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Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests

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Abstract. The percentage of above-canopy Photosynthetic Photon Flux Density (%PPFD) was measured at 0, 50 and 100 cm above the forest floor and above the main understory vegetation in stands of (1) pure *Betula papyrifera* (White birch), (2) pure *Populus tremuloides* (Trembling aspen), (3) mixed broad-leaf-conifer, (4) shade-tolerant conifer and (5) pure *Pinus banksiana* (Jack pine) occurring on both clay and till soil types. %PPFD was measured instantaneously under overcast sky conditions (nine locations within each of 29 stands) and continuously for a full day under clear sky conditions (five locations within each of eight stands). The percentage cover of the understory layer was estimated at the same locations as light measurements.

Mean %PPFD varied from 2 % at the forest floor under *Populus* forests to 15 % above the understory vegetation cover under *Betula* forests. Percent PPFD above the understory vegetation cover was significantly higher under shade intolerant tree species such as *Populus*, *Betula* and *Pinus* than under shade tolerant conifers. No significant differences were found in %PPFD above the understory vegetation cover under similar tree species between clay and till soil types. The coefficient of variation in %PPFD measured in the nine locations within each stand was significantly lower under deciduous dominated forests (mean of 19 %) than under coniferous dominated forests (mean of 40 %). %PPFD measured at the forest floor was positively correlated with %PPFD measured above the understory vegetation and negatively correlated with cumulative total percent cover of the understory vegetation (R^2 = 0.852). The proportion of sunflecks above 250 and 500 µmol m^{-2} s^{-1} was much lower and %PPFD in shade much higher under *Populus* and *Betula* forests than under the other forests. Differences in the mean, variability and nature of the light environment found among forest and soil types are discussed in relation to their possible influences on tree succession.

Keywords: *Abies balsamea*; *Betula papyrifera*; Forest understory; Light environment; *Populus tremuloides*; Succession; Sunfleck; *Thuja occidentalis*.

Introduction

Short-wave radiation intensity between 400 and 700 nm (i.e. Photosynthetic Photon Flux Density: PPFD) plays a major role in the growth, survival, and regeneration of understory boreal forest species (Johansson 1990; Messier et al. 1989; Vales & Bunnell 1988; Ross et al. 1986). While data on photosynthesis, growth and demography are still lacking for many boreal plant species, detailed descriptions of some important microenvironmental characteristics could provide the – much needed – framework for future studies on the ecophysiology and dynamics of boreal forest understory vegetation. In particular, studies of the photosynthetic light environment are relevant to a large range of processes such as photosynthesis, evapotranspiration, reproduction, germination, growth and survivorship (Larcher 1980).

PPFD beneath forest canopies is influenced by several factors, including tree species composition and phenology, stand density and structure, sky conditions and solar angle (Constabel & Lieffers 1996; Messier & Puttonen 1995; Baldocchi & Collineau, 1994; Morgan et al. 1985; Smith 1982; Tasker & Smith 1977; Holmes & Smith 1977; Anderson 1964). Some important quantitative descriptions of the distribution of light in the understory of boreal forests have already been published (Constabel & Liffers 1996; Messier 1996; Messier & Puttonen 1995; Johansson 1987; Ross et al. 1986). These studies have emphasized the spatial, temporal and successional variability of the understory light environment in boreal forests, yet none have dealt specifically with the effects that different tree species, soil types and understory vegetation have on the understory light dynamics. Understory species composition and abundance strongly affect the understory light environment (Constabel & Lieffers 1996; Messier et al. 1989). Boreal forests are often characterized by a dense understory vegetation of herbs and evergreen and deciduous shrubs (de Granpré et al. 1993) which is believed to play an important role in the establishment, growth and survival of shade-tolerant conifer species (Constabel & Lieffers 1996; Kneeshaw & Bergeron 1996).

We wished to answer the following questions:

1. Is there an intrinsic difference in the quantity and spatial and temporal variability of light penetrating through the canopy among different boreal forest types, notably *Populus tremuloides*, *Betula papyrifera*, shade-tolerant conifer, mixed broad-leaf conifer and *Pinus banksiana* forest?

2. Do the two major soil types found in the northwestern section of the boreal forest of Quebec (clay vs till soil types) affect the availability of light reaching the understory vegetation independently of the type of overstory tree composition?
3. What is the effect of understory vegetation on light availability and variability? We did not consider the influence of canopy openings caused by the last spruce budworm outbreak and selected closed (cover at least 85 %) and undisturbed stands of each forest type.

An additional objective was to collect data on the understory light environment for a new plant level model (LIGNUM, described in Perttunen et al. 1996).

Material and Methods

Study area

The study sites were situated in virgin forests on the mainland surrounding lake Duparquet, Québec (48° 30' N; 79° 20' W; elevation 300 m). This region is part of the *Abies balsamea* (Balsam fir)-*Betula papyrifera* (Paper birch) climax vegetation domain as defined by Grandtner (1966). Physiographically it forms part of the northern clay belt, a large region characterized by lacustrine clay deposit left by the proglacial lakes Barlow and Ojibway (Vincent & Hardy 1977). The vegetation composition and its variation along a successional gradient were described by Bergeron & Dubuc (1989). Early successional forests are dominated by *Betula papyrifera*, *Populus tremuloides* and *Pinus banksiana* (Jack pine); in the absence of fire *Abies balsamea* and *Thuja occidentalis* (Eastern white cedar) take over dominance. However, even the oldest forest communities have not reached a steady state as directional succession still occurs more than 200 yr after the last wild fire.

