

Sunflecks in forest communities and their importance for plant life in a forest understorey

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Abstract

Plant life in forest understorey is limited by several environmental factors, esp. by limited light resources (solar radiation). Various adaptations (life strategies) help plants to use heterogeneity of the environment, including moving short-term sunflecks of direct solar radiation, which penetrates through openings between crowns of tall trees to the soil surface. Size, frequency and duration of sunflecks change, depending on stand structure and position of sun on the sky.

Sunflecks occurrence and effects on stomatal conductance, water relations and photosynthesis were studied during sunny days in understoreys of deciduous forests at Báb and Bratislava-Patrónka (both in Western Slovakia, Central Europe), as well as in laboratory conditions.

Sudden increasing of solar radiation (from ca 6 W m^{-2} to 50 and more) caused by natural sunflecks increased stomatal conductance, transpiration rate and net photosynthetic rate ca 50-90 %. Responses of spring and summer herbs were similar. In an annual *Impatiens parviflora*, rapid increasing of radiation in laboratory conditions increased stomatal conductance and photosynthesis by 25-70 %. In all cases plant responses were immediate and steady state was reached up to 400 sec. Long-term sunflecks (more than 30 min) on a plant can cause water stress and temporal wilting of leaves and plants. In sensible plants we can observe damage by light (photoinhibition).

Plants growing in the forest understorey can improve their energy balance by utilizing sunflecks and gaps. And by higher photosynthetic rate large portion of daily carbon gain which is important for carbon balance of a plant (in long period the gain can be up to 60 %).

Key words: heterogeneity, light regime, sunflecks, forest understorey, plant responses, carbon balance

Introduction

Stand microclimate is influenced by vegetation properties, stand structure and architectural features of the canopy (cf. MONTEITH, 1973, 1975).

Temperate-zone forests are complex ecosystems with high species diversity and complex vertical and horizontal structure. Leaf canopy of tall trees is the structural unit of the forests which form the particular and characteristic environment of the forest stand interior, beneath which the understorey species develop and grow (cf. ELIÁŠ, 1984). In the case of the stand microclimate, it reduces solar radiation and wind speed, and increases air temperature in tree crowns (ELIÁŠ et al., 1989). The environment under tree canopy is primarily characterized by light-limited conditions which are clearly manifested in the growing period. Irradiance (I) is considered the most limiting resource also in wet tropical forests (WATLING et PRESS, 2000, PEARCY, 2007).

Radiation regime in a forest stand is also characterized by very large horizontal variability, namely uneven distribution of light flux density on a soil surface (see e.g. ALEKSEYEV, 1975). The variability results from tree canopy heterogeneity and it is manifested by occurrence of sunflecks and gaps. The penetration of direct solar radiation through canopy openings is strongly controlled by the interactions of solar elevation and variation of canopy density with angular elevation (ALEKSEYEV, 1975). Canopy structure, topography, treefall gaps, and sunflecks all contribute to the understory light environment (WAY et PEARCY, 2012).

The sunflecks - brief increases in solar irradiance that occur in forest understories when sunlight is able to directly reach the ground - differ by their irradiance intensity, duration, size, shape and frequency (ELIÁŠ, 1983, 1984, CHAZDON, 1988,). Each sunfleck has only short duration (last for seconds or minutes at a time), but importance of the sunflecks is related to the plants responses and utilization (benefits). Sunflecks create a continually changing pattern of sun and shade patches, both within a tree canopy and on understory forest plants. Despite being present in any given location in these environments <10% of the time, sunflecks contribute 10–80% of the photon flux density (PFD) available for photosynthesis by understory plants (CHAZDON, 1988, CHAZDON and PEARCY, 1991). Thus, factors that affect sunfleck utilization can be important determinants of the carbon balance of understory plants (WAY et PEARCY, 2012).

Sunfleck regimes within forest canopies have not been well studied because of access problems, and some high-frequency measurements of PFD on individual leaves throughout a canopy are only presented as a daily integrated light regime (WAY et PEARCY, 2012).

In this paper we shortly presented results of our studies of sunflecks effects on understory plants in temperate deciduous forests in Western Slovakia (Central Europe).

