

Seasonal variations in leaf area index, leaf chlorophyll, and water content; scaling-up to estimate fAPAR and carbon balance in a multilayer, multispecies temperate forest

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Summary Seasonal differences in phenology between coniferous and deciduous tree species need to be considered when developing models to estimate CO₂ exchange in temperate forest ecosystems. Because seasonal variations in CO₂ flux in temperate forests are closely correlated with plant phenology, we quantified the phenology of forest species in a multilayered forest with patches of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L.) in Brasschaat, Belgium. A scaling-up modeling approach was developed to simulate reflectance at the leaf and canopy scales over a one-year cycle. Chlorophyll concentration, water content, specific leaf area and leaf area index of the forest species were measured throughout an entire year (1997). Scaling-up from the leaf to canopy was achieved by linking the PROSPECT and SAIL models. The result is the annual progression of the fraction of absorbed photosynthetically active radiation (fAPAR) in a 1 km² forest area, which can be directly related to high-resolution, remotely sensed data.

Keywords: chlorophyll content, leaf area index, modeling, phenology.

Introduction

Within the framework of global climatic change studies, characterization of forest carbon balance is a key issue (Fung 1997, Myneni et al. 1997). In the temperate zone, forest CO₂ flux exhibits a strong inter-seasonal variation that is strongly correlated with plant phenology. Relating internal leaf biophysical processes to the forest stand scale requires a scaling-up modeling approach (Jarvis 1995, Chen 1996). To integrate temporally and spatially, a remote sensing approach has been proposed that is linked to the fraction of absorbed photosynthetically active radiation (fAPAR) (Curran 1989, Matson et al. 1994, Waring et al. 1995, Gond et al. 1997). Links between remote sensing and surface quantum efficiency are mainly of

interest for applications at regional and global scales; for example, to estimate global primary production (Prince and Goward 1995, Hunt et al. 1996, Coops et al. 1998). In the present paper, a validation of the scaling-up modeling approach is described and the link with a 1 km² remotely sensed pixel is presented. Scaling-up was achieved by linking the PROSPECT (Jacquemoud and Baret 1990) and SAIL (Verhoef 1984) models.

Materials and methods

Description of forest site

The experimental forest “De Inslag” (51°18′ N, 4°31′ E) is situated in the northeast of the province of Antwerpen (Brasschaat, Campine region, Belgium) and occupies an area of 150 ha. Mean annual temperature at the site is 10 °C (10.4 °C in 1997) and mean annual precipitation is 750 mm (662 mm in 1997). “De Inslag” forest is a mixed multilayer forest characterized by strong vertical and horizontal heterogeneity (de Pury and Ceulemans 1997, Ěermák et al. 1998). The forest is organized into many patches of varying size ranging from 1 to 3 ha. Each patch has a uniform species composition, but there are large differences among patches with respect to the understory species and to some extent the overstory species as well. The forest is mostly 70-year-old *Pinus sylvestris* L. (20–25 m high), with patches of *Quercus robur* L. (20–25 m high) intermixed. The main understory layer is composed of either *Prunus serotina* J.F. Ehrh. (8–10 m high), *Rhododendron ponticum* L. (2–3 m high) or a ground cover of *Molinia caerulea* (L.) Moench. (50–90 cm high).

Sampling procedure and measurements

All measurements were made during 1997. Leaf samples were collected on twenty occasions (approximately every 15 days

from February 5 to December 18, 1997) to monitor temporal variations in chlorophyll concentration and water content. Vegetation area index (V_a) was determined eight times (approximately every 40 days from January 29 to November 19, 1997). These data were used to adjust input parameters for the scaling-up model.

Chlorophyll measurements

At each sampling period, between two and six fresh samples of foliage were collected for analysis of chlorophyll (a and b) concentration. For each species, all samples were obtained from the same tree throughout the year.