The mean annual temperature is 0.6 °C, the mean annual precipitation is 822.7 mm, and the annual frost-free period is 64 days (Bergeron et al. 1983). The soil is a Grey luvisol (Anon. 1978) with a moderate to good drainage; for comparison, stands of *Populus*, *Betula* and *Pinus* were also chosen on adjacent till deposits.

Forest age since fire disturbance has been determined in previous studies by dendrochronological techniques (Bergeron 1991). 29 stands, 20 on clay and nine on till soil, were selected in forests that varied in age since fire from 50 to 230 yr; they represent a wide variety of stand structure and composition types (Table 1). These forests provide a good representation of the range of understory environments found in the unmanaged closed boreal forests of northwestern Québec.

Overstory and understory stand structure

Stand structure in each stand was assessed in plots with a radius of 17 m. DBH (diameter at breast height) and identity were determined for all trees greater than 5 cm in diameter. Percentage cover of the understory vegetation was estimated visually in each of nine 1-m^2 subplots centered around points where light measurements took place (i.e. plot center, and at 2 m and 5 m from the plot center in each cardinal direction). The cover was estimated for three strata at each subplot: between 0 and 50 cm, 50 and 100 cm, and between 100 cm and the top of the main understory vegetation.

Light measurements

PPFD was measured in July and August 1994 at 9 systematic points inside a 17 m wide radius plot in each of the 29 stands: at plot centre and at 2 and 5 m in each cardinal direction. The exact center of the plot was determined at random by throwing a stick within a larger area where the overstory canopy was completely closed. The measurements were carried out at 0, 50 and 100 cm above the forest floor, and above the main understory vegetation cover under overcast sky conditions following the method proposed by Messier & Puttonen (1995) and validated by Parent & Messier (1996). This method is based on the findings that one instantaneous measure made under completely overcast conditions is representative of the main daily %PPFD on both clear and overcast sky conditions. Light measurements in the forest understory were carried out with a hand-held LI-190 point quantum sensor (LI-COR, Inc., Lincoln, NE). Continuous measurements were carried out in an adjacent opening to record the above canopy PPFD using a LI-1000 datalogger.

A subsample of one *Populus*, one *Betula*, three mixed Broad-leaf-conifer, two mixed coniferous and one *Pinus* stand was selected at random within each of these categories to measure light continuously under clear sky conditions; in each stand five sensors were placed above the main understory vegetation. For each of these sensors, the mean of 5-second measures was recorded every minute over one full sunny day on July 15, 1994 using LI-1000 dataloggers.

Data analysis

For each plot, we calculated the mean value, standard deviation and coefficient of variation of the nine instantaneous measures of %PPFD made at 0, 50, and 100 cm above the forest floor and above the main understory vegetation cover under completely overcast sky conditions. Similarly, we calculated the average of

the total percent cover of the understory vegetation made between 0 and 50 cm, 50 and 100 cm, and 100 cm and the top of the main understory vegetation of the nine subplots. The 29 stands were grouped into two different soil types (clay vs till) and five different forest types:
(1) pure *Betula papyrifera*;
(2) pure *Populus tremuloides*;
(3) mixed broad-leaf conifer (stands with between 25 % and 75 % broad-leaf species based on total basal area);
(4) shade-tolerant conifer (stands with more than 75 % conifers);
(5) pure *Pinus banksiana* (Table 1).

One-way or two-way ANOVA were used to test for significant differences in light environment among forest and soil types. The Tukey HSD multiple comparison test was used to compare means. Simple and/or multiple linear regressions were used to test for relationships between light, understory vegetation and stand characteristics.

Results

Effects of forest and soil types on understory vegetation and mean daily %PPFD

The 29 stands selected for this study varied in time since fire, density, soil type, height, average DBH, percent broad-leaf composition, mean basal area, mean understory vegetation percent cover and mean percent understory light (Table 1). In order to be able to isolate the effects of forest and soil types, we separated the analyses of the five different forest types on clay soil (i.e. 20 stands) with those made on the three forest types that were found on both clay and till soils (i.e. nine stands on till and 10 stands on clay). See Table 1.

According to a multiple regression applied to the 20 stands growing on clay soil, height of the overstory trees was positively related and total basal area was negatively related to mean daily %PPFD measured above the understory vegetation (R^2 = 0.335; Table 2).

Table 1. Stand characteristics.

