



METABOLIC PLASTICITY AND RESPIRATORY IN PLANTS AND ECOSYSTEMS IN A CHANGING ENVIRONMENT

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INTRODUCTION

The plant response to fluctuations in environment is critical to predicting plant and ecosystem responses to climatic change. The responses of diverse ecophysiological plant processes, for example, the respiration and carbon balance can be revisited from a perspective of the phenotypic plasticity. Phenotypic plasticity is defined how the capacity of an organism for to produce different phenotypes in response to environmental heterogeneity and resources availability with alterations in the morphological, anatomical, physiological and biochemical traits and not genetic changes (Bradshaw, 1965, Sultan, 2000). The phenotypic plasticity can to have effects in the structure, diversity and functioning of the ecosystems and is a fundamental evolutionary strategy of sessile organisms for to responses to the natural selection and anthropogenic drivers, for example, the soil use change or increase atmospheric of the CO₂.

The respiratory process release the energy stored from starch and sugars formed during the photosynthesis and converted in ATP in the process called oxidative phosphorylation. The capacity of formation and use of ATP by plants in various metabolic reactions during the growth, the development and the maintenance of plants can be affected by environmental conditions and, consequently, the responses of plants to some of these key factors in a scenario of change global. Additionally, the age or ontogeny of organs and whole plants are other elements that are involved in the plant respiration with effects in different scales from cellular to ecosystem. The respiration is a mechanism that can be affected by different environmental conditions while some environmental conditions that can induce alternative oxidase include drought that is associated to high irradiance and increase of temperature leaf, considered an abiotic resource fundamental in a scenario of change global.

Numerous research has explored the physiological and biochemical responses of the photosynthesis, growth and biomass allocation responses of the plants to factors associated with the global change, specially, to increase of elevated atmospheric concentration of CO₂ [CO₂]. However, the response plant respiration (*R*) to environmental changes both in the time short and large on plant function and future [CO₂] is unclear. Here, we show a approach of importance of metabolic plasticity and respiratory in plants and ecosystems in a changing environment.

Respiration and carbon cycle, a key ecophysiological process influenced by age of forests

Forest ecosystems play a central role in the global carbon cycle; they sustain approximately 80% of terrestrial net primary production (*NPP*) and 50% of global *NPP* (Whittaker 1975, Field *et al.* 1998) and are a major part of the terrestrial carbon sink that removes approximately 30% of anthropogenic carbon emissions each year (Canadell *et al.* 2007). It is well established, however, that aboveground *NPP* in forests declines with age (Ryan *et al.* 1997, Acker *et al.* 2000, 2002), potentially diminishing the capacity of old-growth forests to remove atmospheric *C* (Harmon *et al.* 2004, Miller *et al.* 2004, Pregitzer and Euskirchen. 2004, Magnani *et al.* 2007).

Current understanding of the mechanisms governing the age-related decline in *NPP* are embodied in two competing hypothesis (Gower *et al.* 1996, Ryan *et al.* 2004). The “respiration hypothesis” suggests that *GPP* remains constant but *NPP* declines following canopy closure early in stand development

because of increasing plant respiration (R_a) associated with the accumulation of woody biomass. More recently, the respiration hypothesis has been modified to include increased partitioning of C below ground as a factor contributing to the age-related decline in NPP (Ryan *et al.* 2004). The decline in carbon use efficiency (CUE), defined as the ratio of NPP/GPP , with stand age suggests that increasing R_a has a role in the age-related decline in NPP (Mäkelä and Valentine 2001, DeLucia *et al.* 2007). In contrast, the alternate “ GPP hypothesis” posits that R_a is a fixed fraction of GPP , and the age-related decline in GPP causes NPP to decrease. A number of factors, including increasingly unfavorable water relations and nutrient limitations in large trees, may contribute to the decline in GPP in old forests (Yoder *et al.* 1994, Ryan *et al.* 1997, 2006). The near constant fraction of GPP partitioned to R_a supports the GPP hypothesis (McCree and Troughton 1966, Litton *et al.* 2007) and should lead to a constant CUE with stand age.

Understanding the mechanisms governing the age-related decline in NPP and the corresponding balance between R_a and GPP is central to the ability to predict responses of terrestrial ecosystems to global change (Potter *et al.* 1993, Running and Coughlan 1988). To date, there have been few direct tests of these competing hypotheses (*e.g.* Ryan *et al.* 2004) and none have measured GPP independently from R_a to test their relative contribution to the age-related decline in forest NPP .