Pinus sylvestris needles of each of the three age classes (emerged in 1995, 1996 and 1997) were sampled from the same twig. The most accessible branches were chosen in the southern crown extremities. During 1997, *P. sylvestris* trees in the "De Inslag" forest retained their 1995 needle age class until the beginning of October and the new, 1997 needles were present from the end of May. Two fascicles (with two needles each; i.e., four needles) were sampled from both one- and two-year-old needles, whereas three-year-old needles were analyzed individually. Needles were cut into 1-cm lengths, and sections of the second and the third cm (from the tip) were analyzed for chlorophyll (expressed on a projected area basis). Samples were prepared in the field and transported in the dark in an insulated box to the laboratory where the samples were stored at 4 °C. Analyses required five days to complete because of the time required for efficient acid extraction. Chlorophyll was extracted by the DMF method (Moran 1982, Porra et al. 1989). Chlorophyll absorption was measured spectrophotometrically at wavelengths of 664 and 647 nm (UV-160, Shimadzu Corp., Japan).

Similar analyses were made for *Q. robur*. In this case, sampling involved taking a 1-cm² leaf disc from two randomly chosen leaves. Because access to the tree crown 20 m above-ground was difficult, a tree near the edge of a patch with low branches was selected for leaf sampling. Leaf samples from the understory species *P. serotina* and *R. ponticum* were also analyzed. For *P. serotina*, three leaf samples were collected randomly from the top, middle and lower layers of the canopy. For *R. ponticum*, single leaves from three leaf age classes were selected from sun and shade layers. For analysis, samples comprised one leaf characterized by age and position on 20 occasions during the experiment in 1997. The *M. caerulea* samples were taken under a *Q. robur* crown, where the *M. caerulea* population was very dense. Single samples were taken at the base and the tip of the leaves 16 times between April and November 1997.

Water content and leaf area measurements

Water content and mean surface area of the collected leaves were determined from fresh samples of each of the five species (on the day that samples were collected for analysis of chlorophyll). Percentage water content (W) was determined from the fresh (M_f) and dry (M_d) mass of leaves (Ludlow 1982):

$$W = 100(M_f - M_d)/M_d. \quad (1)$$

For *P. sylvestris*, 20 needles of each age class on one branch were collected per sample day. For *Q. robur*, *P. serotina* and *R. ponticum*, all the leaves on one branch were collected to ensure a consistent and unbiased sample. For *M. caerulea*, samples were collected on different plants in a 50 m² area.

Vegetation area index measurements

Vegetation area index (V_a) was measured on eight days during the year with a pair of light sensing instruments (LAI-2000, Li-Cor, Inc., Lincoln, NE). The LAI-2000 measures half of the total surface area of leaves and wood (branches, stems, etc.), and not the projected area. Because these measurements need a sky with completely diffuse light, cloudy days without rain were selected (uniform overcast sky) for the field campaigns. One sensor, which was fixed at the top of a nearby tower (40 m high) above the forest, measured incident radiation every 15 s. The second instrument was used to measure the light regime in each of the nine patches. Both instruments had caps obscuring one quarter of the optical sensor adjacent to the handle to screen the operator from the field of view of the sensors. Ten measurements were made per patch. When an understory was present, an 8-m extendable pole was used to place the instrument 9–10 m aboveground, over the understory, but beneath the overstory canopy. Measurements at ground level were used to determine the total V_a of the forest and hence, by difference, a measure of both overstory and understory V_a . The same patches of forest were measured on each occasion to record seasonal variation in V_a (four patches for *P. sylvestris*, three for *Q. robur*, two for *R. ponticum*, and one each for *P. serotina* and *M. caerulea*).

Leaf area index (L) was calculated from estimated V_a . For the deciduous forest species, mean values of V_a during winter were used as estimates of woody area index (W_a) ($W_{aQuercus} = 0.91$, $W_{aPrunus} = 0.66$, $W_{aRhododendron} = 1.13$). The value of $W_{aPrunus}$ was used for *R. ponticum*. For *P. sylvestris*, because the LAI-2000 measures half the total needle surface area of the hemispherical needles, we accounted for the clumping of the needles into shoots by using an equation that incorporates a silhouette factor (STAR = 1.35 in our case) (Stenberg et al. 1995). Woody area index cannot be evaluated by this method. To estimate canopy L , we used Equation 2a for flat-leaved species and Equation 2b for *P. sylvestris*:

$$L = V_a - (W_a/2), \quad (2a)$$

$$L = 2V_a/STAR. \quad (2b)$$

Additional measurements were made to complete the scaling-up exercise. A manual spectroradiometer (LI-1800, Li-Cor, Inc., Lincoln, NE) was used to measure soil reflectance (400–1100 nm). The proportions of direct and diffuse PAR were monitored above the forest canopy by means of a shadow band system installed at the top of the 40-m tower.

