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Light passage through leaf litter: variation among northern hardwood trees

David J. Schimpf^{*}, Nicholas P. Danz¹

Department of Biology, University of Minnesota, Duluth, MN 55812-2496, USA

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Abstract

Leaf litter may influence the environment for germination and photosynthesis of seedlings and other small plants through its effects on transmitted light. We measured red : far-red ratios (R/FR) and photosynthetically active radiation (PAR) transmitted through individual dead leaves from 10 species of deciduous trees of the northern hardwood region of eastern North America. The leaves were collected from the forest litter between spring snowmelt and canopy budbreak, when irradiances on the forest floor are highest. Mean transmittance of PAR varied among species from about 0.5 to 20% for dry leaves and from about 2 to 38% for wet leaves. Transmittance of PAR was greatest for dead leaves from shade-tolerant late-successional species, least for those from shade-intolerant early-successional species, and intermediate for those from moderately shade-tolerant species. Shade leaves transmitted more PAR than sun leaves of the same species, significantly so for *Quercus rubra*, *Acer saccharum*, and *Fagus grandifolia*. Transmitted R/FR was greater for late-successional species than for early-successional species, especially for shade leaves. These ratios tended to be higher for wet leaves than for dry leaves. Shade leaves tended to have higher ratios of transmitted R/FR than sun leaves of the same species, significantly so for *Q. rubra*, *A. saccharum*, and *F. grandifolia*. Changes in both canopy species composition and the proportion of shade leaves during succession in these forests should bring about concomitant environmental trends toward greater favorability for the germination of seeds or spores needing high R/FR, as well as for photosynthesis by plants that are short enough to be covered by leaf litter. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

The amount and type of leaf litter in terrestrial ecosystems may influence the recruitment of plants

^{*} Corresponding author. Tel.: +1-218-726-7265; fax: +1-218-726-8142

E-mail address: dschimpf@d.umn.edu (D.J. Schimpf)

¹ Present address: Center for Water and the Environment, Natural Resources Research Institute, University of Minnesota, Duluth, MN 55811, USA.

from seeds or spores and the growth of established plants short in stature. The effects of litter are both chemical and physical (Facelli and Pickett, 1991). Among the possible physical effects are those on the spectral photon flux densities below the litter. If litter changes the ratio of red : far-red photon flux densities (R/FR), it may then alter phytochrome-mediated developmental processes such as seed germination (Vázquez-Yanes et al., 1990), spore germination (Raghavan, 1989; Hartmann and Weber, 1990),

or de-etiolation (Smith, 1995). To the degree that litter diminishes photosynthetically active radiation (PAR), photosynthetic rates of plants below the litter may be reduced. When litter is found below living foliage, the green leaves greatly diminish the light reaching the dead leaves. In forests, the properties of litter will therefore have their greatest influence on photobiology at the soil surface within canopy gaps or during periods when deciduous trees are leafless.

In northern hardwood forests of eastern North America there are several weeks in April and May, after snowmelt and before new canopy leaves emerge, when irradiances at the forest floor reach their highest annual values (Hutchison and Matt, 1977). Photoperiod is nearing its maximum, and temperatures and soil moisture are sufficient for plant growth. A guild of herbaceous species, the vernal flora (or spring ephemerals), uses this temporal window of resource richness for nearly all of its annual photosynthesis (Greller, 1988). This is also the season when other plants on the forest floor have opportunities to make large photosynthetic gains.

We studied characteristics of sunlight that had passed through dead leaves gathered from the litter layer of northern hardwood forests between snowmelt and leaf-out. Our objectives were to test for differences among species, differences between sun leaves and shade leaves within a species, differences dependent on whether the adaxial (upper) or abaxial (lower) surface of the blade faced the sun, and differences associated with the wetness of the leaf.