Stand type		Age (yr)	Soil types	Density (#/ha)	Height (m)	Average DBH (cm)	Basal area (m^2/ha)	Broadleaf (%)	Understory cover (%)[1]	Understory height (cm)	PPFD (%)[2]	PPFD (CV%)
Deciduous												
Betula papyrifera	1	70	Clay	919	18.0	14.4	21.2	88.4	75.5	147.2	14.4	23.9
	2	70	Clay	1315	18.5	15.6	18.0	97.7	78.0	105.5	12.9	17.0
	3	70	Clay	1542	17.5	13.8	22.7	84.0	77.5	175.2	12.1	20.3
	4	70	Till	863	16.5	19.5	23.3	96.5	106.0	264.4	18.5	20.7
	5	70	Till	594	16.0	20.1	19.6	93.5	133.5	206.1	12.7	6.4
Populus tremuloides	1	50	Till	2065	17.5	15.3	24.6	100.0	114.5	358.3	11.1	22.3
	2	50	Till	2566	18.0	14.4	25.9	100.0	113.0	186.1	10.9	16.5
	3	50	Till	2008	18.5	14.6	17.4	100.0	107.0	200.0	8.7	22.7
	4	50	Clay	1414	22.0	17.5	34.5	89.0	70.0	351.7	8.2	25.1
	5	50	Clay	1528	19.5	17.1	34.8	97.7	81.0	294.4	8.9	16.5
	6	50	Clay	1966	20.0	18.0	46.5	99.1		277.8	11.9	21.0
	7	70	Till	1103	22	22.3	49.7	96.0	114.0	303.9	13.4	18.2
	8	70	Clay	948	24.5	23.9	34.6	97.4	136.0	384.6	10.5	19.0
Mixed coniferous-deciduous												
Mixed	1	70	Clay	1556	16.0	16.6	33.9	73.1	63.0	126.7	6.0	37.5
	2	70	Clay	1499	17.0	16.3	31.1	48.4	56.5	177.8	5.9	45.3
	3	70	Clay	1556	17.0	16.8	33.8	33.6	57.0	122.2	4.6	29.6
	4	70	Clay	780	16.5	17.1	17.8	45.1	62.5	115.0	10.2	20.7
	5	108	Clay	1400	22.0	16.9	31.4	68.1	48.0	141.6	9.5	37.6
Coniferous												
Abies-Picea glauca		70	Clay	1924	17.0	12.9	25.0	13.5	52.5	111.1	8.9	47.4
Picea glauca		70	Clay	863	14.5	21.1	30.1	16.7	35.5	88.9	12.8	21.5
Picea mariana		70	Clay	1938	18.5	14.6	32.4	3.4		55.6	6.4	28.5
Thuja occidentalis	1	230	Clay	799	18.0	26.2	41.0	9.6	69.0	140.0	4.4	30.8
	2	230	Clay	654	18.5	25.6	38.6	5.6	73.0	204.4	5.7	40.1
Pinus banksiana	1	70	Clay	746	24.5	20.1	29.1	25.9	109.0	350.2	14.6	16.7
	2	70	Clay	1245	23.5	19.4	33.8	13.3	99.5	355.6	11.6	25.3
	3	70	Clay	1174	24.0	20.3	30.8	7.8	117.5	422.2	10.2	29.5
	4	70	Till	1754	18	15.1	35.5	0.1	77.5	197.2	10.8	56.4
	5	70	Till	2065	19.5	14.3	36.8	6.3	69.5	179.4	11.3	39.1
	6	70	Till	3041	18.5	14.1	38.5	6.0	29.5	150.0	14.7	36.3

Note: [1]Cumulative total percent cover of all understory layers; [2] Mean daily percent PPFD measured above the understory vegetation;[3]Coefficient of variation among nine subplots.

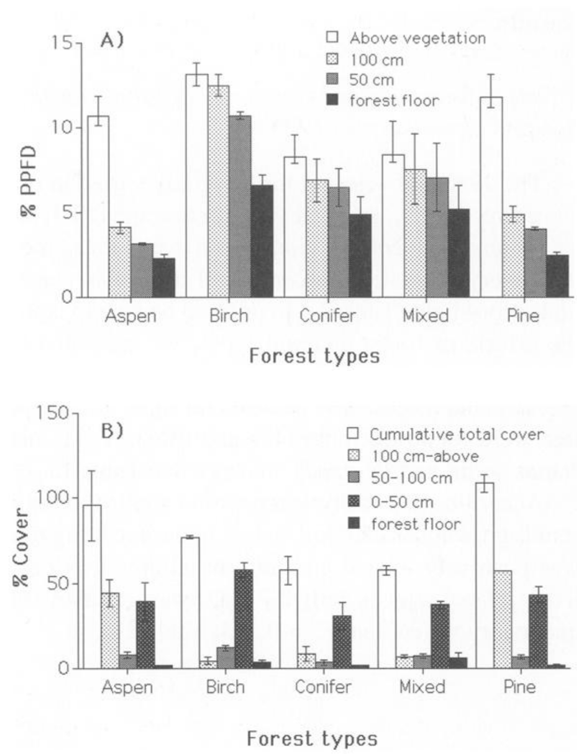

Fig. 1. A. Comparison of the mean daily %PPFD, at different heights; **B.** Percentage understory cover for different layers among closed forests of *Populus tremuloides* (Aspen), *Betula papyrifera* (Birch), Shade-tolerant conifers (Conifer), Mixed coniferous/broad-leaf (Mixed), and *Pinus banksiana* (Pine) growing on clay soil. One repetition is the mean of nine measurements made in a 17-m radius plot. *N* varies from 3 to 5.

