The light environment in plant canopies is characterized by rapid fluctuations in photon flux density (PFD) because of the occurrence of sunflecks. These sunflecks can contribute most of the PFD available for photosynthesis and thus the mechanisms that control their utilization can have a significant impact on the carbon gain within canopies or in understories. When sunflecks are infrequent, their utilization is constrained by the induction requirement of the photosynthetic apparatus. The induction requirement has been shown to involve three separate factors consisting of an increase in the capacity for regeneration of ribulose bisphosphate that is important in the first 1–2 min after a light increase, the light activation of ribulose 1,5-bisphosphate
carboxylase that occurs over the first 5–10 min of induction, and an increase in stomatal conductance. Under the conditions of multiple sunflecks occurring in varying succession characteristic of canopy light regimes, the induction state of a leaf is a function of the up and down regulation of these three factors. The induction state determines the readiness of a leaf to respond to a sunfleck in terms of the maximum assimilation rate that can be achieved during it. Post-lightfleck CO₂ assimilation occurring because of the utilization of high-energy metabolite pools built up during the lightfleck can substantially enhance the utilization of short lightflecks. This buildup occurs because of a transient uncoupling of electron transport and carbon assimilation rates as 3-phosphoglyceric acid pools are reduced allowing for initially elevated electron transport rates during a lightfleck. Simulation modeling and measurements have shown that under natural sunfleck regimes in forest understories the induction state of leaves may limit daily assimilation by 10 to 25%. Post-lightfleck CO₂ fixation, on the other hand, does not significantly enhance sunfleck use in this environment because the short sunflecks for which it is most important make little contribution to the available sunfleck PFD. Within crop canopies, where the contribution of short-duration sunflecks is much greater, simulation modeling indicates a more important role for post-lightfleck CO₂ fixation.

I. Introduction

Leaves in forest understories or within plant canopies experience rapid fluctuations in the photon flux density (PFD) available for photosynthesis because of the changing patterns of sunfleck and shade. Sunflecks are the direct beams of sunlight that penetrate through small gaps in a canopy, and although present for only a small fraction of the day, they often contribute a large fraction of the PFD available for photosynthesis by understory plants. These sunflecks have long been recognized by ecologists as being important for the survival and growth of forest understory plants (Lundegarth, 1921; Evans et al., 1960). Sunflecks are hard to define precisely because they vary so much in both their temporal and spatial characteristics. Long duration sunflecks (>10 min) grade into gap light environments of the type created by treefalls. At the other end of the time scale, changes in PFD of an order of magnitude or more can occur in sunflecks as short as a second because of canopy movements in the wind. Within canopies themselves, the transient nature of the light regime is often striking, with leaves in some canopies receiving more than 1000 sunflecks per day on days with just moderate breezes (Pearcy et al., 1990). The steady-state conditions usually applied in measurements of leaf gas exchange do not hold under these transient light conditions characterizing sunflecks and canopy light environments. Instead, it is necessary to understand, in addition to the steady state photosynthetic characteristics, the transient response characteristics of the leaves in order to gain an understanding of the mechanisms regulating the use of sunflecks. Only in the past 10 years or so has the necessary technology in terms of rapid response infra-red CO₂ analyzers and computer-based data acquisition systems been available for this kind of characterization of transient responses.

The environmental and physiological controls on assimilation rate that operate during sunflecks are quite different than those operating under steady-state conditions. In the steady-state, the fluxes of carbon can be understood in terms of the concentrations of substrates and the effective resistances of specific diffusional and metabolic steps, which combine to determine the overall rate of assimilation. For photosynthesis under transient light conditions, the dynamic elements of the system that give it time dependence come into play. The dynamic elements consist of the metabolite pools that are built up and depleted as the photosynthetic rate changes over a time scale of seconds, the light-regulated enzymes that activate and deactivate over a time scale of minutes, and the stomata which open and close over time scales of minutes. Because the light-regulation

Abbreviations: A₁–assimilation rate at time T; A₂₅ – steady-state assimilation rate; Aᵢ₃₀₅ – assimilation rate corrected to a constant intercellular CO₂ pressure; CAP–carboxyarabinitol 1-phosphate; cᵢ–intercellular CO₂ pressure; F6P – fructose 6-phosphate; FBP – fructose 1,5-bisphosphate; FBPase – fructose 1,5-bisphosphate; GADPH – glyceraldehyde 3-phosphatedehydrogenase; gᵢ – stomatal conductance; ISᵢ – induction state at time T; LUE – lightfleck use efficiency; PCRC – photosynthetic carbon reduction cycle; PFD – photon flux density; PGA – 3-phosphoglyceric acid; PQ – plastoquinone; RSP – ribose 5-phosphate; Ru5P – ribulose 5-phosphate; Ru5P kinase – ribulose 5-phosphate kinase; Rubisco – ribulose 1,5-bisphosphate carboxylase; RuBP – ribulose 1,5-bisphosphate; SBP – sedoheptulose 1,7-bisphosphate; SBPase – sedoheptulose 1,7-bisphosphatase; TP – triose-phosphate; Tᵢ – time constant, time required for a process to change 0.63 of the final-steady state in response to a step change in the environment.