Material nad methods

Field measurements were conducted in the oak-hornbeam forest at Báb, former IBP Forest Research Site (JURKO et DUDA, 1970, BISKUPSKÝ, 1975), and in natural deciduous forest stands near Bratislava-Patrónka (MASAROVÍČOVÁ et ELIÁŠ, 1986). We documented sunflecks effects in natural conditions. Micrometeorological measurements in the oak-hornbeam forest at Báb were surveyed by ELIÁŠ (1989). Spatial and temporal variations in solar radiation were studied and the measurements were performed during selected days, using Li-Cor instruments (cf. ELIÁŠ, 1979, 1983, and ELIÁŠ et al., 1989). Stomatal conductance was measured by Li-60 porometer, tranpiration rate, the leaf water deficit (WSD) was estimated by 2h saturating of discs cut out from leaves, leaf water potencial by the pressure chamber method (cf. ELIÁŠ, 1983, MASAROVÍČOVÁ et ELIÁŠ, 1986). Net photosynthetic rate (PN) in the forest was photosynthetic rate (P_N) in the forest was measured by the gasometric method in an open system with a simple assimilation chamber (for details see MASAROVÍČOVÁ et ELIÁŠ, 1986). In the course of of sampling days we registered natural dynamics of sunfleck occurrence in microhabitats as well as their as well as their influence on charactericteristics of plant eco-physiology.

Lightflecks effects on understory species were studied in laboratory conditions in Institute of Experimental Biology and Ecology in Bratislava. Photosynthesis responses to rapid irradiance changes were measured – I was suddenly increased or decreased in order to find out the sensitivity of two forest herbs (*Aegopdoium podagraria* and *Impatiens parviflora*) to reduce (short-time) I changes (cf. MASAROVÍČOVÁ et ELIÁŠ, 1986).

Results

Sunfleck light regime

The horizontal heterogeneity of the light climate of the deciduous forest was large, including sunflecks (DUDA, 1975, 1986, ELIÁŠ, 1983). In the oak-hornbeam forest at Báb incident PAR at the top of the canopy was reduced by approximately 50 % by the the upper 4- to 5-m-thick layer of leaves, and about 5 % and less penetrated to the ground (ELIÁŠ et al., 1989). Tree crowns filtered up to 75 % of incident PAR. In summer period (shade phase) I at soil surface was low (about 3% of the total I), also in the course of a cloudless, sunny day. I was usually lower than 30 W m^{-2} , but in sunflecks it exceeded the , but in sunflecks it exceeded the values by one or two orders of magnitude. In the by one or two orders of magnitude. In the sampling day we registered at a sampling day we registered at a point sensor point sensor five peaks five peaks of of I : two high between 9.30 and 11.00 and then three in the afternoon I : two high between 9.30 and 11.00 and then three in the afternoon (at 12.30 and between 14.00 and 15.00) (Fig. 1). In the microhabitats, the frequency of sunflecks was higher in the morning, effecting stomatal conductance and water relations of understorey plants.

Plant responses to sunflecks

Stomata responses

Daily variations in stomatal conductance were large in understory plants. The highest values were evidently recorded always in bright sunflecks, neglecting inter-species differences in absolute values (cf. also ELIÁŠ, 1992). Maximum values of stomatal conductance reaching in various individual sunflecks during a day varied from one sunfleck to another in the same leaves (cf. ELIÁŠ, 1983). In the course of a day, stomatal conductance of a leaf oscillated day, stomatal conductance of a leaf oscillated between the lowest value in full shade between the lowest value in full shade and the highest one and the highest one in bright sunfleck. In the morning, the leaf was in bright sunfleck. In the morning, the leaf was frequently sunlit by movingunlit by moving sunflecks sunflecks and its stomatal conductance, therefore, was and its stomatal conductance, therefore, was close to daily close to daily maxima. In the afternoon, the maxima. In the afternoon, the I intensity of moving sunflecks decreased and sstomatal tomatal conductance of the leaf conductance of

the leaf was, therefore, usually close was, therefore, usually close to semi-shaded and shaded leaves.