While the age-related decline in NPP is well established (Ryan *et al.* 1997, Pregitzer and Euskirchen 2004), underlying mechanisms remain uncertain. Myriad genetic, physiological and ecosystem processes may contribute to the age-related decline in NPP ; these processes are broadly classified into two groups, those affecting plant respiration (R_a) and those affecting canopy photosynthesis (GPP), giving rise to two competing hypotheses for the decline in NPP (Fig. 1; Gower *et al.* 1996, Ryan *et al.* 1997). The continuing increase in wood biomass and presumably maintenance respiration with constant leaf area after canopy closure gave rise to the hypothesis that the age-related decline in NPP is caused by increasing C losses to respiration (Yoda *et al.* 1965, Whittaker and Woodwell 1967, Odum 1969, Ryan *et al.* 1997). The “photosynthesis-respiration imbalance hypothesis” (Gower *et al.* 1996), hereafter referred to as the “respiration hypothesis,” suggests that GPP remains high during stand age and that increasing respiratory costs reduce NPP (Fig. 1a).

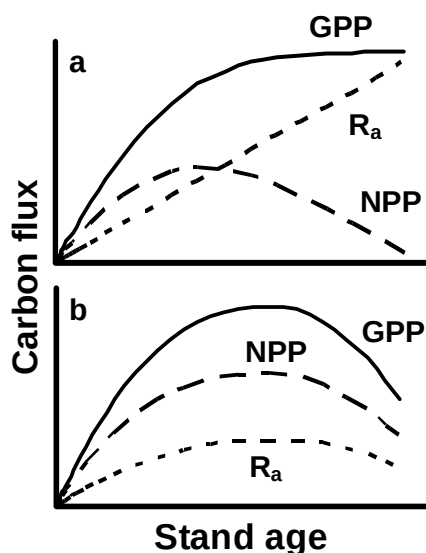


Figure 1. The “respiration hypothesis” (a) and the “ GPP hypothesis” (b) describing how changes in autotrophic respiration (R_a) and gross primary production (GPP) contribute to the age-related decline in forest net primary production (NPP).

That R_a scales with biomass is rooted in the almost universal observation that basal whole organism respiration varies with body size in animals (Hedin 2006) and plants (Reich *et al.* 2006). Woody tissues that provide support and conduction for large trees require a substantial investment in live biomass and

it is assumed that respiratory costs increase in proportion to this investment (Waring and Schlesinger 1985). However, the decline in tissue specific rates of sapwood R (Carey *et al.* 1997, Lavigne and Ryan 1997, Ryan *et al.* 2004) may produce a less than isometric scaling. Specific rates of leaf R also decline with tissue age across a season suggesting that R may change with phenology.

The “ GPP hypothesis” (Fig. 1b) posits that R_a is a fixed fraction of GPP and that declining GPP rather than the increasing R_a causes the age-related decline in NPP . This hypothesis is derived from the observation of Thornley (1969) that plants allocate C to maximize photosynthesis and growth. Because R_a and growth ultimately depend on sugars from photosynthesis, these two processes should remain balanced and R_a should be proportional to GPP (Dewar *et al.* 1998, Litton *et al.* 2007). It is assumed that the decrease in leaf area index (LAI) commonly observed in old stands generates a corresponding decrease in GPP . Because instantaneous R_a is regulated by the availability of sugars and the energy demand by tissues (Atkin and Tjoelker 2003, Gonzalez-Meler *et al.* 2004), differences in short-term and long-term changes in R_a may reflect a shift of dominant processes.

The competing hypotheses give rise to testable predictions at short (seasonal) time scales. If R_a is proportional to biomass and the decline in NPP with age is driven by increasing R_a (“respiration hypothesis,” Fig. 1a) then CUE , the ratio of NPP/GPP , should decrease as the ratio of woody tissues to foliage increases with stand age. Alternatively, if R_a is a fixed fraction of GPP and the decline in NPP is driven by age-related decreases in GPP (“ GPP hypothesis,” Fig 1b), then CUE should remain constant over time. Furthermore, asynchronous changes among GPP , R_a and NPP should lead to short term variation in the relationship between carbon gain and growth (instantaneous CUE ; CUE_i) during the growing season. Until recently these predictions have not been tested with direct measurements of GPP , R_a and NPP as stands age.

The respiration hypothesis had become firmly entrenched as the “textbook” explanation for declining NPP until Ryan and Waring (1992) demonstrated that the increases in wood maintenance respiration in old-growth stands of lodgepole pine were too small to explain the decline in NPP . Ryan *et al.* (2004) concluded that a decline in GPP coupled with increased partitioning of C to belowground pools and foliar respiration explained the decline in aboveground NPP with stand age in *Eucalyptus* plantations. This study also illustrates that tissue respiratory costs are not constant at either long or short time scales (Gonzalez-Meler and Taneva 2005). While increasing wood respiration may play a role, these studies suggest that age-related decreases in GPP coupled with change in C partitioning may be the dominant processes driving decreases in NPP with stand age.

