Trees (2003) 17:117–126
DOI 10.1007/s00468-002-0213-3

ORIGINAL ARTICLE

John S. Roden

Modeling the light interception and carbon gain of individual fluttering aspen (*Populus tremuloides* Michx) leaves

Received: 19 October 2001 / Accepted: 14 August 2002 / Published online: 25 September 2002

Abstract Poplars (*Populus* spp.) have a particular petiole morphology that enhances leaf flutter even in light winds. Previous studies have shown that this trait enhances whole canopy carbon gain through changes in the temporal dynamics and spatial distribution of light in the lower canopy. However, less is known about the effects of flutter for leaves at the top of the canopy (“sun leaves”). A computer simulation model was developed that uses latitude, time of day, day of year, azimuth and a slope component, which was varied at a 3 Hz frequency over an arc of rotation to create the flutter motion, and generate data on light interception for both surfaces of a fixed or fluttering leaf. The light files generated (10 Hz) were input into a dynamic model of photosynthesis to estimate the carbon gain for both fluttering and fixed leaves. As compared to leaves fixed at various angles and azimuths, fluttering leaves had a more uniform light interception. Depending on their angle and azimuth, fixed leaves may not always be intercepting high photon flux density (PFD) even when exposed to full sun. Leaf flutter continuously randomizes leaf angles creating uniform PFD inputs for photosynthetic reactions regardless of variation in leaf orientation and solar position. These effects on light interception could have positive impacts on carbon gain for leaves at the top of the canopy.

Keywords Leaf flutter · Light dynamics · Poplar · Light interception · Canopy motion

Introduction

Leaves at the top of a canopy are often assumed to be experiencing high radiation loads and are commonly referred to as “sun leaves” (Boardman 1977; Björkman 1981). Although these leaves may not be affected by canopy shading, they can experience temporally dynamic light environments due to diurnal fluctuations in solar position (Myneni and Impens 1985), cloud movement (Knapp and Smith 1987) as well as leaf and/or canopy motion (Norman and Tanner 1969; Desjardins et al. 1973; Tang et al. 1988; Roden and Pearcy 1993a). The transient characteristics of light interception created by leaf movement may be related to the aerodynamic and biomechanical properties of leaves, petioles and stems (Norman and Tanner 1969; Finnigan 1985; Pearcy 1990). Aspen (*Populus tremuloides* Michx.) leaves are particularly influenced by wind since they possess a flattened, non-rigid petiole oriented perpendicular to the blade creating the characteristic leaf flutter habit (Niklas 1991).

Previous studies (Lakso and Barnes 1978; Hongliang and Hipps 1991; Roden and Pearcy 1993a) have demonstrated that leaf flutter modifies the dynamic and spatial distribution of light in the lower canopy. Flutter increases light penetration into the lower canopy while modifying the number and duration of sunflecks any understory leaf might receive (Roden and Pearcy 1993a). Flutter creates an understory light environment that is more dynamic temporally and more evenly distributed spatially. Flutter enhances lower canopy carbon gain since understory poplar leaves are very efficient at photosynthetic utilization of rapidly fluctuating sunflecks (Roden and Pearcy 1993b).

Although it has been demonstrated that leaf flutter influences lower canopy light environments, little is known regarding the light interception of individual fluttering leaves. Roden and Pearcy (1993a) postulated that reductions in light interception by fluttering leaves at the top of a canopy would not significantly influence upper canopy carbon gain. The photon flux density (PFD) intercepted by fluttering “sun leaves” may still be sufficient to saturate the photosynthetic apparatus. Even if the mean PFD intercepted is below light saturation, leaves exposed to rapidly fluctuating light environments may fix nearly as much carbon as leaves in constant high PFD due to post-illumination CO_2 fixation (Roden and

J.S. Roden (✉)
Department of Biology, Southern Oregon University,
1,250 Siskiyou Blvd., Ashland, OR 97520, USA
e-mail: rodenj@sou.edu
Tel.: +1-541-5526798, Fax: +1-541-5526415

Pearcy 1993b). However, these ideas have previously been untested.

Light sensors attached to both surfaces of fluttering and fixed sun leaves demonstrate that light interception can rapidly fluctuate between the upper and lower surface (Roden and Pearcy 1993a). However, even the smallest photodiodes available tend to inhibit the flutter motion and would provide only a snapshot in time for one particular leaf orientation. Therefore, modeling this problem seemed tractable and appropriate since it allows testing of many different leaf orientations, solar positions and flutter characteristics. The light interception of individual fluttering leaves can be estimated from physical relationships and well-established assumptions of diurnal and seasonal variation in solar constants and atmospheric transmission. In addition, the complexity of light dynamics created by canopies and clouds that have to be considered if light interception is directly measured, can be ignored in a computer simulation.

With the development of dynamic models that estimate photosynthetic rates from high frequency PFD inputs (Pearcy et al. 1997), carbon gain can be estimated for individual fluttering leaves. This study attempts to determine if flutter significantly modifies the carbon gain of poplar leaves exposed to full sun. The hypothesis tested is that individual fluttering leaves exposed to full sun will possess comparable photosynthetic rates to leaves fixed in position.

Model description – equations for light interception

The simulations were divided into two major components: (1) a light interception model and (2) a photosynthesis model.

Light interception model

The goal of the light interception model was to estimate the cosine of the angle between the solar beam and a line normal to the blade (θ) also known as the cosine correction (Fig. 1). The equation is given by (Jones 1986),

$$\cos\theta = [(\sin\lambda \bullet \cos\eta) \bullet (-\cos\alpha \bullet \sin\chi) - \sin\eta \bullet (\sin\alpha \bullet \sin\chi) + (\cos\lambda \bullet \cos\eta) \bullet \cos\chi] \bullet \cos\delta + [\cos\lambda \bullet (\cos\alpha \bullet \sin\chi) + \sin\lambda \bullet \cos\chi] \bullet \sin\delta \tag{1}$$

where the symbols λ, η, δ, α and χ represent latitude, time of day as an hour angle, day of year (solar declination), azimuth orientation, and a slope component (leaf angle) respectively. Leaf azimuth angle is the deviation, in radians, from true north of a line normal to the petiole/mid-vein axis. Solar declination is the seasonal change in maximum solar elevation calculated from the day of year (Jones 1986). The incident light normal to the solar beam was then calculated using the solar constant above the atmosphere (1,360 W m^{-2}), an estimate of the transmission coefficient for a relatively clear atmosphere (0.8), and solar elevation (Jones 1986). The incident light was converted to photosynthetically active radiation in molar flux units (μmole photons m^{-2} s^{-1}) assuming a typical solar spectrum and multiplied by the cosine correction ($\cos\theta$, Eq. 1) to estimate incident PFD for any leaf angle and position. This model applies only to light interception of individual leaves without canopy shading (by neighbors), or atmospheric effects (cloud cover or changes in humidity and/or particulates).

