



Impact of anomalous climates on carbon allocation to biomass production of leaves, woody components, and fine roots in a cool-temperate deciduous forest



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ABSTRACT

We investigated carbon allocation in a cool-temperate forest in central Japan in years of contrasting climate anomalies: an early spring warming induced by the El Niño Southern Oscillation in 2002 and a low summer photosynthetic photon flux density (PPFD) induced by a stationary rain front in 2003. Observations of eddy flux, biometric variables, and chamber measurements from 1999 to 2006 and interannual variations in fine root net primary production (frNPP) were analyzed in conjunction with a terrestrial biosphere model simulation with multiple biometric constraints. Compared to the annual means (excluding 2002 and 2003), the low summer PPFD in 2003 reduced the annual gross primary productivity (GPP; −6%), soil respiration (SR; −11%), and ecosystem respiration (RE; −5%). Under the low summer PPFD, CO₂ fluxes commonly decreased but components of the NPP were not affected. The low variation in NPP is explained by previous findings that NPP is more sensitive to climate conditions before or during the early stage of the growing season. The early spring warming in 2002 increased the GPP (8%) and woody tissue NPP (wNPP; 55%) and decreased the frNPP (−33%) and SR (−6%). Although early spring warming prolonged the growing season, the foliage NPP (fNPP) and litterfall were invariant. The increase in wNPP and the decrease in frNPP imply that the forest decreased frNPP in favor of wNPP under the high spring temperature. Although the frNPP was estimated by model-data integration, we argue that the decrease in frNPP is plausible because the decrease in SR cannot be explained without the contribution from fine root respiration. These results suggest that increasing or decreasing patterns of component fluxes cannot necessarily be inferred from the GPP. Factors such as the nature and duration of climate anomalies and allocation shift between components of the NPP may need to be considered when characterizing carbon allocation under anomalous climate events.

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1. Introduction

Carbon allocation plays a key role in the dynamics of the terrestrial carbon cycle. It influences carbon flux, standing biomass production, and soil carbon accumulation by controlling the investments of photosynthate into leaves, woody organs, and fine roots (Friedlingstein et al., 1999). In general, forests allocate photosynthates to maximize plant growth and minimize

limitations by adjusting the balance between aboveground and belowground resource supplies (Enquist and Niklas, 2001). For example, nitrogen fertilization experiments have shown that an alleviation of nutrient limitations induced an allocation shift from the belowground to aboveground components (Gower et al., 1992; Haynes and Gower, 1995; Maier and Kress, 2000; Giardina et al., 2003; Janssens et al., 2010). Several studies have reported that carbon allocation changes with stand age (e.g., competition for light resources promotes aboveground production in young stands; Davidson et al., 2002; Ryan et al., 2004), whereas belowground resource limitation overwhelms the light limitation in older stands (Chapin et al., 2002). These studies have confirmed that changes in environmental conditions are a key factor for understanding the mechanisms underlying carbon allocation.

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Anomalous climate events may be useful for investigating the mechanism of carbon allocation because they abruptly change the environmental conditions in forest ecosystems. The frequency of anomalous climate events has been increasing in recent decades (e.g., Alexander et al., 2006; Huntington, 2006; Min et al., 2010). In particular, the intense and persistent El Niño events that occurred during the 1980s (e.g., 1982–1983, 1987–1988, and 1997–1998) influenced the carbon cycle of forest ecosystems. For example, the El Niño event in 1998 induced above-average temperatures in the spring across the Canadian inland and western coast. In response to this high temperature anomaly, a high anomalous carbon sequestration (net ecosystem production; NEP) was observed in a boreal deciduous forest in Saskatchewan (Black et al., 2000) and in secondary Douglas fir stands on Vancouver Island (Morgenstern et al., 2004). Although in numerous studies the forest response to anomalous climates has been investigated as a factor of changes in vegetation indexes, photosynthesis (gross primary productivity; GPP), and carbon sequestration (e.g., Asner et al., 2000; Black et al., 2000; Foley et al., 2002; Nemani et al., 2003; Morgenstern et al., 2004; Saigusa et al., 2010), our understanding of the climate control of carbon allocation remains limited. Potential changes in the carbon allocation associated with climate anomalies may alter woody biomass and forest soil carbon accumulation, and in turn influence the subsequent overall carbon emission and feedback to climate change.

This study investigated the impact of anomalous climates on the carbon allocation of a cool-temperate forest in the Takayama Forest Research Site, Japan. Multi-year biometric observations are available for the majority of the Takayama site's carbon cycle components, such as woody tissue net primary productivity (wNPP), foliage NPP (fNPP), aboveground and belowground woody biomass, litterfall, recruitment, and mortality, with the exception of fine root NPP (frNPP). One year data of frNPP were compensated by estimates from a model-data integration technique, in which a process-based biosphere model is combined with multi-year biometric observations to inversely estimate the plausible carbon allocation to fine roots. The availability of observed carbon cycle components (GPP, fNPP, wNPP, and litterfall) constrains unnecessary freedom in the simulation of frNPP; thus, a reliable estimate of frNPP is expected.