Analysis

The scaling-up method is based on two models. At the leaf scale (PROSPECT model) and at the canopy scale (SAIL

model) the reflectance, transmittance and absorption of PAR were simulated for each forest species. Initially, the PROSPECT model simulated the probability of light being intercepted by leaves, and then either absorbed, reflected in a direction depending on leaf inclination and angle of incidence, or transmitted through the leaf. The PROSPECT model requires five parameters for each species: (1) number of layers inside the leaf (from the surface area/fresh volume ratio); (2) chlorophyll (a + b) concentration; (3) leaf equivalent water thickness (from water content and surface area); (4) leaf protein concentration; and (5) leaf cellulose and lignin concentration summed together (Jacquemoud et al. 1995).

Scaling-up from the leaf to the canopy was performed with the SAIL model, assuming an idealized horizontal canopy composed of layers of flat leaves distributed homogeneously, with a random leaf azimuth distribution. Despite the limitations of this assumption, we applied it to estimate L . The SAIL model incorporates (1) leaf/needle reflectance; (2) transmittance; and (3) absorption values from the PROSPECT model. In addition, the SAIL model requires estimates of (4) L ; (5) leaf inclination angle; (6) diffuse/direct irradiance; and (7) soil reflectance.

Results and discussion

Temporal variation in chlorophyll concentration differed among species (Figure 1). In *P. sylvestris*, chlorophyll concentration also varied with position within needles (Table 1). Needle tips were eliminated because of their irregular shape (Flower-Ellis and Olsson 1993) and the difficulty in calculating accurately projected needle area. Mean chlorophyll concentration of the next two centimeters from the needle tip, which was higher than in the remainder of the needle, was expressed in relation to the relative proportions of the three age classes of needles (cohorts). The same projected needle area was assumed for each age class (1995, 1996 and 1997); i.e., each annual cohort comprised one-third of the total needle area. An exception was made for 1997 needles during the period between bud burst (just before May 29) and the attainment of maximum chlorophyll concentration (September 11). During this period, current-year (1997) needles were growing, necessitating an adjustment to the weighting by needle area. When bud burst occurred, the 1997 needles represented only about 1% of the total needles in the pine canopy. This percentage increased from 4% on June 9, to 11% on July 3, to 22% on August 13. The needles were fully grown by September 11. Each age-class comprised one-third of the needle area of the canopy from October 9. In winter as well as during spring, we observed an apparent increase in chlorophyll concentration (from April 10 to May 22). Just before bud burst in 1997, the concentration of chlorophyll a + b reached a maximum of 580 mg m^{-2} . During the summer, chlorophyll concentration remained stable. At the end of the summer, the 1995 needles fell after they had lost most of their chlorophyll (September 11: 624 mg m^{-2} ; September 24: 389 mg m^{-2} ; October 9: 29 mg m^{-2}). The seasonal curve showed a steep decline in chlorophyll concentration between September 11 and October 9. During