2. Materials and methods

2.1. Plant materials

We collected dead leaves in May 1995. Those of *Fagus grandifolia*, beech, (Latin nomenclature follows Gleason and Cronquist (1991)) came from forest just south of Munising, Michigan, USA, 46°24' N, 86°40' W. We collected *Populus grandidentata* (big-tooth aspen) leaves from forest within Duluth, Minnesota, USA, 46°49' N, 92°05' W, and those of the following eight species from forest 30'' directly north of there: *Acer rubrum* (red maple), *Acer saccharum* (sugar maple), *Betula alleghaniensis* (yellow birch), *B. papyrifera* (paper birch), *P. balsamifera* (balsam

poplar), *P. tremuloides* (trembling aspen), *Quercus rubra* (red oak), and *Tilia americana* (basswood). We assigned species to successional categories based on the literature (Burns and Honkala, 1990; Barnes, 1991). We classified paper birch and all three *Populus* as shade-intolerant early-successional species; basswood, red maple, yellow birch, and red oak as mid-successional species of moderate shade tolerance; and beech and sugar maple as highly shade-tolerant late-successional species.

The soil at Munising was classified as a Kalkaska sand, a spodosol, by Berndt (1977). The Duluth sites have sandy-loam soils (Agricultural Experiment Station, 1977) in glacial till derived largely from mafic igneous bedrock (Schwartz, 1949). We collected balsam poplar leaves from saturated soil and all other species from well-drained locations, consistent with where the producing trees grew. We deliberately attempted to obtain a variety of leaf shapes and sizes within species, and the relative numbers of sun and shade leaves is not intended to be representative. We chose leaves that had intact blades, which came disproportionately from upper strata of the litter. Continuous snow cover in the previous winter at Duluth began in late November, which is typical; October through November averaged 2.4°C warmer than normal, with total precipitation 1.3 cm (11%) above normal (National Climatic Data Center, 1994b). Continuous snow cover at Munising did not begin until early January (National Climatic Data Center, 1995), which is much later than typical; October through December averaged 3.0°C warmer than normal, with total precipitation 9.3 cm (45%) below normal (National Climatic Data Center, 1994a). These conditions may have affected the properties of the leaves we collected. We softened the dead leaves in cold tap water and flattened them between blank newspaper in a plant press while they dried at room temperature. For each, one sector of its blade about 2 cm in diameter was bordered with ink to aid repeated observation of the same area. Each sector chosen for delineation lacked large veins and holes visible to the naked eye.

2.2. Light measurement

Light measurements were made when clouds did not block the direct solar beam, within 1.5 h of solar noon at Duluth, MN, USA, 46°49' N, 340 m above sea

level, between 29 May and 22 August. For each leaf, we first measured the incident photon flux density of PAR (400–700 nm) on a horizontal surface with an LI-190SA Quantum Sensor and LI-1000 Datalogger (LI-COR, Lincoln, NE, USA) set on instantaneous mode. These values ranged between 1630–1940 $\mu\text{mol s}^{-1} \text{m}^{-2}$. We immediately appressed the leaf over the sensor and recorded transmitted PAR twice, once with each surface of the marked sector of the blade facing up. We recorded incident R/FR photon flux densities (wavebands centered at 660 and 730 nm, respectively) on a horizontal surface with an SKR 110 sensor and SKR 100 meter (Skye Instruments, Limited, Llandrindod Wells, UK) set on Ratio and range 0–200 $\mu\text{mol s}^{-1} \text{m}^{-2}$; the incident flux densities in the red waveband varied between 130 and 180 $\mu\text{mol s}^{-1} \text{m}^{-2}$. We immediately appressed the marked sector of the blade over the sensor and recorded the transmitted R/FR with each of the surfaces of the leaf facing up; the meter was reranged to 0–20 $\mu\text{mol s}^{-1} \text{m}^{-2}$ if the leaf was so opaque that this modification was needed to produce a stable reading. Both types of radiation measurements were first performed using ‘dry’ leaves (equilibrated with atmospheric humidity). We then soaked these leaves in cold tap water for at least 2 h, and made the same series of measurements after blotting the excess surface water from the marked sector of the blade.

Clear-sky midday readings of PAR were taken at ground level every 0.5 m along a transect in the forest at Duluth on 17 May 1995. Positions in the direct shadow of trunks were excluded; this set estimated the maximum PAR incident on the litter before budbreak. The 1940 $\mu\text{mol s}^{-1} \text{m}^{-2}$ we observed in the course of transmission measurements estimated the maximum PAR incident on litter in gaps.

A freehand transverse section was made from each leaf after wetting the blade, then observed in transmitted light at 400 \times . Sections containing two layers of palisade mesophyll cells or one layer of greatly elongated palisade mesophyll cells were classified as sun leaves. Those having a single layer of shorter palisade mesophyll cells were classified as shade leaves. ‘Leaf type’ means sun leaf or shade leaf.