Fixed leaves maintain the same “slope” (leaf angle, χ) throughout the day. For a fluttering leaf, the slope angle was modified to generate a twisting motion along a fixed petiole/mid-vein axis (Fig. 1). The blade travels through an arc of rotation (ϕ) and then returns to the initial leaf angle. The arc of rotation can be varied to test different flutter motions, however, the default was 140°, which was estimated from canopy observations and slow motion photography of aspen leaves in a wind tunnel. The motion was simulated with a sin wave since it adequately models the deceleration and acceleration of a leaf blade as it approaches and departs from the point at which it changes direction.

Calculations were made at a frequency of 50 Hz with the slope component changing directions (every 17th calculation) to simulate a 3 Hz frequency in leaf flutter with a slight offset to avoid aliasing. Roden and Pearcy (1993a) determined that aspen leaves flutter at a frequency of 3 Hz from spectral analysis of sunfleck dynamics in the understory. However, it must be noted that this analysis does not relate to the frequency of return to the blade’s original position, but the number of times the leaf was at any particular angle. Over any complete flutter cycle the same leaf angle will occur twice, once in both the forward and return direction. From an engineering standpoint, aspen leaves flutter at approximately 1.5 Hz.

When aspen leaves flutter, not only does the leaf angle change, but so also does the azimuth angle. A number of tests were run to also determine the simultaneous effect of changing azimuth direction (simulated using a sin wave function, at variable frequencies) as well as leaf angle. These were compared to runs using fixed azimuth angles as described above.

The light interception was calculated for both the abaxial and adaxial surface of the leaf. The side of the leaf that does not receive direct beam radiation was assumed to be receiving diffuse light. Diffuse light was estimated from solar elevation and the incident radiation on a horizontal surface at any time,

$$I_{\mathrm{diffuse}} = 0.25 \bullet I_{\mathrm{horizontal}} \bullet \left[1 - \left(0.8^{1/\sin\beta} \bullet \sin\beta\right)\right] \tag{2}$$

where β is solar elevation (estimated from λ, δ, and η, Jones 1986).

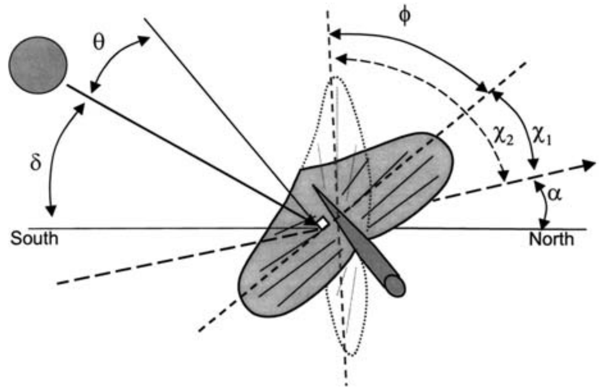

Fig. 1 Diagram showing the major angles used to calculate light interception for any leaf orientation. The symbols δ, α, χ, ϕ, and θ represent solar declination (day of year), azimuth orientation, and a slope component (leaf angle), the arc of rotation and the angle between the solar beam an a line normal to the blade, respectively. See text for details

Photosynthesis model

For these experiments photosynthesis was most appropriately estimated using a dynamic model. The biochemical components of the photosynthetic apparatus respond to changes in PFD at time scales ranging from tenths of seconds to minutes. To my knowledge, there are no gas exchange systems that utilize a cuvette that would allow a leaf to flutter and thus adequately test these questions. Fortunately, Pearcy et al. (1997) have developed a robust model that receives 10 Hz light data and provides detailed output of numerous photosynthetic parameters. Their dynamic model (for C_3 plants) is a modification of the Farquhar-von Caemmerer-Berry model (Farquhar et al. 1980) that includes pool sizes of metabolites, light activation and deactivation of PCR-cycle enzymes, and a dynamic model of stomatal conductance. This model has been shown to accurately predict the measured total carbon assimilation of leaves exposed to natural and artificial lightfleck regimes whereas steady-state solutions were off by as much as 50% (Pearcy et al. 1997).

Materials and methods

Testing and parameterization

The dynamic model of photosynthesis (Pearcy et al. 1997) was parameterized to match known photosynthetic responses of aspen leaves to steady state and dynamic light environments. Measurements of photosynthetic gas exchange were performed with both a transportable system as describe in Roden and Pearcy (1993b; see also Pfitsch and Pearcy 1989) and an open, fast-response laboratory gas exchange system that utilizes a small chamber volume and high flow rates (described in Sassenrath-Cole and Pearcy 1992) suitable for studying responses to fast light transients. Although, a detailed analysis of steady-state and dynamic gas exchange characteristics of aspen will not be presented here (see Roden and Pearcy 1993b) those data were used to parameterize the photosynthesis model. The Appendix contains a list of parameters used in that model.

One additional gas exchange experiment was performed to determine if flashing light on both sides of a leaf modifies its carbon gain as compared to light from one side only. A special double-sided cuvette was designed (R.W. Pearcy, University of California, Davis) that exposed the leaf to light from both the abaxial and adaxial side. It has been observed using steady state gas exchange systems (Roden, unpublished data) that the abaxial surfaces of aspen leaves have similar photosynthetic capacities to adaxial surfaces. However, the question for leaf flutter was whether an alteration of light exposure between both surfaces could be modeled as exposure on a single surface. Photosynthetic gas exchange was measured on aspen leaves exposed to either a constant PFD of 1,800 μmol m^{-2} s^{-1} on each surface or illumination alternating between abaxial and adaxial surfaces at a frequency of 0.2, 1 and 5 Hz.