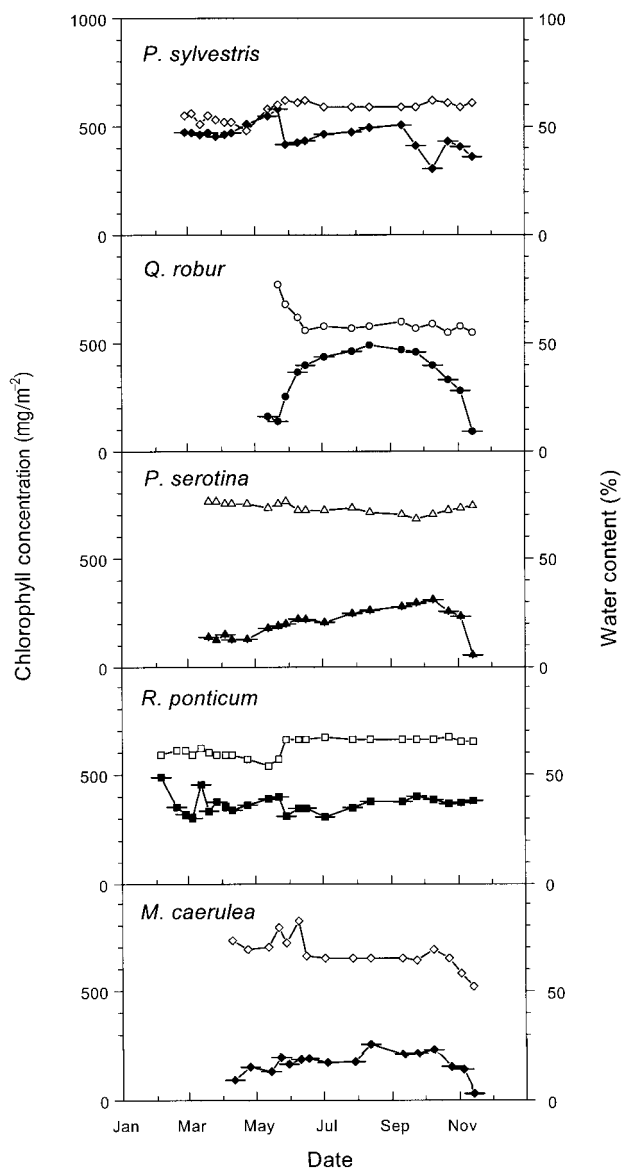


Figure 1. Time courses of leaf chlorophyll (a + b) concentration (closed symbols) and water content (open symbols) during 1997 for the five main species (*P. sylvestris*, *Q. robur*, *P. serotina*, *R. ponticum* and *M. caerulea*) in "De Inslag" forest, Brasschaat, Belgium.

autumn, the chlorophyll concentrations of the 1996 and 1997 needles gradually decreased.

Quercus robur also showed a seasonal trend in chlorophyll concentration (Figure 1). After a rapid increase in spring (from May 22 to June 7), a maximum chlorophyll concentration of 491 mg m^{-2} was reached on August 13. A progressive decline started on October 9 and continued until leaf fall (after November 14).

In the understory, the chlorophyll concentration of *P. serotina* steadily increased (Figure 1) from bud burst on March 20 to the end of summer on October 9. The maximum concentration of chlorophyll was low compared to that of the overstory species (only 309 mg m^{-2}). We noted that the chlorophyll concentration reached a maximum in *P. serotina* leaves at the

Table 1. Chlorophyll concentration (mg m^{-2}) of two pairs of *P. sylvestris* needles calculated from the tip of the needle to the base (6th cm) for (A) 1995 needles measured on November 14, 1996; (B) 1996 needles measured on February 19, 1997; and (C) 1997 needles measured on August 13, 1997.

Needles/Date	Tip	1st cm	2nd cm	3rd cm	4th cm	5th cm	Base
A	566	418	366	356	320	279	219
B	423	377	432	265	244	191	–
C	585	376	349	315	280	245	191

same time that it reached a minimum in *P. sylvestris* needles (October 9).

Rhododendron ponticum leaves showed an almost constant pattern of chlorophyll development (Figure 1), except in the winter before the sampling protocol was standardized (this may explain some of the variations in chlorophyll concentration; e.g., February 5 and March 13). Chlorophyll concentration increased until May 22. The development of new leaves was associated with a decrease in chlorophyll concentration and changes in water content occurred (Figure 1). Subsequently, the chlorophyll concentration remained stable throughout the summer, with a maximum chlorophyll concentration of 401 mg m^{-2} on September 24. The grass, *M. caerulea*, had a low chlorophyll concentration, with a maximum of 255 mg m^{-2} (August 13).

The temporal variation in water content for the five main species during 1997 is shown in Figure 1. In spring, when bud burst of the evergreen species occurred, the water content increased consistently (from 50 to 60% for *P. sylvestris* and from 55 to 65% for *R. ponticum*). Later, the water content remained stable. In young leaves of *Q. robur*, water content decreased from 80 to 50% during the spring. The water content then remained stable until leaf fall. Leaves of *P. serotina* showed decreasing water content during spring and summer (from 75 to 70%) but water content increased during the autumn before the leaves fell. For *P. serotina*, the curve of water content was the inverse of the chlorophyll concentration curve. For *M. caerulea*, water content was stable during the summer and decreased in autumn concomitantly with chlorophyll concentration.

Figure 2 shows the development of L for the five species monitored during 1997. The value of L varied during the year for all species, including the evergreen species.