2.3. Statistical treatment

We divided transmitted values of PAR by corresponding incident values of PAR and multiplied by

100 to derive the percentage transmitted. Incident R/FR ratios varied from 1.15 to 1.22; we multiplied all transmitted ratios by 1.20/(observed incident ratio) to adjust them to a common incident ratio. All statistical procedures were done with SAS, release 6.09 (SAS Institute, 1989). It proved necessary to log-transform both the PAR and R/FR quotients to satisfy assumptions of normality, as determined through the Wilk–Shapiro statistic and normal plots of residuals. Wilk–Shapiro values for transformed data were 0.983 (PAR) and 0.990 (R/FR), and the residuals were not different from normal ($P = 0.335$ and 0.921 , respectively). Homogeneity of variances was determined for the log-transformed data using the F -max test on the groups with the highest and lowest variances, and the differences in variance were never significant at $\alpha = 0.05$.

The null hypotheses that transmitted quotients did not differ among species, or between leaf types within species were tested with two-way ANOVA. Hypotheses that transmitted quotients did not differ within leaves according to which surface faced the sun, or within leaves according to dry versus wet condition, were tested with repeated-measures ANOVA. Where significant main effects were found, appropriate multiple comparison tests were carried out. Product-moment correlation coefficients between transmitted PAR and R/FR values were computed.

3. Results

3.1. Effects of leaf surface

There was only one significant difference between upper versus lower surfaces facing the sun in percentage of PAR transmitted—wet basswood sun leaves ($P = 0.016$ for paired t , Bonferroni method); these means were not far apart: 7.9% (upper) versus 8.7% (lower). There were no statistically significant upper versus lower surface differences for transmitted R/FR. Therefore, we used the mean of the values for the upper and lower surfaces facing the sun in all of our other analyses.

3.2. Transmission of PAR

The mean of 22 observations of PAR just above the litter on the forest floor before budbreak was