Intolerant broad-leaf (*Populus*, *Betula*) and coniferous (*Pinus*) species transmitted significantly ($P < 0.10$) more %PPFD as measured above the understory vegetation than shade tolerant conifer and mixed broad-leaf conifer forest types (Fig. 1A). The cumulative total cover (Fig. 1B) and maximum height of the understory vegetation (Table 1) were significantly ($P < 0.05$) higher under *Pinus* and *Populus* than under *Betula*, shade-tolerant conifer and mixed forest types. A multiple regression found both %PPFD measured above the understoy vegetation ($P = 0.040$) and height of the tree canopy ($P < 0.001$) to be positively related to the cumulative total understory cover ($R^2 = 0.802$; Table 2).

The coefficient of variation of %PPFD measured above the understory vegetation also varied greatly among stands (Table 1). It was significantly ($P < 0.05$) higher under *Pinus*, Shade-tolerant conifer and Mixed forest types than under *Populus* forest types (Fig. 2), and was also significantly higher under *Pinus* than *Betula* forest types. Multiple regressions showed that it was positively related to the percentage of conifers in the stand ($R^2 = 0.361$; Table 2).

A two-way ANOVA between the three forest types (*Populus*, *Betula* and *Pinus*) and two soil types showed no effect of soil type, but a small effect of forest type on %PPFD measured above the understory vegetation (Table 3): %PPFD was significantly ($P = 0.028$) higher under *Betula* stands (Table 4). A strong interaction was found between forest and soil types for the cumulative total understory cover (Table 3). This interaction indicated that cumulative total understory plant cover did not change for *Populus* between the two soil types, whereas on till it increased for *Betula* and decreased for *Pinus* (data not shown).

Effects of understory vegetation on light environment

Vertical distribution of both understory vegetation and %PPFD in stands growing on clay was highly variable among forest types (Fig. 1A, B). Both *Pinus* and *Populus* had important understory plant cover between 5 and 50 cm and above 100 cm in height, whereas *Betula*, shade tolerant conifer and mixed types had an important plant cover only between 5 and 50 cm (Fig. 1B). %PPFD decreased as one approached the forest floor for all forest types, but the intensity of the decrease was variable (Fig. 1A). Multiple linear regressions showed that %PPFD measured at the forest floor was related to cumulative percent understory plant cover, total tree

Table 2. Selected multiple linear regressions to predict the effects of various stand structural attributes for stands growing on clay soil type on various attributes of the understory light and vegetation.

		R^2	P
PPFD-above	8.43 + 0.47HEIGHT – 0.24 BA	0.335	0.031
COVER-total	– 45.43 + 5.28 HEIGHT + 2.20 PPFD-above	0.802	< 0.001
CV-above	18.25 – 0.21 CONIFER-percent	0.361	0.005
PPFD-ff	7.675 + 0.469 PPFD-above – 0.097BA – 0.068COVER-total	0.852	< 0.001

PPFD-above: %PPFD as measured above the understory vegetation; COVER-total: Cumulative total understory plant cover; HEIGHT; Average height of the overstory tree canopy; BA: Total basal area of trees > 5 cm DBH; CV-above: Coefficient of variation in percent of PPFD-above; CONIFER-percent: Percentage of conifers within a stand based on BA; PPFD-ff: %PPFD as measured at the forest floor.

Table 3. ANOVA table showing mean-square and *P*-values for % PPFD measured above the understory vegetation, cumulative understory plant cover and % PPFD measured at the forest floor among three forest types (*Populus*, *Betula* and *Pinus*) and two soil types (clay vs till).

		PPFDabove		COVERtotal		PPFDff	
Factors	DF	Mean-Square	*P*	Mean-Square	*P*	Mean-Square	P
Forest type	2	22.77	0.028	673.09	0.202	13.52	0.002
Soil type	1	3.14	0.433	42.38	0.740	0.33	0.626
Forest type × soil type	2	3.01	0.549	3175.40	0.005	19.30	0.001
Error	13	4.79		367.53		1.34	

basal area and %PPFD measured above the understory vegetation ($R^2 = 0.852$; Table 2). When comparing Fig. 1A with Fig. 1B, it is clear that light attenuation within the understory plant cover relates well to its abundance. The proportion of PPFD transmitted by the understory vegetation was negatively related to the cumulative total percent cover (Fig. 3). Overall, %PPFD at the forest floor was significantly ($P < 0.01$) lower under *Populus* and *Pinus* (ca. 2 %), where the largest amount of understory vegetation was found (see Fig. 1B), compared to the other forest types – ca. 5% (Fig. 1A). The coefficient of variation of %PPFD was higher on the forest floor than above the understory vegetation, especially for the *Populus* and *Betula* types (Fig. 2), but there were no significant differences among forest types.

The vertical distribution of both understory vegetation and %PPFD differed significantly between clay and till soil types (Table 4). Differences in vertical light distribution among forest and soil types were related to differences in the vertical understory plant cover. A strong interaction was found between forest and soil types for %PPFD measured at the forest floor (Tables 3 and 4). This interaction indicated that %PPFD at the forest floor did not change for *Populus* between the two soil types, whereas it increased from clay to till for pine and decreased for *Betula*.

Effects of forest type on light dynamics under clear sky conditions

Table 5 presents the mean daily %PPFD measured above the understory vegetation from both instantaneous measures under overcast sky conditions and continuous measurements under sunny sky conditions, and the proportion, frequency and duration of sunflecks higher then 100, 250 and 500 μmol m^{-2} s^{-1}, respectively, for eight different stands. Both the mean daily %PPFD calculated from instantaneous measures made under overcast sky conditions and continuous measures made under clear sky conditions were in fairly close agreement (R^2 = 0.841). The average number of sunfleck events at the 100 μmol m^{-2} s^{-1} level during a full sunny

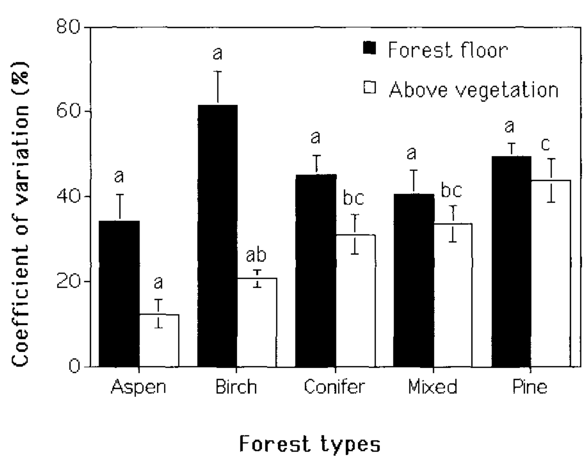

Fig. 2. Comparison of the coefficient of variation of % PPFD measured at the forest floor and above the understory vegetation among the five forest types (see Fig. 1) growing on clay soil. One repetition is the mean of nine measurements made in a 17-m radius plot. *N* varies from 3 to 5.

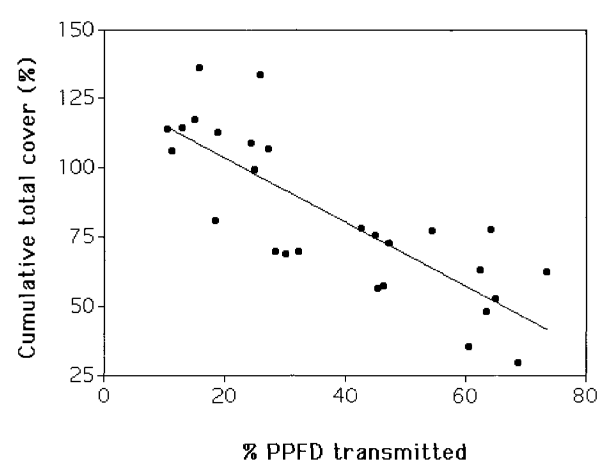

Fig. 3. Relationship between cumulative total percent cover of understory vegetation and percent of above understory vegetation PPFD reaching the forest floor; $Y = 126.93 - 1.163X$; $R^2 = 0.663$; $P < 0.001$. One repetition is the mean of nine measurements made within a 17-m radius plot. $N = 29$.

day varied from 11.4 for fir-white spruce to 30.4 for *Betula* (Table 5), lasting on average 5.4 min for *Picea* and 9 min for *Pinus*. Sunflecks at the 100 µmol m^{-2} s^{-1} level contributed from 59.1 % (*Populus*) to 86 % (*Pinus*) of the total light received during a sunny day (Table 5). No clear trend in the proportion, frequency and duration of 100 and 250 µmol m^{-2} s^{-1} sunflecks was observed among the forest types. The average number of sunflecks at the 500 µmol m^{-2} s^{-1} level events varied from 2 for *Populus* to 12 for *Pinus* (Table 5). Sunfleck proportion at the 500 µmol m^{-2} s^{-1} level was much lower in the deciduous forest types, especially *Populus* (17.9 %), as compared to *Pinus*, shade-tolerant conifer and mixed forest types (32.1 to 56 %) (Table 5).

Fig. 4 shows the diurnal variation of PPFD measured at one location above the understory vegetation for each of four forest types. The one location was selected to be representative of the five locations measured in each stand. Intensity of the diffuse shade light (i.e. not influenced by any direct light) was much higher under *Populus* and *Betula* forest types (ca. 100 µmol m^{-2} s^{-1}) compared to the fir-white spruce and pine types (ca. 30 mmol m^{-2} s^{-1}). Sunfleck events were concentrated at midday in all eight stands investigated.

Table 4. Comparison of % PPFD and percentage understory vegetation cover between clay and till deposits at four heights in the understory of *Populus*, *Betula* and *Pinus* stands.