Output and analysis

The output of the light interception model (10 Hz light data for an entire day) was input into the dynamic model of photosynthesis. The photosynthesis model requires only one light file per leaf as input so the interception of the upper and lower surfaces were compared and the higher value was stored. It may be more realistic to add the PFD intercepted for both leaf surfaces, however the light response of carbon gain (used to parameterize the photosynthesis model) was measured using gas exchange systems that measured light on one surface only. For example, if the light intercepted on both surfaces were added when the leaf was parallel to the solar beam (twice diffuse), then a much higher photosynthetic rate would be predicted than actually measured under low light conditions.

Although the output for the dynamic model (Pearcy et al. 1997) includes many variables such as RuBP pool size, Rubisco activation state, stomatal conductance and steady-state assimilation rates etc., the main variable of interest for this study was the dynamic assimilation rate. The 10 Hz carbon assimilation rate and light interception data were reduced to 10-min averages for diurnal comparisons and graphics. The integrated daily carbon gain for fluttering leaves was compared with fixed leaves for the same conditions.

Results

An example of the light interception for one very short period (Fig. 2) provides a visual description of how the model works. Every 5th data point, representing a 10 Hz frequency (the larger symbols in Fig. 2) was stored in a light file that was used as input for the dynamic model of photosynthesis (which cannot accept inputs faster than 10 Hz). Figure 2 also shows that a 10 Hz frequency captures most of the variation in light interception for leaves that flutter at 3 Hz.

The photosynthesis model parameters chosen (see Appendix) adequately simulated the steady-state light and CO_2 response of a number of replicate aspen leaves (Fig. 3). In addition, the model effectively simulated the dynamic response of carbon assimilation and stomata to a step change in light (Fig. 4). More importantly, the model gave excellent fits to observed photosynthetic responses to flashing light regimes (Fig. 5). Differences in peaks and valleys between the model and gas exchange observations were minor and turn out to be less than 2% of the integrated carbon assimilation. The model also

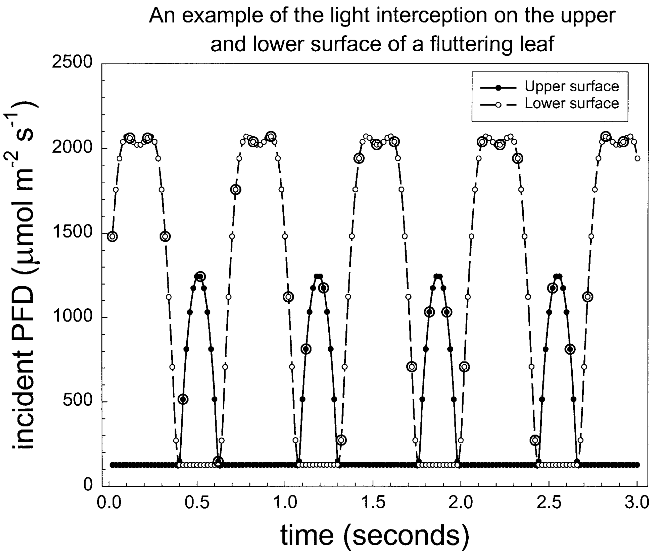

Fig. 2 An example of the output from the light interception model for a fluttering leaf facing east with an initial leaf angle of 75° at 1130 hours (day 155 and latitude 38.5°). The smaller symbols represent a 50 Hz calculation frequency and the larger symbols represent a 10 Hz frequency that was used as input into the dynamic model of photosynthesis

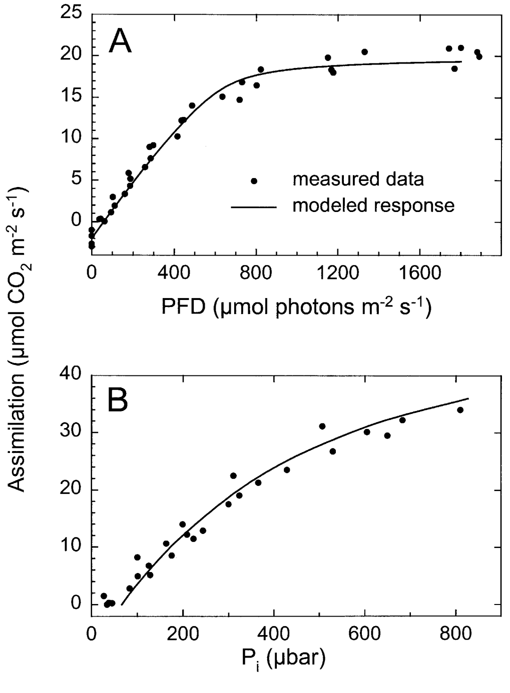

Fig. 3 Modeled and measured light and CO_2 response curves for aspen leaves. Measured values represent four replicate leaves. Measurements were made at a temperature of 25°C and leaf to air vapor pressure deficits of 12–15 mbar

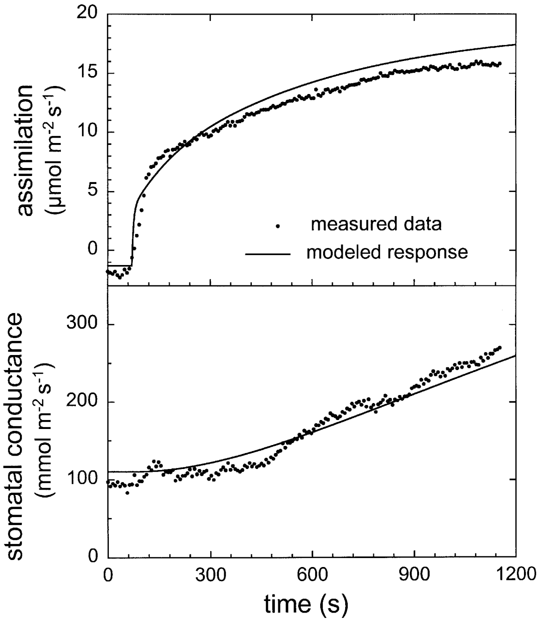

Fig. 4 Modeled and measures time course of photosynthetic induction for aspen following a step change in photon flux density (PFD). Leaf temperature was 24°C and leaf to air vapor pressure deficit was 11 mbar