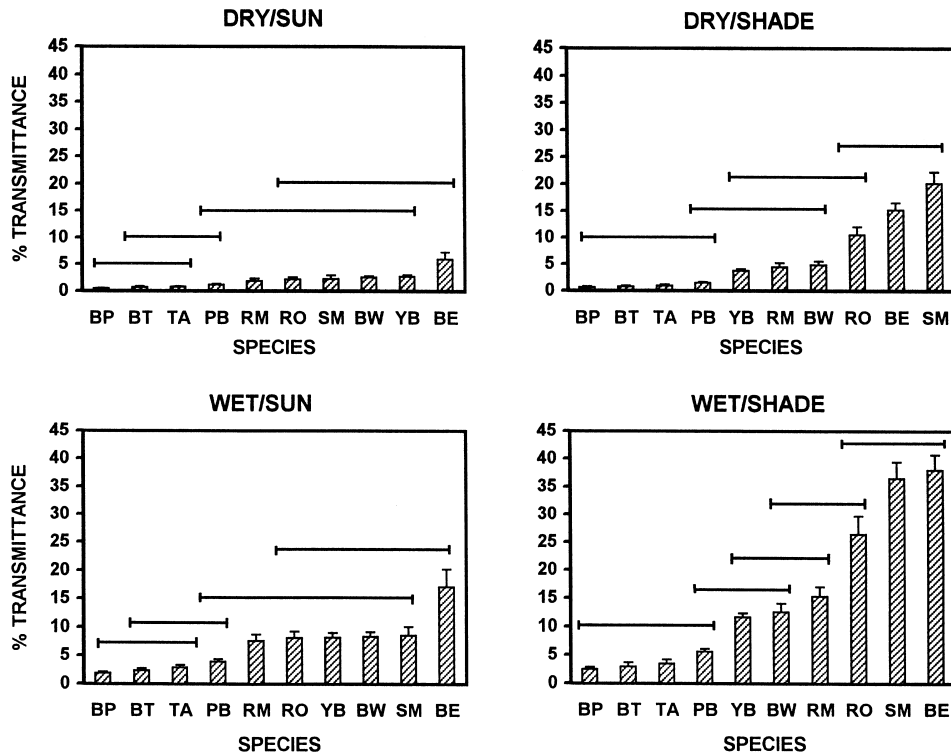


Fig. 1. Interspecific comparisons of transmittance of PAR. Height of bar equals mean transmittance (as %), with 1.0 standard error of the mean indicated (data not transformed). For transformed data, $F = 53.22$ (dry) and $F = 54.78$ (wet) with $P < 0.0001$ for 19, 438 df in both cases. Bars below the same horizontal bracket are not different at $\alpha = 0.05$, using Tukey's HSD. Species codes and number of leaves: BP = balsam poplar ($n = 22$ sun, 7 shade); BT = bigtooth aspen ($n = 20$ sun, 10 shade); TA = trembling aspen ($n = 26$ sun, 7 shade); PB = paper birch ($n = 8$ sun, 23 shade); RM = red maple ($n = 7$ sun, 19 shade); RO = red oak ($n = 38$ sun, 21 shade); SM = sugar maple ($n = 8$ sun, 48 shade); BW = basswood ($n = 30$ sun, 35 shade); YB = yellow birch ($n = 23$ sun, 43 shade); BE = beech ($n = 23$ sun, 40 shade).

$1505 \mu\text{mol s}^{-1} \text{m}^{-2}$ (s.d. = 195); the median value was $1550 \mu\text{mol s}^{-1} \text{m}^{-2}$. The percentage of PAR transmitted differed significantly among species (Fig. 1). For dry leaves, means for all three species of *Populus* were less than 1% for both leaf types, with shade leaves of beech and sugar maple having means of 15 and 20%, respectively. Similar rankings were seen for wet leaves, with all *Populus* species less than 4%, and shade leaves of sugar maple and beech at 36 and 38%, respectively. Means for beech, sugar maple, and red oak were never significantly different from one another, but were always significantly different from those for the three *Populus*. Paper birch always ranked just above the three *Populus* and was not significantly different from at least two of them. The remaining species varied in their rank, depending on leaf type and wetness.

All species/leaf-type combinations transmitted significantly more PAR when wet than when dry ($\alpha = 0.01$, paired t , Bonferroni method). The relative increase was greatest, about four-fold, for leaves having the lowest transmittances, as compared to two- to three-fold for leaves transmitting the highest proportions of PAR (Fig. 1).

Shade leaves transmitted significantly more PAR than sun leaves for beech, sugar maple, and red oak ($\alpha = 0.01$, Student's t for means adjusted by least-squares, Bonferroni method). The relative increase was greatest in sugar maple, least in beech, and more pronounced for dry leaves than for wet leaves from all three of these species (Fig. 1). The remaining species generally showed the same trend, but with much smaller differences between sun and shade leaves that were not statistically significant.