		Forest floor	50 cm	100 cm	Above understory vegetation
%PPFD					
Populus	Till	1.7 (0.3)	4.1 (0.7)	5.6 (1.3)	10.3 (0.5)
	Clay	2.3 (0.3)	3.1 (0.1)	4.1 (0.4)	10.6 (1.2)
Betula	Till	2.7 (0.6)	3.4 (0.7)	4.2 (0.9)	15.6 (2.9)
	Clay	6.6 (0.7)	10.7 (0.2)	12.5 (0.6)	13.1 (0.7)
Pinus	Till	6.1 (1.4)	8.4 (1.0)	9.7 (1.3)	12.1 (1.3)
	Clay	2.4 (0.2)	4.0 (0.1)	4.9 (0.4)	11.8 (1.4)
% understory vegetation cover		Forest floor	5-50 cm	50-100 cm	100 cm -Top of vegetation
Populus	Till	0.2 (0.2)	54.8 (6.1)	20.5 (7.5)	36.5 (11.1)
	Clay	1.5 (0.1)	39.1 (11.3)	7.9 (1.8)	44.3 (7.8)
Betula	Till	0.6 (0.4)	45.7 (3.2)	14.3 (8.9)	59.3 (8.5)
	Clay	3.4 (1.3)	57.5 (4.3)	11.9 (1.6)	4.3 (2.2)
Pinus	Till	5.9 (2.6)	34.5 (12.1)	6.6 (3.7)	11.9 (5.0)
	Clay	1.7 (0.7)	43.2 (4.6)	6.6 (1.4)	57.1 (0.3)

Note: Standard error of the mean is in parentheses.

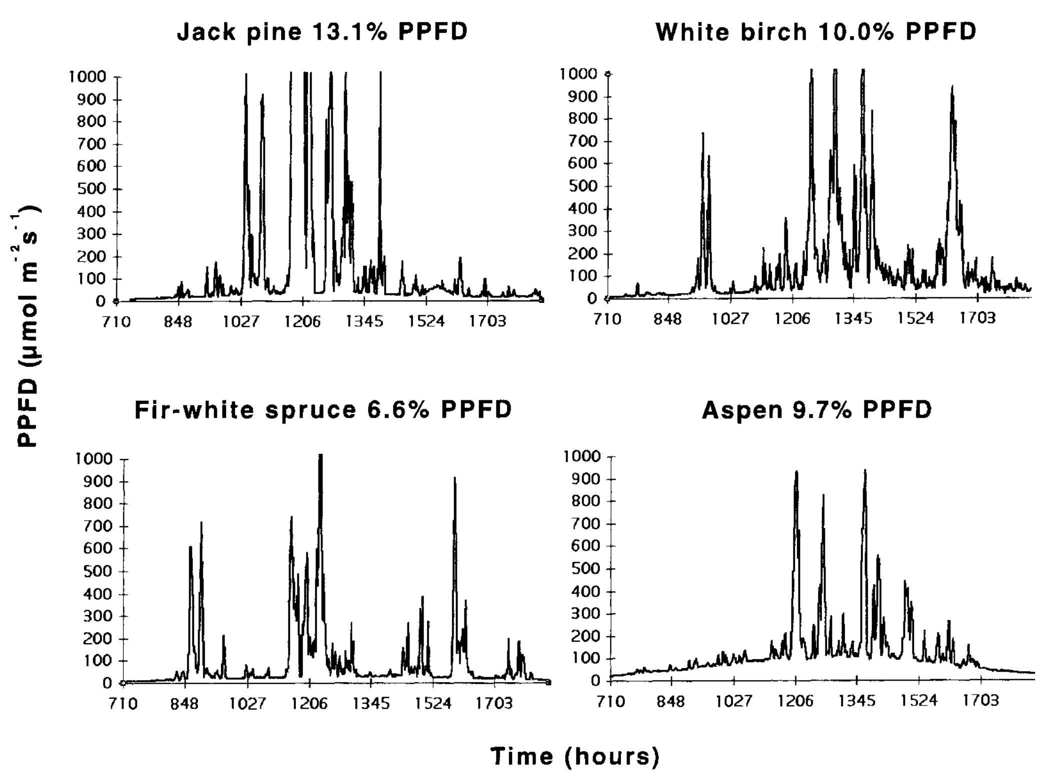

Fig. 4. Comparison of the diurnal variation of PPFD measured at one location above the understory vegetation among *Populus tremuloides* (Aspen 5), *Betula papyrifera* (White birch 2), tolerant conifer (Fir-White spruce), and *Pinus banksiana* (Jack pine 1) forests. The one location selected was representative of the five locations given in Table 5. Y-axis terminated at 1000 µmol m^{-2} s^{-1}.

