3, respectively (Koch and Sillett, 2009; Van Pelt, 2001; Sillett et al., 2010). These evidences also suggest that the community and individual carbon budgets cannot be simply equivalent. Although the driving mechanism for CUE may be complicated (Zhu, 2013), it is clear that CUE can link the carbon dynamics of individual and community scales.

In nature, it is almost impossible to maintain the development of an "even-aged" stand. On the one hand, smaller individuals are more sensitive to competition (Biging and Dobbertin, 1992); on the other hand, larger individuals are more vulnerable to drought and thermal stress (Nepstad et al., 2007) and thus change physiological function (Wu et al., 2017). As a result, U-shaped size-mortality trends are common in natural old forests (Lorimer et al., 2001; Foster et al., 2014, Coomes et al., 2015; Pillet et al., 2017), which means that older populations are normally distributed (Coomes and Allen, 2007). In this case, larger individuals approaching carbon neutrality have higher mortality, and the demography of forest stands recovering from disturbance would tend towards younger, faster-growing trees to grow (Brienen et al., 2015) and hence towards higher carbon use efficiency (CUE) (Malhi, 2015). Correspondingly, their constant (Ryan et al., 2004; Xu et al., 2012) or slowly declining NPP (Luyssaert et al., 2008) may be the main cause for carbon sink existence. Tree mortality was suggested to be associated with size-related exposure to disturbances, which can cause a decline in forest stand biomass accumulation over time (Xu et al., 2012). Obviously, if carbon accumulation is equal or less than the carbon lost by the death of trees (Seedre et al., 2015; Gray et al., 2016), the total biomass of old forests may eventually be closer to a relatively stabilized dynamic equilibrium instead of going up to the maximum, indicating a stable individual distribution. However, stochastic disturbance events are more difficult to detect (Foster et al., 2010), and the mechanism of how disturbance influence tree distribution is also unclear. Thus, finding appropriate approaches to determine and quantify the effect of disturbance on the mortality and biomass of individuals and community is an important part of understanding the mechanism of stand carbon sink.

The mountainous area accounts for nearly one third of the global land. However, only few studies related to forests were conducted on mountain ranges that were less favorable or accessible for land use (Tan et al., 2011), especially those at higher altitudes (> 3000 m). As a typical representative of mountain forests, subalpine forests not only have a wide distribution but also are sensitive to global climate change. Thus, it is extremely necessary to understand the status quo and patterns of carbon functions in subalpine forests.

The aim of this study was to determine whether, in old forests, the medium-sized tree and their stable distribution under the effects of disturbance is the main reason contributing to carbon sinks. Our experiment consisted of two parts: (i) First, we established the relationship between CUE and biomass at the individual and stand level, and

through the quantification of growth and death in the disturbance, we attempted to produce a mathematical derivation to find the most likely individual state in old forests; (ii) Second, based on the eddy-covariance system and multi-annual forest inventory data, the CUE of typical old and middle-aged forests located at an elevation of above 3000 m were actually measured.

Our research objectives were as follows: (i) to construct and verify the general CUE model; (ii) to predict the theoretical value of CUE in old forests based on the impact of the disturbance on individual size, and test our hypothesis; (iii) to clarify the carbon function of the typical subalpine forest in western China.

2. Material and methods

2.1. Growth-based CUE framework

The combination of the CUE definition and the growth-maintenance paradigm provided another expression of CUE (Van Iersel, 2003).

$$\frac{1}{CUE} = 1 + g_r + m_r \cdot \frac{1}{RGR} \tag{1}$$

where g_r and m_r are the growth and maintenance respiration coefficients, correspondingly. According to the thermodynamics of far-from-equilibrium systems, g_r/m_r represents the time to complete an iteration growth (see supplementary information). Thus, based on the iteration growth mode (IGM), a discrete form of the Gompertz curve, i.e. $f(x) = \left(c_m \frac{2b+2}{1-b}\right)^{1-b} x^b - x$ (see supplementary information), an equivalent growth model, RGR, can be represented as:

$$RGR = \frac{f(x)}{x(g_r/m_r)} = \frac{\left(\left(c_m \frac{2b+2}{1-b}\right)^{1-b} x^b - x\right)\frac{m_r}{g_r}}{x} \tag{2a}$$

where $f(x)$ and x are the iteration increment and existing biomass during time g_r/m_r, respectively; b is the metabolic exponent; c_m is a specific constant, and $c_m \frac{2b+2}{1-b}$ is the maximum biomass. In the ideal case, the time of each iteration is the same, and b and c_m are also constant. Given that b is usually equal to 3/4, the above equation can be rewritten as

$$RGR = \left(\left(\frac{14c_m}{x}\right)^{1/4} - 1\right)/(g_r/m_r) \tag{2b}$$

Thus, CUE can be expressed as

$$\frac{1}{CUE} = g_r \Big/ \left(\left(\frac{14c_m}{x}\right)^{1/4} - 1\right) + 1 + g_r \tag{3}$$

Eq. (3) shows that CUE is related mainly to the proportion of the existing biomass in the maximum biomass. This proportion is not only dependent on the existing biomass x but is also closely related to c_m. In essence, c_m is the average $f(x)$ with respect to the independent variable x in the equation $f(x) = \left(c_m \frac{2b+2}{1-b}\right)^{1-b} x^b - x$ (see supplementary information). From a discrete perspective, c_m represents the average iteration increment, indicating the ability of iteration growth, and is related to the species and the environment. Interestingly, if the environment variables have a stable periodicity, c_m can be constant on the periodic scale.

This CUE framework applies also to communities. The only difference is that the community metabolic exponent is 1, because of the constant total leaf area (AL) per unit area in an idealized forest with a constantly closed canopy. Note that the closed community biomass increment here is equivalent to the vertical growth (H) of all individuals within a unit area, and thus community biomass per unit area is proportional to $x^{(1-b)}$ (because of $DBH^2 \propto (H \times DBH^2)^b$ and $(H \times DBH^2) \propto x$). Then, regardless of the value of b, by replacing x with $H^{1/(1-b)}$ (Eq. (2a)), the CUE of the communities can be expressed as: