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# Seasonal patterns of foliar reflectance in relation to photosynthetic capacity and color index in two co-occurring tree species, *Quercus rubra* and *Betula papyrifera*

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ABSTRACT

Although foliar reflectance in the visible wavelengths is largely understood, species-specific relations between leaf spectral properties, pigment content and carbon exchange, and interdependence of these fundamental drivers that ultimately produce large-scale signals complicate understanding of and upscaling in remote sensing applications. We recorded seasonal patterns in foliar reflectance in relation to leaf photosynthetic, biochemical, structural and optical properties in two co-occurring tree species, red oak (*Quercus rubra*) and paper birch (*Betula papyrifera*). Over the course of a growing season, we monitored the timing of phenological events, i.e. bud break, near-complete leaf expansion and leaf fall, on mature trees. On a monthly basis, maximum rate of carboxylation ($V_{cmax}$) and maximum rate of electron transport ($J_{max}$) were estimated from leaf-level gas exchange measurements in the upper crown for three individuals per species. Thereafter, visible and near infrared spectral properties, nitrogen content and specific leaf area were determined for sampled sunlit leaves. These data were compared with color indices extracted from digital images of sampled leaves throughout the growing season.

Studied leaf traits significantly varied between the two species and throughout the growing season. Paper birch was characterized by relatively early bud break and rapid leaf expansion. Hence, interactions between species and day of year could be partly contributed to contrasting spring phenology of paper birch and red oak. Spectral vegetation indices, Chlorophyll Normalized Difference Index (Chl NDI), Photochemical Reflectance Index (PRI) and in particular Red Edge Position (λRE), gave a good indication of leaf physiology over the course of the growing season, more specifically of photosynthesis and leaf nitrogen on an area basis ($N_{area}$). On the other hand, color indices performed rather poorly at tracking key leaf functional traits in this study. Overall, dark green leaves characterized by low Intensity (*I*, derived from HSI color space) displayed highest photosynthetic activity and highest values of spectral vegetation indices.



## 1. Introduction

Forest functioning is principally driven by the biochemical and structural properties of its foliage and seasonal variation therein (Pallardy and Kozlowski, 2008). For decades, remotely sensed information about essential canopy and leaf properties has been obtained through hyper-, multispectral and digital imaging at different scales in space and time (e.g. Gates et al., 1965; Asner, 1998; Kokaly et al., 2009; Garbulsky et al., 2011). Accurate leaf pigment content can be acquired from visible and near infrared regions of leaf reflectance spectra at wavelengths of 400–700 nm and 700–1400 nm, respectively, generated by hyperspectral imaging (e.g. Gamon and Surfus, 1999; Sims and Gamon, 2002; Gitelson et al., 2009). Leaf pigments are indispensable for photosynthesis as they (i) absorb photosynthetically active radiation, covering the visible portion of the light spectrum, and (ii) partly protect the photosynthetic apparatus against stress such as excess light and low temperatures. Although the basic features of foliar reflectance are widely understood, non-linear and species-specific relations between pigment content and leaf spectral properties hinder upscaling exercises required for large-scale remote sensing applications (Ollinger, 2010). Other leaf properties as nitrogen content, water content and leaf thickness are rather estimated from absorption and scattering in the near infrared region and beyond (>1000 nm; Curran, 1989; Smith et al., 2003; Kokaly et al., 2009).

Through digital imaging optical information can be captured, as "greenness", nitrogen status and therefore photosynthetic capacity of leaves (Woebbecke et al., 1995; Kawashima and Nakatani, 1998; Rorie et al., 2011) and canopies (Blinn et al., 1988; Richardson et al., 2007, 2009a,b). Light intensity quantized in the red, green and blue

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bands can be extracted from digital images. These values roughly cover the visible spectrum, but overlap for adjacent wavelengths and are not discrete reflectance values for a given wavelength. As a consequence, no specific physiological information, e.g. leaf chlorophyll or xanthophyll content, can be retrieved from digital images as opposed to reflectance spectra.

Several sources explain variability among key biochemical, physiological and anatomical leaf properties, and some of these differences can be tracked by concomitant changes in leaf spectral and optical properties. Cleland et al. (2007) defined phenology as the study of periodic events in life cycles of plants or animals, as influenced by the environment, especially temperature and precipitation changes driven by weather and climate. In foliage of deciduous trees, changes related to phenology and ontogeny, i.e. developmental stage or age, occur in chlorophyll content, leaf mass per unit area, nutrient content, leaf color, photosynthetic capacity, leaf tissue structure, etc. over the course of the growing season (Merzlyak and Gitelson, 1995; Grassi et al., 2005; Poorter et al., 2009). Insight into and precise estimation of these changes are very useful for modeling of carbon assimilation and budget of forests, particularly the seasonal trends of model parameters as $V_{cmax}$, $J_{max}$, $g_s$ and $R_d$ (Wilson et al., 2000, 2001; Kosugi et al., 2003; Ito et al., 2006; Mo et al., 2008; Reynolds et al., 2009).