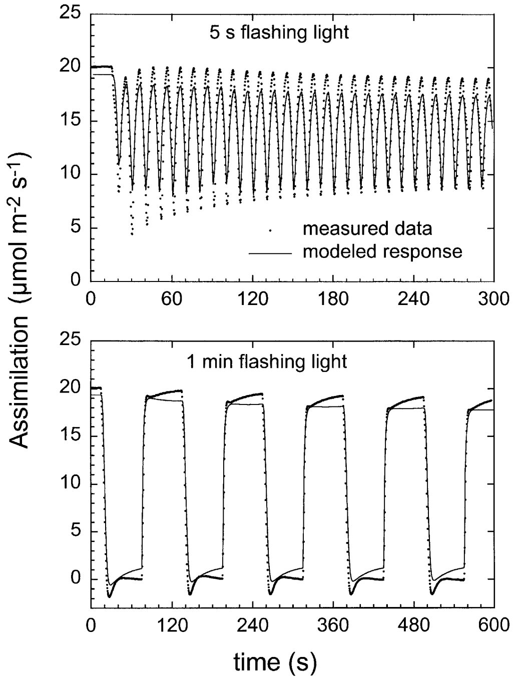

Fig. 5 Measured and modeled photosynthetic response of aspen to a decrease in total PFD with either a 5 or 60 s flashing light treatment. Measurements were made at a temperature of 23°C and leaf to air vapor pressure deficits of 11–13 mbar

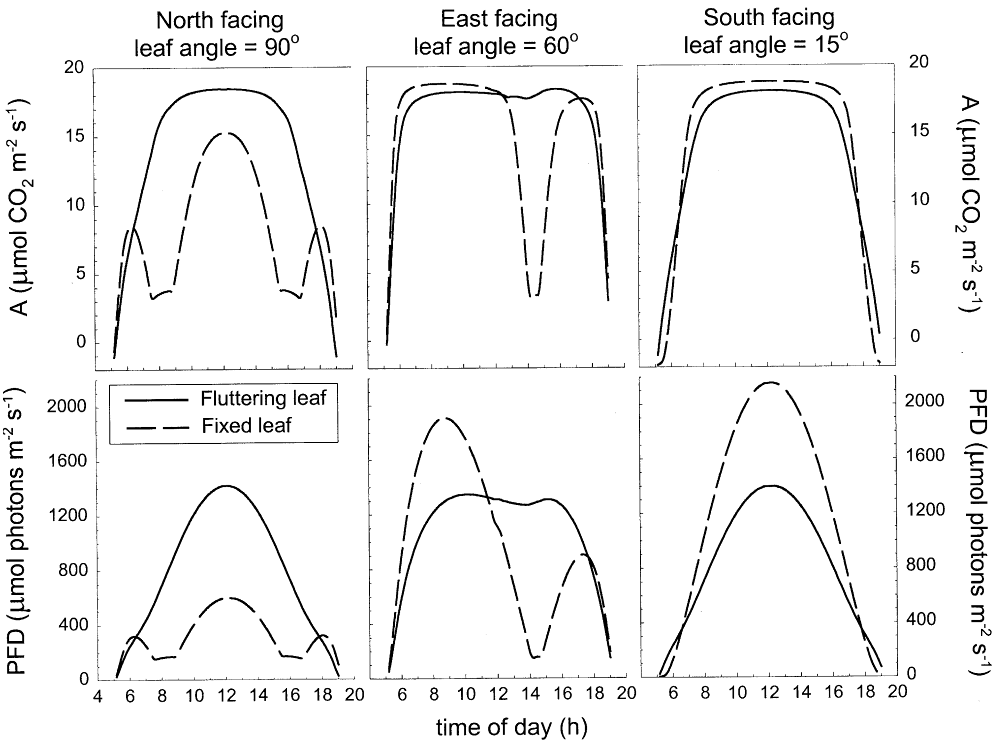

Fig. 6 Representative examples of model simulations of diurnal light interception (*PFD*) and carbon assimilation (*A*) for individual fluttering and fixed aspen leaves at various angles and azimuths

performed extremely well for higher frequency light dynamics (1 and 0.4 s flashing light), although not presented graphically since the model and measured lines were indistinguishable. The model also effectively simulates (data not shown) the photosynthetic response to low light transients (see Roden and Pearcy 1993b).

Gas exchange data collected (R.W. Pearcy, University of California, Davis) using a double-sided cuvette demonstrated that alternating light exposure on the upper and lower side of an aspen leaf had no effect on the assimilation rate as compared to light exposure on one surface only (Table 1). This was true even though the photosynthetic capacity on the abaxial surface was significantly lower than the adaxial surface. This implies that incorporating light interception from both surfaces into one light file for the dynamic model of photosynthesis was adequate to simulate the carbon gain of a fluttering leaf.

Figure 6 shows examples of diurnal trends in light interception and carbon assimilation that demonstrate the effect of leaf flutter for three distinct scenarios. In the first example, a north facing fluttering leaf with an initial leaf angle of 90° (vertical) intercepted 150% more PFD and fixed 70% more carbon than a leaf fixed at the same initial orientation. Clearly, at certain times of the day (0800 and 1600 hours), when the blade was parallel to the solar beam the leaf experienced quite a low light environment and flutter enhanced light interception. Vertically oriented leaves frequently intercept much less PFD than horizontally oriented leaves and so it was expected that flutter should enhance both PFD interception and carbon gain for those leaves.

The second scenario in Fig. 6 was an east facing leaf at a 60° angle. The integrated PFD intercepted was nearly identical between a fixed and fluttering leaf however the fluttering leaf gained 8% more carbon. Although both leaves intercepted a similar total amount of PFD, the PFD was distributed evenly over the day for the fluttering leaf. The east facing leaf fixed at 60° intercepted the greatest amount of PFD mid-morning, however that light was above that which saturates the photosynthetic apparatus (≈800 µmol m^{-2} s^{-1}) and failed to enhance carbon assimilation (Fig. 6). By early afternoon the fixed leaf was parallel to the solar beam and flutter enhanced both PFD interception and carbon gain.