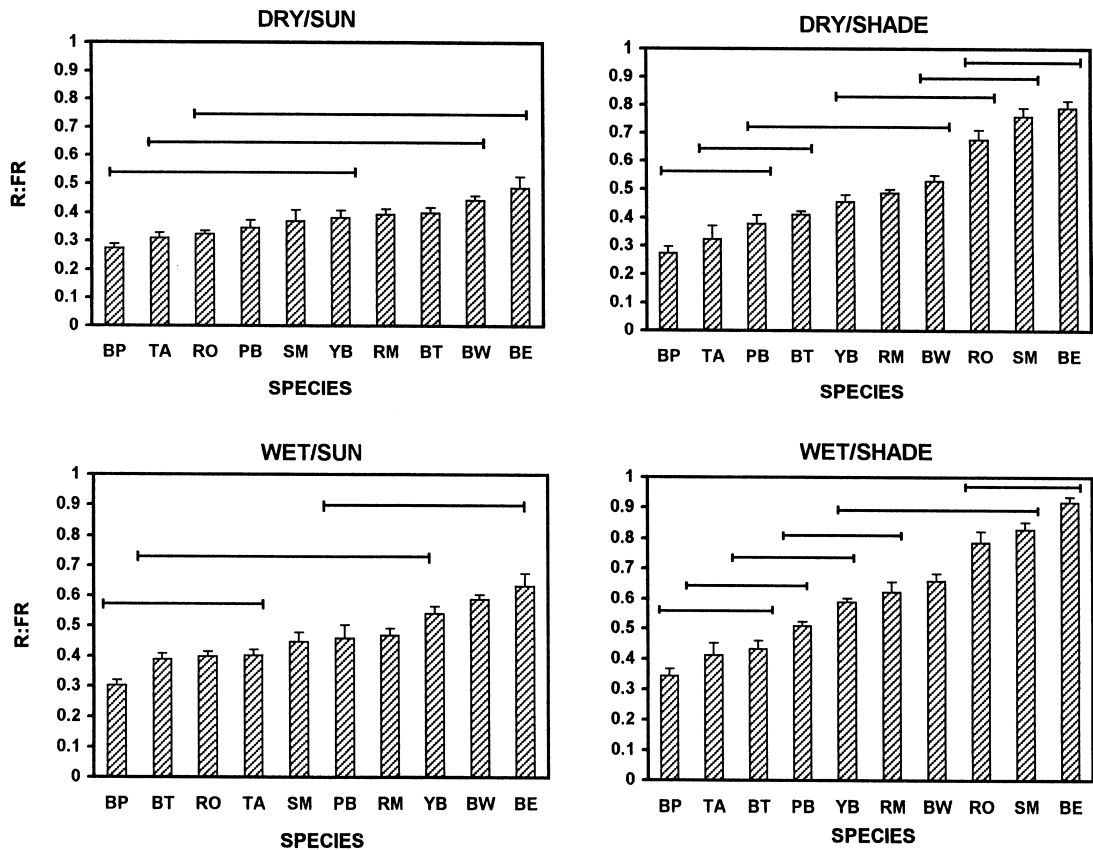


Fig. 2. Interspecific comparisons of transmitted R/FR. Height of bar equals mean ratio, with 1.0 standard error of the mean indicated (data not transformed). For transformed data, $F = 27.05$ (dry) and $F = 35.90$ (wet) with $P < 0.0001$ for 19, 430 df in both cases. Bars below the same horizontal bracket are not different at $\alpha = 0.05$, using Tukey's HSD. For species codes see Fig. 1. Number of leaves: BP $n = 20$ sun, 7 shade; BT $n = 19$ sun, 10 shade; TA $n = 23$ sun, 7 shade; PB $n = 8$ sun, 23 shade; RM $n = 7$ sun, 19 shade; RO $n = 38$ sun, 21 shade; SM $n = 8$ sun, 47 shade; BW $n = 30$ sun, 35 shade; YB $n = 23$ sun, 42 shade; BE $n = 23$ sun, 40 shade.

3.3. Transmitted R/FR

Mean transmitted R/FR ratios differed significantly among species, all of which reduced the ratio well below the incident value (Fig. 2). Ratios were lowest, below 0.3, for dry balsam poplar and highest, just above 0.9 for wet shade leaves, for beech. The range of mean values was narrowest for dry sun leaves and broadest for wet shade leaves. Wet leaves transmitted significantly higher R/FR than dry leaves in the majority of species ($\alpha = 0.01$, paired t , Bonferroni method), but in none of the species or leaf types was the magnitude of this difference nearly as great (Fig. 2) as it was for PAR (Fig. 1). Shade leaves transmitted significantly higher R/FR than sun leaves

for beech, sugar maple, and red oak, in both wet and dry conditions ($\alpha = 0.01$, Student's t for means adjusted by least-squares, Bonferroni method). Most other species showed this same trend to only a slight degree (Fig. 2), with sun/shade differences that were not statistically significant.

3.4. Relationship between PAR and R/FR

Transmitted PAR proportion and R/FR ratio for the same leaf were highly correlated, with $r = +0.86$ (dry) and $r = +0.90$ (wet), $P < 0.001$ in both cases. The relationship between the non-transformed variables appears to be somewhat curvilinear (Fig. 3).