Water relations/Transpiration rate

In sunflecks, transpiration rate of the understory plants was extremely high, in comparison with that in shade areas (cf. ELIÁŠ, 1983). Water saturation deficit increased rapidly Š, 1983). Water saturation deficit increased rapidly from morning to noon from morning to noon and reached maxima in the afternoon. Sunflecks duration longer than 30 minutes caused temporal wilting of leaves in the annual *Impatiens parviflora* (see also ELIÁŠ, 1992).

Photosynthesis responses

The maximum daily values of stomatal conductance were found?measured in sunflecks. In spring and summer, there were significant differences in P_N and g_s between plants in the shade and on sunflecks. Within short-time short-time I changes (17-50) minutes P_N alternations by more than 50% were registered. With *Impatiens parviflora* the change from deep shade (7 W m^{-2}) to bright sunfleck (170 W m^{-2}) caused within 17 min a P_N rise up to 94% (from 0.82 to $13.93 \times 10^{-8} \text{ kg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). In measuring with *Impatiens parviflora* under laboratory conditions, sudden I changes (from 18 to 220 W m^{-2} and conversely) caused P_N changes by 23-74 %. In all cases plants responded instantly to sudden (short-time) I changes within 400 sec. (cf. MASAROVÍČOVÁ et ELIÁŠ, 1986). (cf. MASAROVÍČOVÁ et ELIÁŠ, 1986).

In wilting *Impatiens parviflora* leaves on the sun exhibited water potential -0.8 MPa .

Discussion

Sunflecks light regime

The characteristics of sunfleck light regimes in an understory or in a tree canopy depend on attributes such as the canopy height, and canopy structural characteristics such as the clumping of foliage, the flexibility of branches and petioles, and leaf size (WAY et PEARCY, 2012). The abundance of sunflecks varies greatly both within and amongst forest types, generally the frequency and intensity of sunflecks decreases as tree height and the leaf area index increase (CHAZDON et PERACY, 1991). MIYASHITA et al. (2012) characterized sunfleck distributions in a Japanese temperate deciduous and coniferous forest understory, as well as in gap

sites in each forest type, over an entire year. Unsurprisingly, the evergreen forest understory had the lowest daily accumulated PFD over the year, but also many fewer sunfleck events ($\text{PFD} > 50 \mu\text{mol m}^{-2} \text{s}^{-1}$) than the deciduous or gap plots, since evergreen plots had high leaf area indices year-round. All of the high-intensity sunflecks ($\text{PFD} > 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) that did occur in the evergreen plot were in the growing season (May to October), while the deciduous plot experienced high-intensity light events as early as February.

The temporal nature of sunfleck regimes in understories is determined in part by the earth's rotation and by wind-driven canopy movements. Frequently, sunflecks in forest understories are clustered into periods of multiple sunflecks separated by longer periods with few or no sunflecks. On a clear day, a leaf in the understory may receive only a few sunflecks in the most shaded microsites or up to 300 or more sunflecks. Most of these are shorter than 10 s and only 1–2% are typically large enough to approach full sunlight PFDs because of penumbral effects (PEARCY, 1983, CHAZDON, 1988). However, sunflecks longer than 120 s, which represent only 5% of all sunflecks in forest understories, contribute >75% of the total daily sunfleck PFD (PEARCY et al. 1994).

Plant responses to sunflecks

Water relations and CO_2 exchange in forest herbs were strongly affected by moving sunflecks: in them higher P_N and g_s , and lower leaf water potential were found than in the shade (ELIÁŠ, 1979, 1983, 1984, MASAROVICHOVÁ et ELIÁŠ, 1986). Water relations of seven herbaceous perennials growing in the oak-hornbeam forest were markedly influenced by sunflecks, where g_s and transpiration rate were significantly higher than in shade areas (ELIÁŠ, 1983, 1984). This tendency as well as higher P_N were confirmed in spring and summer species by MASAROVICHOVÁ and ELIÁŠ (1986). Short-term changes of irradiance caused significant P_N changes. Differences were found in the I response of P_N between spring (sun) plants and summer (shade) plants as well as between spring and summer leaves of *Aegopodium podagraria*. During one day P_N and g_s fluctuated, following I of the leaf, from minimum in full shade to maximum in sunflecks. WSD had the opposite tendency.