Discussion

Effects of overstory and understory vegetation on light environment

Few data are available for detailed comparisons of the light environment found among the forests investigated in this study with those of other boreal forests. Messier (1996) compiled most of the data available on understory light in the mixed coniferous-deciduous forest ecosystem of the world. %PPFD above the understory vegetation varies from 2 % in a dense 38-yr-old *Picea abies* stand in Sweden (Johansson 1987) to 60.4 % in an open 70-yr-old *Picea mariana* stand in Alberta (Ross et al. 1986). Values reported in this study generally conformed with those recorded in similar type of closed boreal forests (Constabel & Lieffers 1996; Lieffers & Stadt 1994; Messier & Puttonen 1995; Johansson 1987; Ross et al. 1986), but were much higher than those measured in the heavily shaded understory of coastal conifer forests of the pacific northwest (Canham et al. 1990; Messier et al. 1989), tropical pine forests in Australia (Morgan et al. 1985), temperate deciduous of north America (Canham et al. 1994; Brown & Parker 1994; Canham et al. 1990; Messier & Bellefleur 1988) and tropical forests (Turnbull & Yates 1993; Lawton 1990; Canham et al. 1990; Lee 1989; Morgan et al. 1985; Chazdon & Fetcher 1984; Pearcy 1983).

%PPFD values found under *Populus* forest types in this study were much lower than those reported by Lieffers & Stadt (1994) and Constabel & Lieffers (1996) under similar *Populus* stands (i.e. similar basal area, density and height) in northern Alberta (14 to 40 % PPFD). One possible explanation for the higher %PPFD values found in northern Alberta is that precipitation is both low (500 mm: Anon. 1969) and much lower than in Abitibi (823 mm); this presumably led to *Populus* stands with a lower leaf area index (LAI).

%PPFD measured above the understory vegetation for similar tree species did not vary between clay vs. till soils, even though stands on till usually had lower height and greater density (although with a similar total basal area) (Table 1). This suggests that LAI did not vary much between soil types for a similar tree species. Obvious differences in the type and density of understory vegetation were found (Béland & Bergeron 1993; de Granpré et al. 1993; pers. obs.) between soil types, however, which greatly influenced %PPFD being transmitted to the forest floor. High understory vegetation cover and resulting low %PPFD found on the forest floor of clay *Pinus* stands compared to till could help explain the higher density of advanced conifer regeneration found on till by Béland & Bergeron (1993). However, because of the low number of sample plots for each soil type this should be interpreted with caution.

There is no accepted light threshold value that defines a sunfleck for all forest types (Chazdon 1988), so we present results for thresholds of 100, 250 and 500 μmol m^{-2} s^{-1}. We calculated that sunflecks contributed between 59.1 and 86 %, 28.3 and 74.5 % and 17.9 and 56 % of the total PPFD amount received during a full sunny day for thresholds of 100, 250 and 500 μmol m^{-2} s^{-1}, respectively, above the understory vegetation. These values are comparable to those of Messier & Puttonen (1995) and Washitani & Tang (1991) who used similar methods and thresholds. The importance of sunflecks

Table 5. Sunfleck characteristics measured above the understory vegetation in eight different stands; values are means for five locations within each stand made under completely sunny days. Stands characteristics are given in Table 1.

Stand type	Inst.	Cont.	Sunflecks								
	PPFD (%)	PPFD (%)	>100µm			>250µm			>500µm		
			Prop[1]	Freq[2]	Time[3]	Prop	Freq	Time	Prop.	Freq.	Time
				(%)	(#)	(min.)	(%)	(#)	(min.)	(%)	(#) (min.)
Deciduous											
Aspen 5	8.7	8.3	59.1	27.8	7.1	28.3	8.0	4.9	17.9	2.0	6.4
White birch 2	10.8	8.9	74.9	30.4	7.1	53.0	19.0	5.8	26.9	11.6	4.6
Mixed broadleaf-coniferous											
Mixed 2	5.3	5.4	70.2	19.0	5.7	51.0	8.8	4.9	32.9	5.0	3.1
Mixed 4	11.2	12.5	60.4	20.8	8.3	51.5	14.8	7.4	44.0	11.0	7.9
Mixed 5	9.9	7.7	70.2	18.4	8.2	57.2	12.8	5.7	34.0	6.8	3.7
Coniferous											
Fir-White spruce	7.1	6.2	78.9	11.4	7.3	70.2	6.8	7.5	56.0	5.4	6.1
Black spruce	5.7	6.0	68.5	19.5	5.4	49.7	8.5	4.8	32.1	3.5	5.0
Jack pine 1	13.1	13.4	86.0	26.0	9.0	74.5	18.4	6.7	48.7	12.2	6.2

[1]Proportion of total daily PPFD > 100, 250 and 500 μmol m^{-2} s^{-1}; [2]Mean number of individual sunflecks events for each threshold during a full sunny day; [3]Mean duration of sunflecks in minutes.

was clearly lower under *Populus* for all three thresholds, even though mean daily %PPFD under that forest type was higher than many of the other forest types (Table 5). The higher light intensity found in shade (i.e. including diffuse light only) under *Populus* and *Betula* (Fig. 4) explains why the proportion of sunflecks at the level of 500 µmol m^{-2} s^{-1} in these stands could be so low while at the same time having a mean daily %PPFD as high or higher than some mixed or coniferous forest types (Table 5). Reasons for these differences were not investigated, but they could be due to the even distribution of leaves in *Populus* and *Betula* canopies compared to conifer canopies: conifers tend to have dense crowns with well defined holes between adjacent trees. This can also explain the much lower coefficient of variation of %PPFD measured above understory vegetation in *Populus* and *Betula* forest types (Fig. 2).