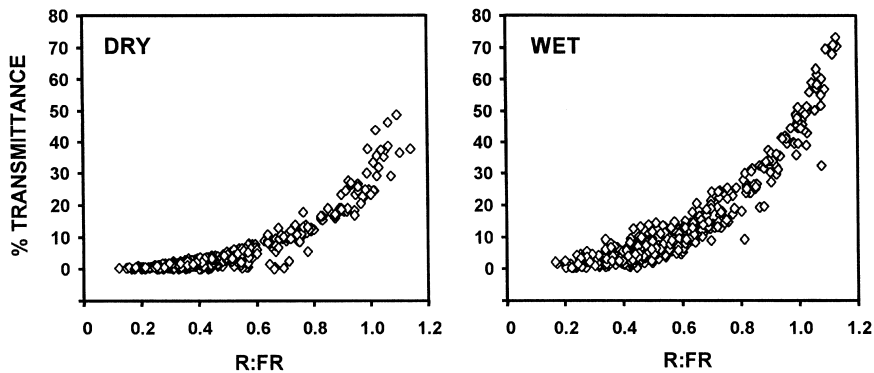


Fig. 3. Scatter plots of transmittance of PAR and transmitted R/FR through the same leaf (data not transformed). Number of leaves = 450 in each scatter plot.

4. Discussion

4.1. Successional trends

In comparing shade leaves, the sequences of species by transmitted percentages in Fig. 1 and by ratios in Fig. 2 correspond closely to successional categories: early-successional species have the lowest values, late-successional species have the highest values, and mid-successional species have intermediate values. In comparing sun leaves the same trend occurs, but there is some overlap among successional categories. The results indicate that leaf litter becomes less of a barrier to photosynthesis as secondary succession proceeds in northern hardwoods. Successional shifts toward greater canopy dominance by sugar maple and beech result in litter with higher transmittance of PAR. Further, sugar maple and beech have ‘monolayer’ crown architectures (Horn, 1971), in contrast to the ‘multilayer’-crowned species that often dominate early in succession. The proportion of the litter in the form of shade leaves would be expected to increase noticeably, based on models of canopy architecture (Campbell, 1977, p. 129), as dominance by monolayer species increases with successional time. This amplifies the effect of the species shift on PAR below the litter.

4.2. Photosynthesis below litter

Assuming a pre-budbreak PAR of $1500 \mu\text{mol s}^{-1} \text{m}^{-2}$ striking the litter beneath trees, as we observed, PAR below the previous year’s litter can be estimated

with a simple absorbance-filter model. This uses mean per-leaf transmittance raised to the power equalling the number of layers of leaves. Leaf-area indices in mesic northern hardwood stands can be expected to range from $5\text{--}6 \text{m}^2/\text{m}^2$ throughout secondary succession (Marks, 1974; Whittaker et al., 1974; Crow, 1978; Aber, 1979), yielding mean litter depths of five to six layers of leaves. In the highest-transmittance scenario for five layers, wet beech shade leaves would yield sub-litter PAR of about $12 \mu\text{mol s}^{-1} \text{m}^{-2}$ ($0.38^5 \times 1500 \mu\text{mol s}^{-1} \text{m}^{-2}$). This would be below the published light-compensation point for some forest-floor vascular herbs (Hicks and Chabot, 1985). The depth of the litter is not five to six layers everywhere. Much of the northern hardwoods’ landscape has pit-and-mound microrelief. Beatty (1984) found litter to average half as deep on mounds, and twice as deep in pits, as on level ground. Litter is also less abundant on fallen wood (Christy and Mack, 1984), upon which some species can establish. PAR would be about $25 \mu\text{mol s}^{-1} \text{m}^{-2}$ under four layers of wet sugar maple shade leaves (0.36^4). Under two layers of dry shade leaves of beech (0.15^2) PAR would be about $35 \mu\text{mol s}^{-1} \text{m}^{-2}$, or under two layers of dry sugar maple shade leaves (0.20^2) about $60 \mu\text{mol s}^{-1} \text{m}^{-2}$. Actual soil-surface values would be slightly greater than these because PAR reflected from buried leaves is partially reflected back from leaves above them. That is, a simple absorbance-filter model underestimates below-litter PAR. Such projected photon flux densities below these lesser numbers of leaves somewhat exceed the light-compensation points that have been reported for vascular herbs from these communities

(Hicks and Chabot, 1985). In contrast, two layers of wet *Populus* leaves (at most, 0.04^2) will suffice to put PAR below the reported light-compensation points, even in this bright-sun scenario. PAR beneath litter in gaps would be about 25% more than the above calculations.