Responses of CO_2 assimilation rates to sunflecks are complex because several components of the photosynthetic apparatus with markedly different time constants (τ , the time to reach 63% of the full response) are involved. Light harvesting and

energy transfer essentially occur instantaneously relative to the timescales usually considered in physiology, while the initial adjustments in photosynthetic carbon reduction cycle metabolites following a change in PFD take no more than a second or so (WAY et PEARCY, 2012). The pattern that emerges from several studies is that plants in shady understories or grown under low-light conditions usually have faster rates of induction and reach 90% of full induction in a shorter time than plants in more open habitats or grown in high-light environments.

At timescales of minutes, the utilization of sunflecks is limited by the induction requirement of CO₂ assimilation. Photosynthetic induction in leaves has been shown to involve light regulation of key photosynthetic enzymes and stomatal opening which requires 20 or more minutes for completion and in effect limits the maximum assimilation rate that can be achieved during a sunfleck (WAY et PEARCY, 2012).

The role of g_s in the dynamics of induction is quite variable, depending on species, growth conditions and the environment. Increases in g_s during induction typically exhibit a short lag before increasing to a maximum over another 10–60 min (WAY et PEARCY, 2012). In response to a sunfleck, stomata exhibit a distinct pulse response. This pulse response consists of an initial lag followed by an increase in g_s that continues in low light long after the sunfleck itself (cf. post-sunflecks effects in ELIÁŠ, 1983). An often slower closing response is then initiated that returns g_s back to the initial levels measured prior to the sunfleck (WAY et PEARCY, 2012).

Sunflecks contribution to carbon gain

Previous studies estimated that sunflecks can be responsible more than 80% of the photons that reach plants in the understory, and up to 35% of carbon fixation. This makes them important sources of energy for plants in the understory of forests (CHAZDON, 1988, CHAZDON and PEARCY, 1991). The amount of energy that a sunfleck provides depends on their duration, size and shape and the intensity of photosynthetically active radiation (PAR), which itself depends on the arrangement of vegetation in the canopy and the position of the sun in the sky (CHAZDON and PEARCY, 1991).

The daily contribution of sunfleck utilization by leaves can be determined by integrating the diurnal course of photosynthesis and PFD and separating carbon gain due to sunflecks from that due to background diffuse PFD. The carbon gain can then be compared with a steady-state model to address the question of how limitations or

enhancements to sunfleck use influence carbon gain (WAY et PEARCY, 2012). The few available studies of this type reveal wide variation, with sunflecks contributing from 30 to 60% of the daily carbon gain in tropical forest understories (PEARCY, 1987, WATLING et PRESS, 2000) but as little as 10–20% for deciduous forest tree seedlings (Schulze 1972, Weber et al. 1985). The low contributions in the deciduous forest may be due to the higher diffuse light level in this habitat and also the low photosynthetic capacity of the seedlings (WAY et PEARCY, 2012). The annual contribution of photosynthesis during sunflecks derived in this way ranged from 9% in sites with the least annual sunfleck PFD to 46% for sites with the greatest sunfleck PFD. Thus, sunflecks can be a significant driver of carbon gain on both a daily and annual basis (WAY et PEARCY, 2012).