A recent review of the literature supports the concept that increases in the partitioning of GPP to R_a as well as decreases in GPP both contribute to the age-related decrease in NPP (Fig. 2). For the forests in this survey, CUE was positively correlated with the fraction of total C in foliage ($CUE = 0.318 + 1.991 \times \text{leaf mass/total mass}$, $r^2 = 0.43$, $P < 0.01$). An important limitation of this dataset is that “age” and “forest type” were confounded and thus it remains questionable if this trend truly represents a generalized age-related phenomenon. Contrary to the results reported by DeLucia *et al.* (2007), Litton *et al.* (2007) found that R_a represents a relatively constant fraction of GPP , and that increased partitioning of C belowground may contribute to the age-related decline in NPP . Although the reasons for increased partitioning of C belowground with age are not well understood, it is likely that different mechanisms contribute to the age-related decline in NPP in different forest types growing under different climate regimes and edaphic conditions (Ryan *et al.* 1997).

Figure 2. Variation in *GPP* (closed symbols) and *NPP* (open symbols) for different forest types from DeLucia *et al.* (2007). *NPP* ($\log NPP = \log AGE \times -0.29 + 13.3$; $r = -0.60$) declined more strongly with stand age than *GPP* ($\log GPP = \log AGE \times -0.14 + 13.5$; $r = -0.41$) (Wilks' Lambda m test, $P < 0.01$).

Competition between tissue maintenance and growth, as well as the supply of nutrients and water to support them, can lead to variation in *C* partitioning to above- and belowground tissues during the growing season (Amthor 2000, Farrar and Jones 2000, Pregitzer 2003). The observation that tissue respiration rates are related to growth and carbohydrates (Gonzalez-Meler *et al.* 2001, Millenaar *et al.* 2001) suggests that current *GPP* controls R_a at short-time scales. The dependency of R_a on *GPP* has been demonstrated in forest stands using isotopes (Ekblad and Höglberg 2001, Bowling *et al.* 2002), girdling (Höglberg *et al.* 2001, Trueman and Gonzalez-Meler 2005) and meteorological approaches (Tang *et al.* 2005). These results contrast with recent observations that current photosynthate cannot always support observed concomitant rates of R_a (Carbone *et al.* 2007, Taneva *et al.* 2006). Reserves in roots and stems can meet the imbalance between *GPP* and R_a when energy demand is high (Korner 2003, Trumbore 2006). Recent studies in grasslands, shrublands and mature forests indicate that *GPP* partitioning to storage and the use of *C* from reserves in R_a varies between tissues and seasonally (Carbone and Trumbore 2007, Keel *et al.* 2006).

Use of *C* isotope ecosystem tracer to directly measure the use of current *GPP* by R_a during the growing season

At any given time during the growing season the relationship between *GPP* and R_a may vary depending on the differential responses of these processes to biotic (growth, reserves) and abiotic (drought, light, nutrient) factors. The balance between respiratory energy demand for growth and maintenance (mass dependent) and the available photosynthates (mass independent) throughout the growing season can be measured with a novel ecosystem isotopic pulse-chase method developed at Gonzalez-Meler's laboratory.

We propose to measure the seasonal variation in *GPP* and components of R_a at the same time that distinctly labeled one-day photosynthate is being respired from leaves, branches, stems and soils over several days. Several critical parameters are determined by following the amount of newly fixed *C* respired from plant tissues and soils during a 7-10 day "chase" period: 1) the total amount of new *C* assimilated during the pulse by canopy photosynthesis; 2) the *MRT* of newly fixed *C* in plant biomass which is derived from the decay kinetics of ^{13}C in respiration at the canopy, leaf, wood and soil respiration levels; 3) the proportion of labeled photosynthate allocated to respiration of the different components of R_a ; 4) the role of storage to support R_a and its components by comparing the amount of labeled ^{13}C respired with the measured R_a .

The feasibility of the ecosystem pulse-chase method was tested in Biosphere II, where young stands of *Populus deltoides* were exposed to two levels of atmospheric CO_2 (Engel *et al.* 2004) and in a large stature *Liquidambar styraciflua* stand exposed to FACE (Norby *et al.* 2002). We manipulated the ^{13}C of the atmospheric CO_2 to label one-day photosynthate and to quantify its fluxes out of the plant community (Table 1).