The third scenario was a south facing, nearly horizontal (15° angle) leaf (Fig. 6). Compared to its fixed counterpart, a fluttering leaf intercepted 31% less PFD. However, the additional PFD absorbed by the fixed leaf at midday was well above saturation. The fluttering leaf gained nearly as much carbon as the fixed leaf because it inter-

Table 1 The carbon assimilation rate of aspen leaves exposed to either continuous light (1,800 µmol m^{-2} s^{-1}) on one surface or alternating light (0.2, 1 and 5 Hz frequency) between the upper and lower surface. Thus, with the alternating light regimes, the leaf was essentially continuously illuminated but on alternating sides

Treatment	Photosynthetic rate (µmol m^{-2} s^{-1})
Constant upper surface	20.7
Alternating – 0.2 Hz	19.5
Alternating – 1 Hz	20.3
Alternating – 5 Hz	20.7
Constant lower surface	14.0

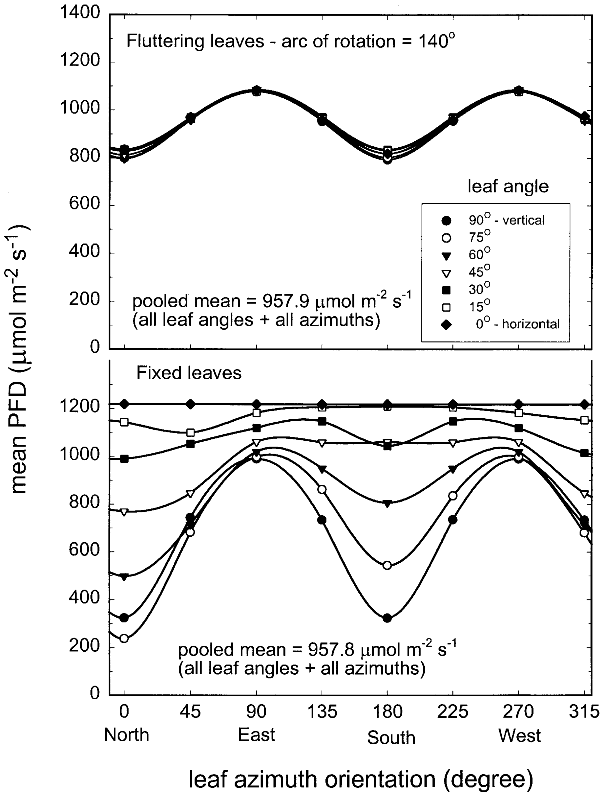

Fig. 7 Simulated effect of leaf orientation and flutter on mean daily light interception for individual aspen leaves in full sun for day 155, latitude 38.5° and a 140° arc of rotation

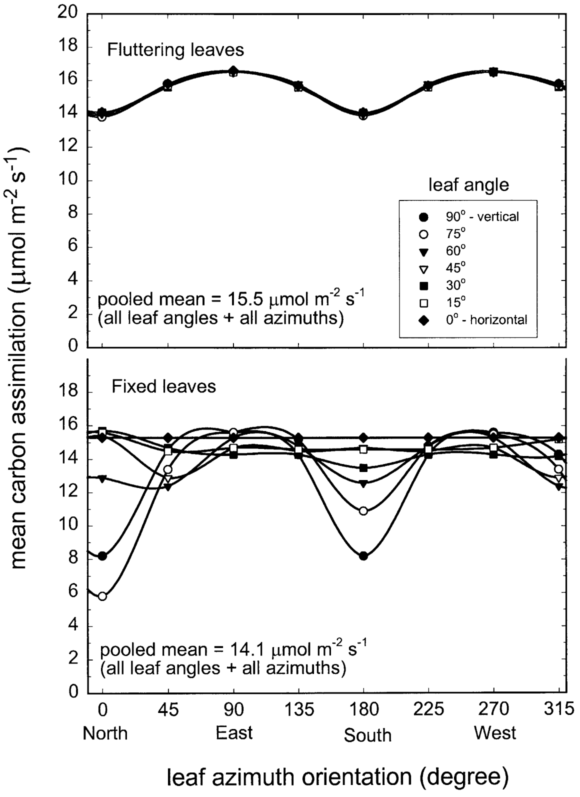

Fig. 8 Simulated effect of leaf orientation and flutter on mean carbon assimilation for individual aspen leaves in full sun for day 155, latitude 38.5° and a 140° arc of rotation

cepted sufficient PFD to saturate photosynthesis and because of efficient utilization of dynamic PFD input (post-illumination CO_2 fixation). Comparing the light interception of fixed leaves in all three scenarios (Fig. 6), it is clear that "sun leaves" may not always be exposed to high PFD. The similarity in light interception for fluttering leaves in all three scenarios implies that flutter creates a more uniform light environment for all leaves even those with very different orientations.

The integrated daily PFD and A were estimated for eight azimuth (45° increments) and seven leaf angles (15° increments) from vertical to horizontal for fixed and fluttering leaves (Figs. 7, 8). If we assume a random azimuth and leaf angle distribution in a population of "sun" leaves, then flutter would not change the total amount of light intercepted (pooled mean for both were ≈958 μmol m^{-2} s^{-1}). In a population of randomly oriented leaves, leaf flutter would essentially continuously re-randomize leaf angles and thus total light interception would remain the same. However, leaf flutter reduced the variability in light interception across the entire range of leaf angles (Fig. 7). Although there were slight differences for fluttering leaves facing north/south versus those facing east/west, all fluttering leaves at any given azimuth intercepted nearly identical amounts of PFD regardless of initial leaf angle. Recall that the leaf angle parameter associated with fluttering leaves was just the angle at which the leaf begins its flutter motion. Although these results were not unexpected, to my knowledge this is the first study to quantify and compare the light interception of fluttering and fixed leaves at various leaf orientations.

Flutter increased the carbon gain for a population of randomly oriented aspen leaves by as much as 10% (Fig. 8). Although flutter may not alter the total light interception for this population, it can still influence carbon gain by creating a more uniform light environment across all members of that population. This enhancement was due to increased light interception and photosynthetic rates for leaves with θ angles close to 90° and little or no effect on carbon gain for leaves with small θ angles. Leaves normal to the solar beam intercepted less light when fluttering, but generally not enough to reduce photosynthetic rates much below light saturation.