In *P. sylvestris*, a storm at the end of April caused L to decrease as a result of damage attributable to the falling of live branches, cones and needles. During summer, L increased with new needle development. In September, the decrease in L coincided with the 1995 needle fall. The generally low values of L for *P. sylvestris* were related to the open canopy structure, with clumping of foliage and large gaps between crowns.

Quercus robur showed development of L typical for deciduous trees with a maximum (2.5) in July–August. The low L for *Q. robur* is characteristic of the Brasschaat forest where the trees appeared weak and were infested by caterpillars and mildew.

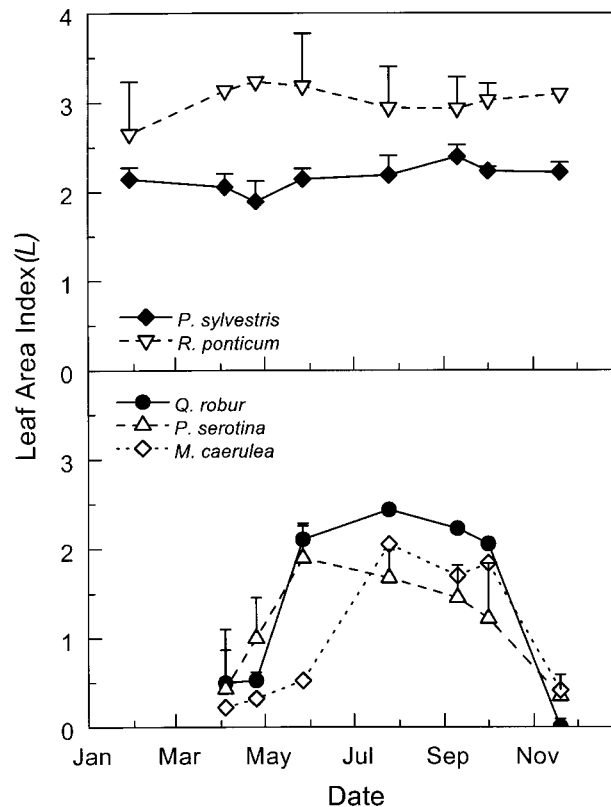


Figure 2. Temporal progression of leaf area index (L) of the five main species in "De Inslag" forest during 1997. A distinction has been made between overstory species (solid symbols) and understory species (open symbols).

Bud burst of the understory species *P. serotina* occurred earlier than bud burst in *Q. robur* but the trees reached a similar value of L during May (1.5). Thereafter, L of *P. serotina* decreased steadily until October (1.0) before the onset of rapid leaf drop in autumn. *Rhododendron ponticum* had a distinct phenological cycle with only small changes in L during the year associated with new growth in spring, reaching a maximum L in April. *Molinia caerulea* displayed a different pattern with slower canopy development during May and June followed by rapid growth to reach maximum L in July, when the foliage and seedheads were fully developed.

Modeling results

PROSPECT was run for every period of field measurements for each species. The 100 outputs (5 species \times 20 sets of measurements) were linearly interpolated to obtain seasonal progressions of leaf absorption, reflectance and transmittance spectra (400 to 2500 nm) (Figure 3).

Canopy reflectance was calculated for each species (assuming a monoculture) during the year with the SAIL model. The parameters included: (1) leaf area index (L); (2) hot spot effect parameter (defined as the ratio of mean leaf size to layer thickness); (3) soil reflectance; (4) sky diffuse radiation above the canopy; (5) zenith and azimuth solar angles; and (6) zenith and azimuth view angles. Data for these parameters were