Forest Canopy carbon uptake Models limits

Variations of physiological features within coenopopulations of understory species on a horizontal plane appeared to be limit for correct modeling of the physiology within a plant stand (ELIÁŠ, 1983). Way and Pearcy (2012) showed that dynamic responses of photosynthesis to sunflecks are not accounted for in current models of canopy carbon uptake, which can lead to substantial overestimates of forest carbon fixation. Since sunflecks are a critical component of seasonal carbon gain for shaded leaves, sunfleck regimes and physiological responses to sunflecks should be incorporated into models to more accurately capture forest carbon dynamics. Comparisons of the diurnal course of leaf level carbon assimilation to the predictions of a steady-state model can provide insights into the physiological and biochemical limitations to sunfleck utilization. The steady-state model is parameterized from a light response curve and then applied to the diurnal course of PFD. Several different equations describing the light response of photosynthesis have been used, but the essential point is that step change in PFD yields an instantaneous step change in assimilation in a model of this type. Using this approach, Pfitsch and Pearcy (1989) found that the steady-state model overestimated daily carbon assimilation by 20 to 30% on clear days with substantial sunfleck activity, but by only 3% on cloudy days when there was no sunfleck activity, which is consistent with a significant induction limitation to sunfleck use in the understory (WAY and PEARCY, 2012).

Further insights into the contribution of sunfleck utilization can be gained by the application of dynamic models of photosynthesis. Several dynamic models directed

at understanding sunfleck use have been developed that start with the widely used Farquhar et al. (1980) model. This model is then modified to make it dynamic by including relevant metabolite pool sizes and light regulation of key enzymes and coupling it to a dynamic stomatal model (Kirschbaum et al. 1988). These models have all been used to reveal large dynamic limitations to daily carbon assimilation in understories, and thus offer a cautionary note regarding reliance on the much simpler steady-state models for understanding carbon budgets of understory plants; similar caveats are likely to apply to tree canopies (WAY and PEARCY, 2012).

Mechanisms of sunfleck tolerance

While sunflecks can be critical to the survival of understory plants, they can be able cause damage. Because the relatively low investment in photosynthetic proteins yields a low light-saturated photosynthetic rate, a classic shade leaf risks photoinhibition and damage from the high PFD of sunflecks, while a classic sun leaf will be ill-suited to shade conditions, overinvesting in photosynthetic proteins that cannot be fully utilized. The sudden and large variations in PFD mean that understory leaves exposed to sunflecks must not only be able to regularly function as shade leaves, but also be able to minimize the potential for damage associated with these crucial, brief bouts of bright light (WAY and PEARCY, 2012). The ability to tolerate sunflecks can involve numerous mechanisms: (i) physical movement to avoid excess PFD, operating on multiple scales (inside chloroplasts, at the whole leaf level, within a tree canopy - rapid leaf movements), (ii) high g_s , to allow for substantial latent heat loss and rapid diffusion of CO_2 into the leaf, (iii) leaf pigments (including anthocyanins and carotenoids). Sunfleck stress tolerance often involves the xanthophyll cycle, which consists of conversions between three xanthophyll pigments (see WAY and PEARCY, 2012, for more details).

Sunflecks cause also increasing of leaf temperature, as it was observed by ELIÁŠ (1983, see also LARCHER, 1995) in understorey plants. WAY and PEARCY (2012) stressed that safely dissipating excess light is critical for preventing damage from sunflecks to leaves, but it does little to protect plants from the direct effects of the rise in leaf temperature that occurs during sunflecks. Leaf temperature increases rapidly during sunflecks as the radiative load on the leaf rises, with temperature increases of up to 10 °C in both tree canopies and understory seedlings. Isoprene emission was identified as a sunfleck tolerance mechanism that protects photosynthetic function.

Emission rates are stimulated by both high-light levels and leaf temperatures, such that isoprene emission ramps up rapidly during sunflecks and declines when the sunfleck ends.

Sunflecks and global change factors interactions

Sunflecks effects should be discussed in relation to global change factors, such as heat and drought stress and elevated CO₂. As discussed above, sudden increases in radiation during sunflecks lead to concomitant rises in leaf temperature, a combination of stresses that can be particularly damaging to leaves. Large leaf sizes, horizontal orientations and low wind speeds in the understory are conducive to achieving high leaf temperatures during sunflecks. While high CO₂ increases induction gain in some species, it appears to have little effect in others; variation in the elevated CO₂ concentration used is unlikely to explain these differences, since different species within a given study responded in opposite manners. Part of this difference may be due to species-specific variation in stomatal behavior (for details see WAY and PEARCY, 2012).