The light-compensation points referenced above are based on observations in typical 'ambient' values of $[\text{CO}_2]$. As forest soil is a source of atmospheric CO_2 , this gas must have greater average concentrations in air beneath litter than in air just above litter. Measurements of $[\text{CO}_2]$ from beneath litter but above mineral soil have apparently not been reported, but $[\text{CO}_2]$ just a few cm above forest litter is known to be higher than typical 'ambient' values (Bazzaz and Williams, 1991; Buchmann et al., 1996). Elevated $[\text{CO}_2]$ will reduce the actual light-compensation points for C_3 plants below litter, and their quantum efficiencies will be higher than what has been reported from laboratory or field studies using air with more typical $[\text{CO}_2]$ (Osborne et al., 1997; Winter and Virgo, 1998). Such plants must still emerge above the litter after the canopy leaves expand if they are to continue net assimilation. In gaps the much greater post-budbreak PPFD at the top of the litter lessens the urgency of such height growth.

A shift in spectral distribution could also influence sub-litter photosynthetic rates; Vázquez-Yanes et al. (1990) found that dead leaves from six species of tropical rain forest trees transmitted light almost entirely at wavelengths above 550 nm. If spectral transmissivity is similar for dead leaves of northern hardwoods, the pre-budbreak light passing through them may have a spectrum that gives greater photosynthetic quantum efficiency than that of the greenish light transmitted through living foliage. This is speculative, because photosynthetic action spectra are poorly known for plants tolerant of deep forest shade.

4.3. Significance for species

This greater PAR below late-successional litter would seem to be of minimal direct benefit to reproduction by the adult sugar maple and beech that produce it, and the lesser PAR beneath litter from earlier-successional species should not inhibit seedling establishment by these two species. This is because both beech and sugar maple have large seed-

lings that expand their cotyledons and first leaves above the litter (Schopmeyer, 1974). The other eight species are incapable of surviving as seedlings above the litter in deep shade, regardless of PAR below the litter. Within canopy gaps or under light shade, young red oak seedlings can easily grow higher than leaf litter; this is also true to a lesser extent for the smaller-seeded red maple and basswood. *Betula* and *Populus* have much smaller seeds and seedlings, and sub-litter PAR may be important for them in gaps, or under light shade in the case of yellow birch; their own litter is likely to provide less PAR for seedling growth than does litter from beech and sugar maple. Thus there is little to suggest that these 10 species have experienced natural selection for leaves to pass or block PAR after they are dead. The patterns we report are likely the byproducts of traits of living leaves that influence the fitness of trees in particular stages or phases of succession.

A further ecological significance is that the litter from beech and sugar maple would be photosynthetically more favorable than that from early-successional trees for establishment by small-seeded shade-tolerant conifers (Simard et al., 1998), small-seeded ground-layer species, species reproducing by spores, or laterally expanding low-growing clones. It would likewise allow more PAR to herbaceous perennials that must emerge through litter each spring. And, if similar interspecific differences in transmittance exist for leaves that come to rest in water, then benthic photosynthesis rates in streams and ponds may be affected by forest canopy composition.

The higher R/FR beneath late-successional litter is likewise probably not beneficial for recruitment of beech or sugar maple seedlings, because neither of these species is known to have light-sensitive seed germination (Farmer, 1997). Indeed, such an influence of light has apparently not been definitively established with respect to overwintered seeds of any temperate canopy trees (Farmer, 1997). Many shrubby or herbaceous species do have germination controlled by R/FR. For them, percent germination may drop proportionately with R/FR decline from about 1.0 to 0.5 (Pons and van der Toorn, 1988). Lower ratios beneath litter cast by early-successional trees may keep more of the seeds dormant in those species capable of forming seed banks (Eriksson, 1995). These tree-species effects may largely disappear

where litter is more than about three layers thick, beneath which even wet beech shade leaves will have depressed R/FR to about 0.5 ($(0.90/1.20)^3 \times 1.20$).

4.4. Predictive value

The strong correlation between transmittance of PAR and transmitted R/FR allows some prediction of one if the other is known (Fig. 3). It also means that R/FR is a reliable indicator of the extent of pre-budbreak or within-gap shading by the litter, essentially independent of daytime sky conditions, a parallel to what Smith (1982) concluded for shading by green canopies. If the very low transmittance of shorter wavelengths reported for tropical leaf litter by Vázquez-Yanes et al. (1990) is also true for northern hardwoods, then it would appear that sub-litter diaspores could not use short-wavelength sensors (Chory, 1997) as effectively as they could use phytochrome for assessing the overall light climate.

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