The goal of the current study was to evaluate the sensitivity of allocation patterns to interannual climate variability using observations-constrained modeling. Specifically, we evaluated the allocation pattern in years of contrasting climate anomalies: the early spring warming induced by El Niño in 2002 and the mid-summer low photosynthetic photon flux density (PPFD) in 2003. By analyzing the carbon allocations in 2002 and 2003, we characterized how carbon allocation is affected by contrasting anomalous climates.

2. Materials and methods

2.1. Study site

This study was conducted in the Takayama Forest Research Site, which is located in a mountainous region in the central part of the main island of Japan (36° 08' N, 137° 25' E, 1420 m above sea level). The site is characterized by a cool-temperate climate, with a mean annual temperature and annual precipitation of 7.2 °C and 2275 mm, respectively.

Deciduous broadleaf trees dominate the forest (*Quercus crispula*, *Betula ermanii*, and *Betula platyphylla* var. *japonica*), occupying 66.1% of the basal area; the forest floor is covered by evergreen dwarf bamboo (*Sasa senanensis*). The forest is a secondary forest and is approximately 50 years old (Saigusa et al., 2002). The growing season leaf area index is approximately 5 m² m⁻² for canopy

trees and 2 m² m⁻² for understory species (Nasahara et al., 2008). The typical tree height is approximately 20 m (Ohtsuka et al., 2005). The soil type is a dystric cambisol with a thick organic layer containing considerable organic carbon (318 MgC ha⁻¹; Jia and Akiyama, 2005).

Eddy fluxes have been measured since the summer of 1997. Beneath the eddy covariance tower, a permanent 100 m × 100 m study plot was established to monitor tree growth by measuring biometric variables, including NPP (foliage, wood, and the understory *Sasa*), woody biomass (aboveground and belowground), stem mortality, and recruitment (Ohtsuka et al., 2007, 2009). frNPP was measured for one year from June 2000 to June 2001 using the minirhizotron method, in which fine roots in the soil-minirhizotron tube boundary layer are observed with a charge-coupled device camera (Satomura et al., 2006). Diurnal and seasonal changes in SR were measured continuously for 24–48 h once or twice a month by the open-flow infrared gas analyzer method using four chambers near the flux tower (Mo et al., 2005).

The years 2002 and 2003 were characterized by contrasting climate anomalies. In 2002, the Takayama site was under the influence of an El Niño event that induced an early spring warming, early foliation, and an anomalously long growing season (Saigusa et al., 2005). Because of the high temperature anomaly in the spring (Fig. 1a), NEP in 2002 began to increase earlier (DOY 130–140) than in other years (approximately DOY 150) (Saigusa et al., 2005). In the summer of 2003, the Takayama site experienced an unusually long rainy season (accompanied by high precipitation; Fig. 1b) induced by a stationary rain front (Saigusa et al., 2010). As a consequence, the PPFD was substantially lower during the summer in 2003 than in other years (Fig. 1c). The monthly PPFD in July was 32% lower in 2003 than in previous years, which caused a 26% lower GPP in July 2003 compared to previous years (Saigusa et al., 2010). In the period 1999–2006, the mean annual NEP was the highest in 2002 (0.75 MgC ha⁻¹ yr⁻¹) and the lowest in 2003 (–0.37 MgC ha⁻¹ yr⁻¹).

2.2. Terrestrial biosphere model: biome-BGC

The present study employed a prognostic terrestrial biosphere model, the Biome-BGC model (Thornton et al., 2002). The model is driven by daily surface meteorological data (daytime, minimum, and maximum air temperatures; precipitation; vapor pressure deficit; and shortwave radiation) and plant eco-physiological parameters for prescribed vegetation types. The model is designed to simulate carbon, nitrogen, and water cycles in a terrestrial ecosystem on a daily basis and is composed of (1) four vegetation compartments, leaf, stem (live and dead), fine root, and coarse root (live and dead); (2) four litter compartments, labile, unshielded and shielded cellulose, and lignin; and (3) four soil compartments, fast, medium, and slow microbial and recalcitrant soil organic matter.

The photosynthetic mechanism is based on the Farquhar biochemical photosynthesis model (Farquhar et al., 1980). The GPP was calculated as the sum of photosynthesis from leaves under illuminated and shaded conditions. Stomatal conductance was modeled as the product of the predefined maximum stomatal conductance and climate regulation factors using a Jarvis-type model (Jarvis, 1976). Autotrophic respiration (AR) was treated as the sum of maintenance and growth respirations (MR and GR, respectively), with the maintenance driven primarily by nitrogen content in the living tissue with temperature dependency (Q₁₀ model) and growth respiration dependent on the predefined fractions of sequestered carbon allotted to vegetation components. Heterotrophic respiration (HR) is primarily driven by nitrogen content in each litter and soil organic matter pool and calculated with a rate constant and a product of two scalar potentials: the Lloyd–Taylor-type temperature scalar potential (Lloyd and

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