Aspen leaves are not fixed in azimuth orientation and the true flutter motion is more complicated than simulated here. In order to test the effects of a more complicated leaf motion, the model was modified to include variation in azimuth angle as well as the slope angle. Although all leaf angles were not tested with this new version, the results confirm the basic premise that flutter creates a more uniform light environment. When flutter changes azi-

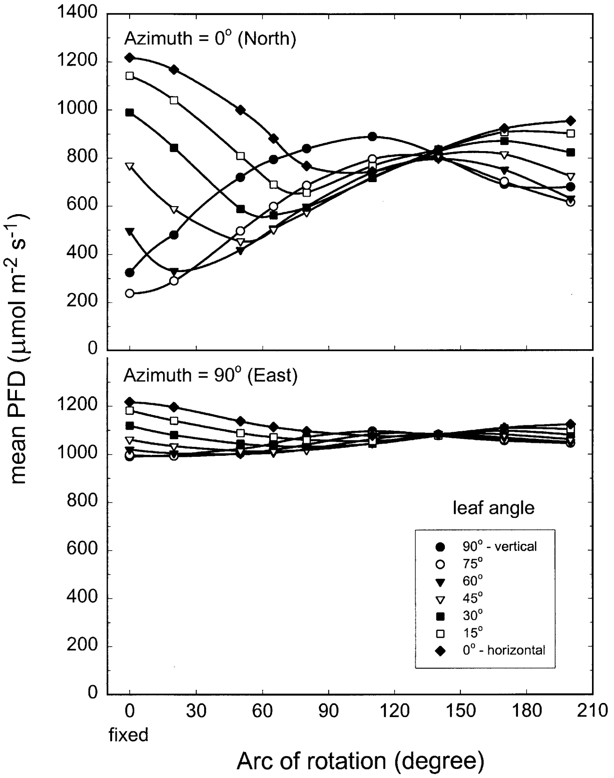

Fig. 9 Simulated effect of rotation angle and flutter on light interception at two contrasting azimuth angles for individual aspen leaves in full sun for day 155 and 38.5° latitude

muth angles as well, the slight variation in light interception for fluttering leaves oriented north/south versus east/west (as in Fig. 7) disappeared (the line became flat, data not shown). Thus, flutter simply acts to re-randomize not only leaf angles but azimuth angles as well, eliminating all difference in light interception within a randomly oriented population of leaves.

The model uses a default arc of rotation of 140° estimated from observations of aspen leaves in the field and wind tunnel studies using slow motion photography. However, the arc of rotation in nature is variable and depends on wind speed. Under light breezes, aspen leaves move through a much smaller arc. Therefore, the light interception of fluttering leaves at various rotation angles was estimated for two contrasting azimuth angles (north and east). As the arc of rotation increased the light interception became more uniform across the leaf angles tested (Fig. 9). Arc of rotation angles greater than 200° were not tested since they were not considered a realistic possibility for aspen leaves.

Using 65° as a typical low wind speed arc of rotation, the PFD interception and carbon gain was estimated for various azimuth orientations and leaf angles. Although a 65° arc of rotation does not eliminate variation in PFD interception in a randomly oriented population of aspen leaves, those leaves still gained 5% more carbon than leaves fixed in position (Fig. 10).

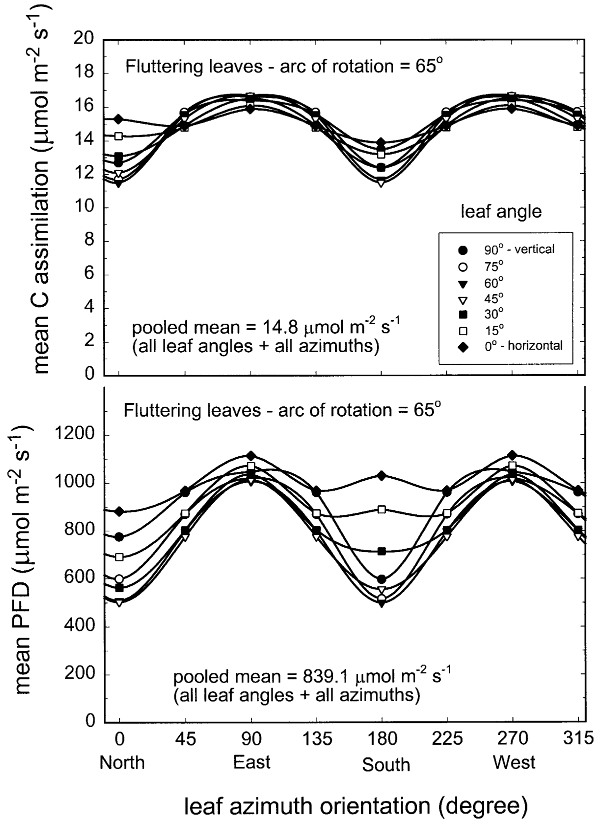

Fig. 10 Simulated effect of flutter, over a 65° arc of rotation, on light interception and carbon assimilation for individual aspen leaves in full sun at various leaf angles and azimuths for day 155 and 38.5° latitude

Discussion

The results using the double-sided cuvette (Table 1) indicate that aspen leaves may not be limited by gradients in light absorption and photosynthetic capacity within the leaf. Gradients in light absorption through different layers of the mesophyll have been demonstrated previously (Terashima and Saeki 1985; Vogelmann et al. 1989; Cui et al. 1991) leading to gradients in photosynthetic capacity (Terashima and Saeki 1985; Evans et al. 1993). Thus, rapidly alternating light on each side of a leaf could potentially reduce the limitations imposed by such gradients. The vertical orientation and thickness of aspen leaves may reduce these gradients such that no benefit of alternating light was observed. If the gradients in photosynthetic capacity are large, such as in very thick leaves, then alternating light exposure could be detrimental if the lower surface does not have the capacity to utilize the additional light energy input. This also was not the case for aspen leaves (Table 1). One might predict that species with leaves that flutter, should have relatively thin leaves with similar photosynthetic capacities on the abaxial and adaxial surfaces.

Clearly, this model is a simplification of the complex leaf flutter motion. Modeling the exact movement of fluttering leaves would require sub-models that simulate petiole twisting and bending. In addition, as leaves flutter, the blade does not remain flat but becomes slightly cupped. Observations from slow motion photography of fluttering poplar leaves suggests that random effects due to variations in wind speed and turbulence would also need to be accounted for. However, adding layers of complexity may not provide additional information. For example, when changes in azimuth direction were included, the basic story of reduced variability in light interception for a population of randomly oriented leaves was maintained. Any factor that modifies leaf angle or azimuth on a rapid time scale should have similar effects on light interception and carbon gain to those presented in this modeling exercise.