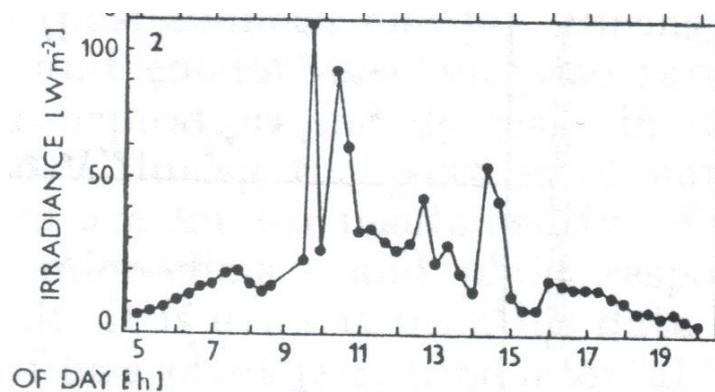


Fig. 1 Variation of irradiance at point sensor situated in the forest stand (2 meters above soil surface) in course of a day (July 13, 1977).

Conclusions

1. Radiation regime in a forest stand is characterized by very large horizontal variability, namely uneven distribution of light flux density on a soil surface. The variability results from tree canopy heterogeneity and it is manifested by occurrence of sunflecks and gaps.

2. The sunflecks contribute evidently to the photon flux density (PFD) available for photosynthesis by understory plants, affect their stomatal conductance, water relations and photosynthesis as well as leaf temperature.
3. Sunfleck utilization increases daily and annual carbon gain of the understorey plants and can be important determinant of the carbon balance of the plants.
4. These dynamic responses and sunflecks contribution to light and carbon fixation in forest canopies, have to be incorporate into models of forest carbon fluxes and improve their performance in this way.
5. Much more research is needed to better understanding and generalization these dynamic responses (including several functional groups), and also effects of climate change on these dynamics.

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Summary

Život rastlín v podraze lesa je limitovaný viacerými ekologickými faktormi, predovšetkým však nedostatkom svetelných zdrojov (slnečného žiarenia). Rôzne adaptácie (životné stratégie) umožňujú rastlinám využívať heterogenitu prostredia, vrátane pohybujúcich sa krátkotrvajúcich škvŕn priameho slnečného žiarenia, ktoré preniká medzerami medzi korunami vysokých stromov až k povrchu pôdy. Veľkosť,

frekvencia a zotrvanie svetelných škvŕn sa menia v závislosti od štruktúry porastu a polohy slnka na oblohe.

Výskyt a vplyv svetelných škvŕn na vodivosť prieduchov, vodný režim a fotosyntézu rastlín sme sledovali počas slnečných dní v podrade opadavých listnatých lesov v Bábe a v Bratislave-Patrónke (obidve západné Slovensko), ako aj v laboratórnych podmienkach.

Náhle zvýšenie úrovne slnečného žiarenia (z ca 6 W m^{-2} na 50 a viac) v dôsledku prírodnej svetelnej škvŕny zmenilo/zvýšilo vodivosť prieduchov, rýchlosť transpirácie a rýchlosť fotosyntézy ca o 50-90 %. Reakcie jarných a letných druhov bylín boli podobné. Pri *Impatiens parviflora* v laboratórnych podmienkach náhle zvýšenie žiarenia zvýšilo vodivosť prieduchov a fotosyntézu o 25-70 %. Vo všetkých prípadoch reakcie boli bezprostredné a rovnovážny stav sa dosiahol do 400 sec. Dlhšie zotrvanie svetelnej škvŕny (viac ako 30 minút) na rastline môže vyvolať vodný stres a spôsobiť prechodné vädnutie exponovaných listov, prípadne celých rastlín. Pri citlivejších rastlinách sa môže pozorovať poškodenie svetlom (fotoinhibícia).

Rastliny rastúce v podrade lesa môžu vďaka svetelným škvŕnám a svetlinám získať podstatné množstvo slnečnej energie do energetickej bilancie. A vďaka zvýšenej rýchlosti fotosyntézy veľkú časť celodenného zisku uhlíka, ktorá je významná pre uhlíkovú bilanciu rastliny (v dlhšom období môže predstavovať zisk až do 60 %).

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