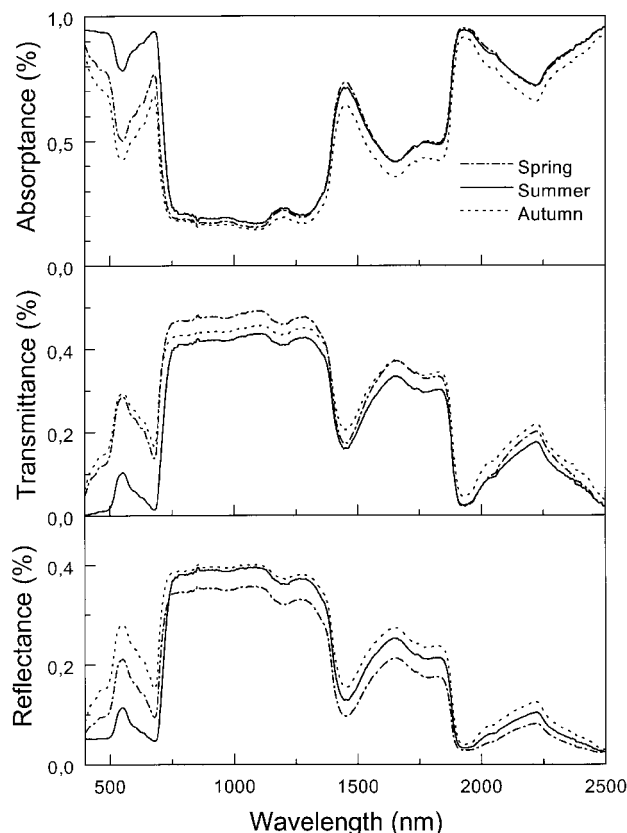


Figure 3. Absorbance, transmittance and reflectance simulated at the leaf scale by the PROSPECT model. Examples in spring, summer and autumn for *Q. robur* are shown.

linearly interpolated to correspond to the output of the PROSPECT model. The required SAIL model output is the seasonal progression of canopy reflectance spectra for each species (400 to 2500 nm; Figure 4).

The ratio of PAR absorbed to PAR transmitted by the canopy was taken as fAPAR. Absorbed and transmitted PAR were determined with the SAIL model by numerically integrating the absorbed and transmitted radiation (from 400 to 700 nm) by the canopy layer, taking into account the direct downward and diffuse downward fluxes of PAR and the upward fluxes of incoming and reflected PAR. To validate the scaling-up approach, we used lines of 25 quantum sensors (400–700 nm) mounted under the *P. sylvestris* canopy in the forest. To calculate fAPAR, we used total incident PAR radiation above the canopy (continuously measured at the top of the tower). By comparing the measured intercepted PAR with the simulated fAPAR in August and October 1997, we observed differences of 3 and 4% for *P. sylvestris* and 40% for *P. serotina* (Figure 5). Underestimation of L as input in the SAIL model may explain the high value for *P. serotina*. Nevertheless, we used this validation to scale up the different species to the 1 km² area. The canopy fAPAR of each species was then weighted by the species composition of each forest patch (de Pury and Ceulemans 1997) to determine fAPAR for a 1 km² area (Figure 6). The forest surface of 1 km² centered on the tower was

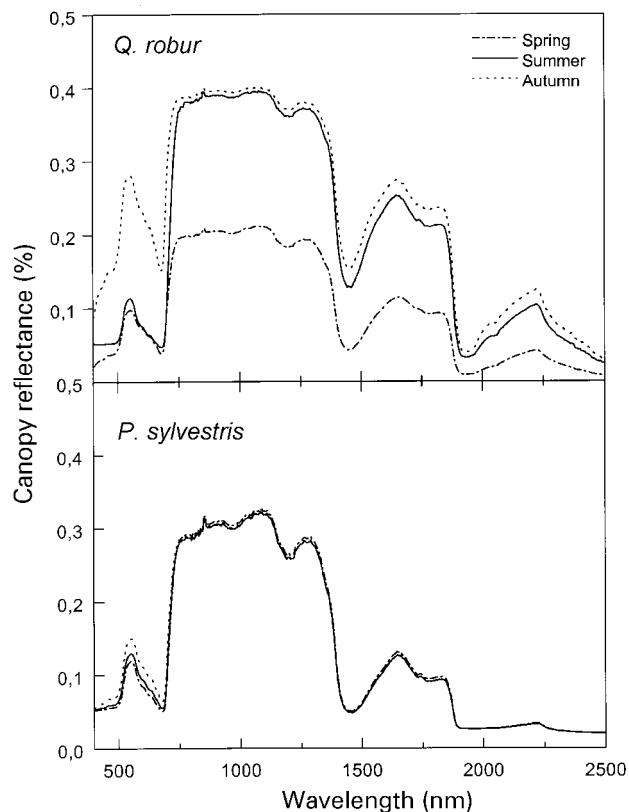


Figure 4. Reflectance values simulated at the canopy scale by the SAIL model. Examples in spring, summer and autumn for *Q. robur* and *P. sylvestris* are shown.