At very low wind speeds, aspen leaves begin to vibrate until some threshold is reached where a full flutter motion begins. This threshold varies, but wind speeds as low as 1 m s^{-1} can initiate flutter (Roden and Pearcy 1993a). Once leaves begin to flutter, the motion seems unaffected by wind speed until very windy conditions prevail. Under high wind speeds poplar leaves tend to cease fluttering and fold over to become more aerodynamic (Vogel 1989). Although an arc of rotation of 140° appears optimal (Fig. 9), the benefits of flutter can extend over a wide range of flutter habits, even those generated by relatively light winds (Fig. 10). More work is needed on the biomechanics of aspen blades and petioles (Niklas 1991), to determine if they have been selected for any specific arc of rotation.

Regardless of how leaves flutter, the subsequent redistribution of light could have a potential benefit for a randomly oriented population of leaves (Fig. 8). Other studies have also postulated that carbon gain is maximized when light is distributed evenly over many leaves (DeWit 1966; Sprugal 1989; Roden and Pearcy 1993b). A population of fixed leaves would have some intercepting very little PFD while others were well above light saturation (Fig. 6). However, a population of fluttering sun leaves will all intercept very similar amounts of light which is close to the level at which the photosynthetic apparatus is saturated. This was the primary reason for the enhanced photosynthetic rates for a fluttering population of leaves. At the very least, this study supports the hypothesis that flutter may not substantially reduce the carbon gain for leaves at the top of the canopy.

Enhanced carbon gain with flutter was also a function of greater lightfleck use efficiency (LUE) which is the ratio of carbon gain during light transients compared to the carbon gain predicted by an instantaneous response to the steady-state assimilation rate (Chazdon and Pearcy 1986). A number of studies have demonstrated that plants can use short frequent lightflecks more efficiently than longer less frequent lightflecks (Chazdon and Pearcy 1986; Lakso and Barnes 1978; Roden and Pearcy 1993b). The LUE was close to 100% (no difference from steady-state) for all fixed leaves, but ranged from 105 to 115% for fluttering leaves. Aspen leaves can efficiently utilize flashing light regimes due, in part, to post-illumination CO_2 fixation (Chazdon 1988; Pearcy 1990; Roden and Pearcy 1993b). The photosynthesis model predicted (data not shown) that fluttering leaves maintained high stomatal conductances, constant metabolite pools sizes (RuBP) and highly activated Calvin cycle enzymes (in particular Rubisco). Thus leaves at the top of the canopy remain, throughout most of the day, in a highly induced state and are able to efficiently take advantage of all light transients. Fixed leaves also maintained high stomatal conductances, however, the photosynthesis model predicted reductions in the activation state of Rubisco (to approx. 50% of maximum) when fixed leaves were parallel to the solar beam for extended periods.

This analysis was based on a population of leaves randomly distributed in terms of leaf angles and azimuths. Although aspen leaves do appear randomly oriented in terms of azimuth, they tend to be more vertical than horizontal. A brief survey of a small aspen canopy revealed that all leaf angles from 0 to 90° were represented although angles between 45° and 60° were the most common (Roden, unpublished data).

Roden and Pearcy (1993a) found that flutter increased light penetration into the lower canopy. Increased light penetration must come at the expense of reduced light interception of fluttering sun leaves. However, this model predicts no change in total light intercepted for a randomly oriented population of sun leaves. It is possible that a non-random leaf angle distribution or reduced arc of rotation for fluttering leaves could potentially account for reduced upper canopy light interception and thus increased light penetration (e.g. leaves with a more horizontal orientation). A more detailed study of leaf angles and azimuths for an entire aspen canopy would highlight deviations in the assumption of randomness and their effects on light interception. Another possibility is that the degree of clumping of leaves changes during windy conditions. Observations of canopy motion during windy conditions support the idea that groups of leaves tend to be more clumped due to directional forcing by the airflow. Greater clumping would reduce the extinction coefficient for light penetration. This might also reduce the uniformity of upper canopy light capture but to what extent is unknown.

The model presented here predicts the light interception of an individual leaf only and thus ignores canopy effects (e.g. clumping). For instance, a leaf on the east-facing outer portion of a canopy will receive full sun in the morning and canopy shade in the afternoon, complicating the effects of flutter over the course of the day. The complexity involved in modeling the light interception of an entire canopy would be quite daunting. These and other factors that modify PFD interception may lessen the photosynthetic enhancement predicted by this model.

Conclusions

The assumption made by Roden and Pearcy (1993b) that flutter will have minimal effects on the carbon gain of upper canopy leaves due to their exposure to direct solar radiation was well founded. This study also points to the possibility that not only will flutter enhance lower canopy light environments and carbon gain (Roden and Pearcy 1993a, 1993b), but potentially the upper canopy as well. Flutter acts to continuously re-randomize leaf orientations (both leaf angles and azimuth) in a population of leaves and thus may not alter overall light interception. However, at any particular time, fixed "sun" leaves can be exposed to light levels well above and well below that which would saturate photosynthesis. By redistributing the light, flutter can reduce the amount of time any leaf is above or below light saturation, and thus enhance carbon gain.

The flutter of upper canopy leaves will modify the lower canopy light environment as well. This study implies that whenever a leaf is parallel to the solar beam, flutter will enhance its own light interception and reduce the amount of direct beam radiation penetrating to the canopy below. This will certainly benefit the upper canopy leaf's carbon gain and may have only a modest effect on leaves directly below depending on how close they were to light saturation. Whenever an upper canopy leaf is normal to the solar beam it is intercepting more light than required to support maximal photosynthetic rates and shading the lower canopy to the greatest extent. In this situation, flutter will increase light penetration into the lower canopy where leaves are light limited, without significantly reducing the fluttering leaf's carbon gain. Thus flutter could create a spatially uniform and temporally dynamic light environment for the entire canopy.

Acknowledgements I would like to thank Bob Pearcy and Lou Gross for modifying their dynamic model of photosynthesis to handle 10 Hz data, Lin Roden for tirelessly running hundreds of model simulations and Bob Pearcy for reviewing an earlier version of this manuscript.