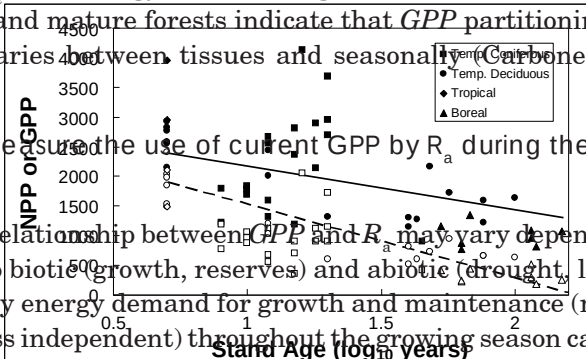


Table 1. Photosynthesis (GPP ; $gC\ m^{-2}$) during the day of the pulse, MRT (days) of the pulse day photosynthate in biomass, labeled R_a ($gC\ m^{-2}$) and the proportion of labeled photosynthate respired from belowground (% $C\ R\ bg.$) at ORNL FACE (*Liquidambar styraciflua*) and Biosphere II mesocosms (*Populus deltoides*) at ambient (400ppm) and elevated CO_2 (800ppm). ORNL results are averages from two replicates repeated over the growing seasons of 2003-6. Biosphere II data are average of three time points during 2002-3.

	GPP	MRT	R_a	% $C\ R\ bg.$
ORNL FACE				
Late spring	12.9 ± 2.1	2.78 ± 0.03	6.8 ± 0.1	53.6 ± 0.2
Summer	11.2 ± 1.6	2.71 ± 0.04	6.6 ± 0.4	63.4 ± 2.9
Early Fall	7.3 ± 0.4	4.17 ± 0.38	3.7 ± 0.5	47.8 ± 1.9
BIOSPHERE II				
Ambient CO_2	3.3 ± 0.7	2.70 ± 0.03	2.5 ± 0.2	40.7 ± 2.1
Elevated CO_2	6.2 ± 0.4	2.44 ± 0.15	4.4 ± 0.4	41.8 ± 5.8

The respired label was chased for at least 150 hours after the original pulse day. As indicated above, we used the short-term relationship between GPP , R_a and C retained (instantaneous CUE ; CUE_i) to integrate the observed responses. Experiments in *P. deltoides* showed a relative constant relationship between R_a and GPP during the growing season and across atmospheric CO_2 concentrations (Table 1). Atmospheric CO_2 did not significantly affect CUE_i in the long term (ambient vs. elevated) or in the short-term (pulse day at ambient conditions in the elevated chambers) regardless of the variations in daily canopy photosynthesis or C allocated to belowground R (Table 1). At ORNL FACE the isotopic composition of atmospheric CO_2 was readily changed for one day in the elevated rings (Table 1; note that the chase phase is done at the long-term CO_2 conditions). Experiments, repeated over several growing seasons, revealed that changes in R_a mostly followed changes in daily GPP , but changes in C allocated to respiration belowground were independent of GPP for most of the growing season (Table 1). Upper canopy leaves were the aboveground component of R_a that had the largest seasonal decline in rates of label respired. CUE_i , the relationship between instantaneous GPP and C -retained (NPP), is a valuable metric for testing the respiration versus GPP hypotheses. Values of CUE_i varied from 0.41 in summer to 0.49 in early fall, suggesting that forests can modulate respiratory costs independently of variations of daily GPP . This supports a compromise between the two hypotheses. The MRT ($-1/k$) of photosynthate at the canopy level is a function of total respiration (Table 1); the faster the respiration rate, the shorter the MRT of the labeled photosynthate. The MRT of one-day photosynthesis decreased by seven hours in the *P. deltoides* plantation exposed to elevated CO_2 (Table 1), whereas it increased by almost 1.5 days in early fall compared to the rest of the growing season in ORNL FACE plantation. Changes in MRT without large changes in CUE_i suggest strong control of total respiration by canopy photosynthesis late in the season, and changes in C allocated to respiration may reflect compensatory energy demand between tissues that are C sinks and tissues that supply C .

Existing FACE experiments overcome the technical difficulties of delivering an isotope tracer to an intact ecosystem (Andrews et al. 1999, Norby et al. 2002, Matamala et al., 2003, Pataki et al. 2003). However, these experiments conducted close to maximum LAI could not always address the role of storage in supporting R_a and growth. The amount of stored C used in respiration can be quantified if the amount of labeled R_a is less than total R_a . Using a ^{14}C pulse-chase labeling technique, Carbone and Trumbore (2007) found that despite large changes in C partitioning, belowground respiration in grasslands and shrublands was supported primarily by reserves. The pulse-chase measurements can coincide with phenological changes in temperate forests to quantify the contribution of C reserves to R_a and NPP . For example, pulse-chase experiments early in the season when stem or root growth may be at their maximum and GPP may be limited by abiotic factors will reveal the amount of stored C used for respiration of roots, stems, and leaves at different canopy layers. These relationships can then be compared with pulse chase experiments done at maximum GPP and late in the season during leaf senescence to reveal respiration and GPP controls.

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