considered to comprise two layers (overstory and understory) making up 100%. The species composition of the patches in the 1 km² area was: *P. sylvestris* = 24%; *Q. robur* = 16%; *P. serotina* = 16%; *R. ponticum* = 4%; *M. caerulea* = 25% and bare soil = 15%. The fAPAR of the species was summed for 1997, taking into account the species' surface area. From this analysis, seasonal variation in fAPAR (at 1 km² scale) can be interpreted geographically. The main contribution to the development of fAPAR for the 1 km² area came from the deciduous

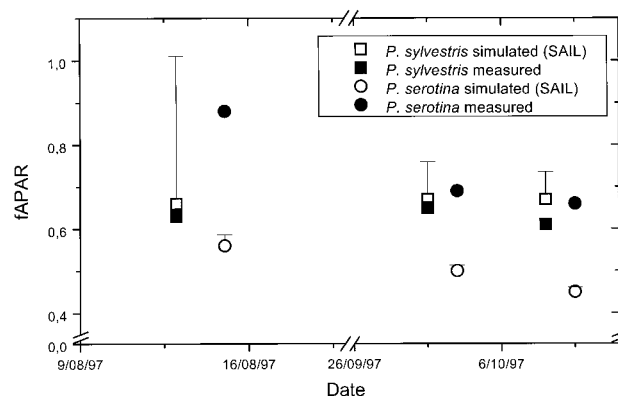


Figure 5. Comparison of fAPAR simulated by the PROSPECT + SAIL models and measured fAPAR under a *P. sylvestris* canopy.

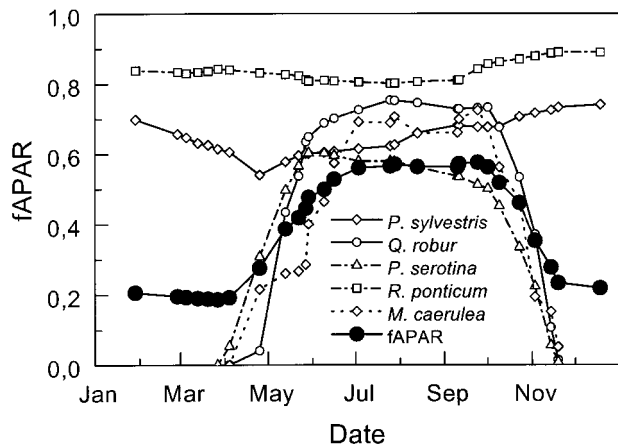


Figure 6. Temporal progression of fAPAR for the five main species (*P. sylvestris*, *Q. robur*, *P. serotina*, *R. ponticum* and *M. caerulea*) in “De Inslag” forest during 1997. Values were weighted by the species composition of the forest to determine fAPAR for a 1 km² forest (●).

species because of the strong contrast between winter and summer fAPAR. This result is of crucial importance because the “De Inslag” forest is commonly regarded as a uniform pine stand.

The understory plays an important role in the carbon budget of this 1 km² area because of the large understory summer fAPAR capacity (fAPAR values of 0.6 for *P. serotina*, 0.85 for *R. ponticum* and 0.7 for *M. caerulea*). Taking into account the species composition of the layers should greatly enhance carbon budget studies because of the importance of biodiversity and its impact on surface properties. With the information we obtained we intend to interpret a 1 km² remotely sensed signal. Ecosystem complexity is routinely observed by high-resolution temporal series of, for example, 1 km² NOAA-AVHRR data sets. It should be possible to determine which part of the Earth’s surface is driving a time series of reflectance observations measured by an observing satellite system. The linearity between species composition and remotely sensed measurements can now be investigated with this kind of surface description and the temporal development of the different species.

Conclusions

Monitoring the seasonal development of species in a mixed forest is a key step for several modeling approaches. Estimation of the carbon allocation of biomass in a stand is a challenge for description of the carbon cycle. In this paper, we have described the seasonal development of a mixed-stand (evergreen and deciduous), multilayer (overstory, understory and ground cover canopies) for a forested area. The temporal progression of estimated fAPAR will facilitate initiation of a new direction of research in connection with remote sensing and ecosystem modeling.