Appendix

Appendix 1

Parameter values, definitions, and symbols for the dynamic model of photosynthesis (see Pearcy et al. 1997) used to model carbon gain in aspen leaves

Parameter	Symbol	Value	Units
Maximum stomatal conductance	$g_{s.max}$	500	mmol m^{-2} s^{-1}
Minimum stomatal conductance	$g_{s.min}$	50	mmol m^{-2} s^{-1}
Boundary layer conductance	g_b	1,440	mmol m^{-2} s^{-1}
Time constant for biochemical signal increase in guard cell	$\tau_{g.i}$	22.2	s
Time constant for biochemical signal decrease in guard cell	$\tau_{g.d}$	420	s
Time constant for increase in osmotica in guard cell	τ_k	1,080	s
Time constant for increase in water in guard cell	τ_{H2O}	600	s
Rate of non-photorespiratory respiration	r_d	2	μmol m^{-2} s^{-1}
Maximum rate of electron transport	$V_{j.max}$	120	μmol m^{-2} s^{-1}
Maximum rate of carboxylation	$V_{c.max}$	150	μmol m^{-2} s^{-1}
Quantum yield for electron transport	α_j	0.085	mol mol^{-1}
Curvature factor for electron transport	θ_j	0.9	Dimensionless
Maximum pool size for RuBP and its immediate precursors	R_{max}	150	μmol m^{-2}
Maximum pool size of high-energy substrates for RuBP regeneration	T_{max}	160	μmol m^{-2}
Apparent Michaelis-Menton constant of carboxylation for R	K_r	75	μmol m^{-2}
Apparent Michaelis-Menton constant of carboxylation for T	K_t	20	μmol m^{-2}
Minimum RuBP regeneration rate in the dark	$V_{f.min}$	0.01	relative to max
Minimum carboxylation rate in the dark	$V_{c.min}$	0.20	relative to max
Rate of decay of photorespiratory intermediates in *G* pool	Ψ	0.04	s^{-1}
Time constant for light activation increase of carboxylation activity	$\tau_{c.i}$	300	s
Time constant for deactivation of carboxylation activity	$\tau_{c.d}$	1,200	s
Time constant for light activation/deactivation of RuBP regeneration	τ_r	60	s

References

Björkman O (1981) Responses to different quantum flux densities. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopedia of plant physiology. Springer, Berlin Heidelberg New York, pp 57–107

Boardman NK (1977) Comparative photosynthesis of sun and shade plants. Annu Rev Plant Physiol 28:355–377

Chazdon RL (1988) Sunflecks and their importance to forest understorey plants. Adv Ecol Res 18:1–63

Chazdon RL, Pearcy RW (1986) Photosynthetic responses to light variation in rain forest species. II. Carbon gain and light utilization during lightflecks. Oecologia 69:524–531

Cui M, Vogelmann TC, Smith WK (1991) Chorophyll and light gradients in sun and shade leaves of *Spinacia oleracea*. Plant Cell Environ 14:493–500

DeWit CT (1966) Photosynthesis of crop surfaces. Adv Sci 23:159–162

Desjardins RL, Sinclair TR, Lemon ER (1973) Light fluctuation in corn. Agron J 65:904–908

Evans JR, Jakobsen I, Ögren E (1993). Photosynthetic light-response curves. II. Gradients of light absorption and photosynthetic capacity. Planta 189:191–200

Farquhar GD, Caemmerer S von, Berry JA (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 149:78–90

Finnigan JJ (1985) Turbulent transport in flexible plant canopies. In: Hutchison BA, Hicks BB (eds) The forest-atmosphere interaction. Reidel, Boston, pp 443–480

Hongliang T, Hipps L (1991) The properties of sunflecks in a flexible plant canopy, and their relationship to turbulence. The 20th conference on Agricultural and Forest Meteorology, Salt Lake City, Utah, no. 4165

Jones HG (1986) Plants and microclimate: a quantitative approach to environmental plant physiology. Cambridge University Press, Cambridge

Knapp AK, Smith WK (1987) Stomatal and photosynthetic responses during sun/shade transitions in subalpine plants: influence on water use efficiency. Oecologia 74:62–67

Lakso AN, Barnes JE (1978) Apple leaf photosynthesis in alternating light. Hortic Sci 13:473–474

Myneni RB, Impens I (1985) A procedural approach for studying the radiation regime of infinite and truncated foliage spaces. II. Experimental results and discussion. Agric For Meteorol 34:3–16

Niklas KJ (1991) The elastic moduli and mechanics of *Populus tremuloides* (Salicaceae) petioles in bending and torsion. Am J Bot 78:989–996

Norman JM, Tanner CB (1969) Transient light measurements in plant canopies. Agron J 61:847–49

Pearcy RW (1990) Sunflecks and photosynthesis in plant canopies. Annu Rev Plant Physiol Plant Mol Biol 41:421–453

Pearcy RW, Gross LJ, He DX (1997) An improved dynamic model of photosynthesis for estimation of carbon gain in sunfleck light regimes. Plant Cell Environ 20:411–424

Pfitsch WA, Pearcy RW (1989) Steady-state and dynamic photosynthetic response of *Adenocaulon bicolor* (Asteraceae) in its redwood forest habitat. Oecologia 80:471–476

Roden JS, Pearcy RW (1993a) Effect of leaf flutter on the light environment of poplars. Oecologia 93:201–207

Roden JS, Pearcy RW (1993b) Photosynthetic gas exchange response of poplars to steady-state and dynamic light environments. Oecologia 93:208–215

Sassenrath-Cole GF, Pearcy RW (1992) The role of RUBP regeneration in the induction requirement of photosynthetic CO_2 exchange under transient light conditions. Plant Physiol 99:227–234

Sprugal DG (1989) The relationship of evergreeness, crown architecture, and leaf size. Am Nat 133:465–479

Tang Y-H, Washitani I, Tsuchiya T, Iwaki H (1988) Fluctuation of photosynthetic photon flux density within a *Miscanthus sinensis* canopy. Ecol Res 3:253–266

Terashima I, Saeki T (1985) A new model for leaf photosynthesis incorporating the gradients of light environment and of leaf photosynthetic properties of chloroplasts within a leaf. Ann Bot 56:789–499

Vogel S (1989) Drag and reconfiguration of broad leaves in high winds. J Exp Bot 40:941–948

Vogelmann TC, Borman JF, Josserand S (1989) Photosynthetic light gradients and spectral regime within leaves of *Medicago sativa*. Philos Trans R Soc Lond Ser B 323:411–421