There may be biologically significant differences in the shade cast by different canopy species within particular forests, which differences might lead to predictable patterns of tree-by-tree replacement (Canham et al. 1994; Horn 1971; Fox 1977; and Woods & Whittaker 1981). Here we demonstrated that stands dominated by shade intolerant (deciduous or coniferous) species transmitted more light than those dominated by shade tolerant conifer species (Fig. 1).

Finally, we showed that the understory plant cover exerted a strong control on forest floor light conditions, and therefore on any further successional development of the forest community. This was especially evident under *Populus* and *Pinus* forest types, on clay soil, where we found the lowest forest floor %PPFD even though it was relatively high above the understory vegetation. As discussed by Constabel & Lieffers (1996), as understory saplings grow in height above the main understory cover one can expect a marked improvement in growth rates. The height at which this accelerated growth occurs will vary among forest types (Table 1). The vertical and interspecific differences in the mean, variability and nature of %PPFD found in the understory among forest and soil types in this study will probably greatly influence the recruitment, growth, reproduction, and survival of understory plant species of the boreal forest, and therefore to strongly regulate stand dynamics.

Implications for regeneration and stands dynamics

Our study and others (reviewed by Messier 1996) show that closed boreal forests cast a lighter shade than most other types of closed forests. Such higher %PPFD values might be necessary for the understory vegetation to grow and survive because of the limited resources and short growing season associated with boreal forest ecosystems. For the same forest, Parent & Messier (1995, 1996) found almost no understory vegetation and very poor growth of seedlings of *Abies balsamea* under a closed forest of *Picea mariana*that transmitted less than 3% PPFD; Kneeshaw et al. (1996) reported a much lower density of advanced regeneration under *Populus* compared to conifer or mixed broad-leaf conifer forest types; Béland & Bergeron (1993) found a very low density of advanced conifer regeneration under *Pinus*, and Simard et al. (subm.) found that shade tolerant conifer recruitment occurs on microsites with more than 5 % PPFD. We hypothesize that the very low %PPFD found at the forest floor under *Populus* on both clay and till deposits, *Pinus* on clay deposit and *Betula* on till deposit (Table 4) in this study (ca. 2 %) could limit the establishment and growth of many species, even shade tolerant conifer species such as *A. balsamea*. This could be seen as an adaptation by shade intolerant species to allow for a dense understory vegetation to inhibit the establishment and early growth of the more shade tolerant conifer species that normally replace them.

This adaptation could further be seen as being advantageous for a species like trembling *Populus* that can resprout from root suckers and grow as much as 2.5 m the first year under favorable conditions (Peterson & Peterson 1992). *Populus* regeneration strategy could then be viewed in another way: high light transmission and nutritionally rich litter produced by *Populus* overstory trees allows for the development of a dense and tall understory vegetation cover. This understory vegetation reduces light to such a low level that it impedes the establishment and growth of shade-tolerant conifers. *Populus* , because of its ability to resprout from below-ground roots and rapidly grow tall (Peterson & Peterson 1992), can better profit from any opening that might occur than small and slow growing shade-tolerant conifers. This strategy could enable *Populus* to grow above the understory vegetation and reach the higher light level found in gaps, perhaps explaining the recurrence of *Populus* in older stands in Abitibi (Paré & Bergeron 1995). Our hypothesis supports the ideas of Chazdon (1986) and Terborgh (1985) who stated there is a clear advantage for understory tree species to select life history characteristics that enable them to grow in height quickly.

Paliwal et al. (1994), comparing various understory species growing in a European beech forest, showed that early successional species had slower photosynthetic induction increases and faster induction losses than late successional species: haft time induction increases went from 2.5 min for early successional species to 0.8 min for late successional ones whereas half time induction losses went from 5.1 min for early successional species to 19.5 min for late successional ones. Such differences in the frequency distribution of PPFD values found among forest types in this study (Table 5) are presumably important for understory species since different species have different abilities to respond to short pulses of high and low PPFD (Küppers et al. 1996; Paliwal et al. 1994; Sims et al. 1994; Yanhong et al. 1994; Pfitsch & Pearcy 1992; Gross 1982).

Conclusion

This study has shown that understory light availability and dynamics in closed broad-leaf conifer forests are influenced by the interactions of (1) overstory tree species composition, (2) abundance and vertical distribution of understory vegetation, and (3) soil type through its influences on the type and abundance of understory vegetation. The light environment found in forests dominated by broad-leaved trees was different in two major ways from that found under conifer dominated forests: (1) %PPFD was much less variable and (2) the intensity of PPFD in diffuse shade light was much higher. This study confirms other studies that have shown that shade intolerant (deciduous or coniferous) species transmit more light than shade tolerant tree species. Finally, our result suggest that the low conifer regeneration found under *Populus* and *Pinus* as reported by several authors (Béland & Bergeron 1993; Kneeshaw et al. 1996; Simard et al. subm.) is the direct results of the dense understory vegetation that reduces %PPFD at the forest floor to levels that inhibit conifer seedling establishment and growth (Parent &Messier 1995; ; Simard et al. 1996) (i.e. < 3 % PPFD).

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