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References

- Ěermák, J., F. Riguzzi and R. Ceulemans. 1998. Scaling-up from individual tree to the stand level in Scots pine. *Ann. Sci. For.* 55:63–88.
- Chen, J. 1996. Optically based methods for measuring seasonal variation of leaf area index in boreal conifer stands. *Agric. For. Meteorol.* 80:135–163.
- Coops, N., R. Waring and J. Landsberg. 1998. Assessing forest productivity in Australia and New Zealand using a physiologically-based model driven with averaged monthly weather data and satellite-derived estimates of canopy photosynthetic capacity. *For. Ecol. Manag.* 104:113–127.
- Curran, P. 1989. Remote sensing of foliar chemistry. *Remote Sens. Environ.* 30:271–278.
- de Pury, D. and R. Ceulemans. 1997. Scaling-up carbon fluxes from leaves to stands in a patchy coniferous/deciduous forest. *In Impacts of Global Change on Tree Physiology and Forest Ecosystems*. Eds. G.M.J. Mohren, K. Kramer and S. Sabate. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 263–272.
- Flower-Ellis, J. and L. Olsson. 1993. Estimation of volume, total and projected area of Scots pine needles from their regression on length. *Stud. For. Suec.* 190:3–19.
- Fung, I. 1997. A greener north. *Nature* 386:659–660.
- Gond, V., F. Veroustraete and R. Ceulemans. 1997. Modeling strategy for a multi-layer mixed forest using remote-sensing data. *In Impacts of Global Change on Tree Physiology and Forest Ecosystems*. Eds. G.M.J. Mohren, K. Kramer and S. Sabate. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 279–286.
- Hunt, R., S. Piper, R. Nemani, C. Keeling, R. Otto and S. Running. 1996. Global net carbon exchange and intra-annual atmospheric CO₂ concentrations predicted by an ecosystem process model and three-dimensional atmospheric transport model. *Global Biogeochem. Cycles* 10:431–456.
- Jacquemoud, S. and F. Baret. 1990. PROSPECT: a model of leaf optical properties spectra. *Remote Sens. Environ.* 34:75–91.
- Jacquemoud, S., J. Verdebout, G. Schmuck, G. Andreoli and B. Hosgood. 1995. Investigation of leaf biochemistry by statistics. *Remote Sens. Environ.* 54:180–188.
- Jarvis, P. 1995. Scaling processes and problems. *Plant Cell Environ.* 18:1079–1089.
- Ludlow, M. 1982. Measurement of stomatal conductance and plant water status. *In Techniques in Bioproductivity and Photosynthesis*. Eds. J. Coombs and D.O. Hall. Pergamon Press Ltd., Oxford, England, pp 49–58.
- Matson, P., L. Johnson, C. Billow, J. Miller and R. Pu. 1994. Seasonal patterns and remote spectral estimation of canopy chemistry across the Oregon transect. *Ecol. Appl.* 4:280–298.
- Moran, R. 1982. Formulae for determination of chlorophyllous pigments extracted with *N,N*-dimethylformamide. *Plant Physiol.* 69:1376–1381.
- Myneni, R., C. Keeling, C. Tucker, G. Asrar and R. Nemani. 1997. Is spring coming earlier? *Nature* 386:698–702.

- Porra, R., W. Thompson and P. Kriedemann. 1989. Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls a and b extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. *Biochim. Biophys. Acta* 975:384–394.
- Prince, S. and S. Goward. 1995. Global primary production: a remote sensing approach. *J. Biogeogr.* 22:815–835.
- Stenberg, P., T. Kuuluvainen, S. Kellomäki, J. Grace, E. Jokela and H. Gholz. 1995. Crown structure, light interception and productivity of pine trees and stands. *Ecol. Bull.* 43:20–34.
- Verhoef, W. 1984. Light scattering by leaf layers with application to canopy reflectance modeling: the SAIL model. *Remote Sens. Environ.* 16:125–141.
- Waring, R., B. Law, M. Goulden, S. Bassow, R. McCreight, S. Wofsy and F. Bazzaz. 1995. Scaling gross ecosystem production at Harvard Forest with remote sensing: a comparison of estimates from a constrained quantum-use efficiency model and eddy correlation. *Plant Cell Environ.* 18:1201–1213.