Leaf properties also vary with species (Knapp and Carter, 1998; Wright et al., 2004). Wright et al. (2004) described a universal leaf economics spectrum along which leaf properties alter depending on the leaf growth strategy of plant species, i.e. quick or slow return on investment in nutrients or dry mass in leaves. In this study, two co-occurring temperate deciduous tree species were followed throughout the growing season, i.e. *Quercus rubra* L. (northern red oak) and *Betula papyrifera* Marsh. (paper or white birch). While red oak is a mid- to late-successional tree species in the Northeastern US, paper birch is a typical pioneer species recolonizing disturbed forest areas (Burns and Honkala, 1990). Birch trees are characterized by fast growth rates, high photosynthetic rates and indeterminate growth habit, i.e. continuous leaf production and shoot extension over several weeks or months at the start of the growing season (Bassow and Bazzaz, 1998; Wang and Kimmins, 2002). In contrast, mid- and late-successional trees are often believed to accommodate lower rates of growth and photosynthesis and/or (semi-)determinate growth habit, i.e. a single growth flush at the start of the growing season when a relatively short period of shoot elongation occurs (Marks, 1975; Bassow and Bazzaz, 1997, 1998). We speculate that along the leaf economics spectrum paper birch has a more 'quick-return' strategy in comparison with red oak.

To our knowledge, this is the first study to document leaf reflectance in relation to photosynthetic parameters, $V_{cmax}$ and $J_{max}$, and other functional properties measured on mature individuals of two co-occurring deciduous tree species over the course over a growing season. In this manuscript the following questions were answered: (i) do phenology and key functional leaf properties differ between two temperate deciduous tree species of different growth habit; (ii) how do leaf spectral, optical, photosynthetic and structural properties relate over the course of the growing season; (iii) do the spectral and optical signatures of leaves reflect their physiology throughout the growing season, and differences therein between the two studied species.

## 2. Materials and methods

### 2.1. Experimental site

The study was conducted at Harvard Forest, Petersham (MA; 42°32′N, 72°11′W, elevation 340 m a.s.l.) in a 70- to 80-year-old mixed deciduous stand along the Prospect Hill tract at the EMS annex walk-up tower. At this location, forest composition was dominated by *Q. rubra*, *Acer rubrum* L. (red maple), *Betula lenta* L. (black birch) and *Tsuga canadensis* L. (eastern hemlock). Two abundant, co-occurring species with a contrasting growth habit were chosen for this study, i.e. *Q. rubra* and *B. papyrifera*. Ten representative trees of each of the two species were selected. The trees chosen were typical of the stand size class, about 20 m tall. Three out of the ten individuals were located within 10 m of a small access road. This allowed for tree crown access for leaf-level measurements using an aerial lift. Meteorological data were obtained from the Fisher Meteorological Station located at an open field plot near the experiment (Boose, 2001). Air temperature was recorded at 15-min intervals at 2.2 m above the ground (Vaisala HMP45C, Campbell Scientific Inc., Logan, UT, USA). Precipitation was monitored with a Met One 385 heated rain gage (Campbell Scientific Inc., Logan, UT, USA; top of gage 1.6 m above the ground).

### 2.2. Ground observations

Phenology observations were made at 4–7 day intervals from April 5 through May 31 and from September 15 through October 30, using the method described by Richardson and O'Keefe (2009). Ground observations were done on all ten individuals per tree species. Three phenological stages were defined: (i) bud break as the date when recognizable leaves appeared from 50% of the buds on an individual; (ii) near-complete leaf development as the date when 50% of the leaves on an individual had reached 75% of their final, mature size and; (iii) leaf fall as the date when 50% of leaves on an individual had dropped (Richardson and O'Keefe, 2009). All dates were derived from linear interpolation between adjacent observations.

### 2.3. Crown measurements

#### 2.3.1. Phenology observations

From May until October, crown measurements were made on the three accessible mature individuals per species on a monthly basis. From up in the canopy, bud development and shoot growth, i.e. the duration and pattern of shoot growth phases were followed. To this end, a label was attached to five branches of each selected tree during the first field campaign. Leaves emerging between the label and the end of the branch were counted on a monthly basis.

#### 2.3.2. Gas exchange measurements

Each month, three to four leaves were selected in the upper, sunlit crown layer. Leaf gas exchange was measured with a portable open-path gas exchange measurement system (LI-6400, Li-COR, Lincoln, NE, USA). Photosynthetic response to intercellular $CO_2$ concentration ($A_n/C_i$) was measured under photosynthetically active radiation (PAR) of 1500 μmol m$^{-2}$ s$^{-1}$ which provides >95% saturation and block temperature was set to 25 °C. Response curves were generated by measuring leaf photosynthesis at ten $CO_2$ concentrations in the following order: 380 180 100 70 45 380 600 720 1000 and 2000 ppm. Once in a while, dark respiration ($R_d$) was measured at PAR = 0 μmol m$^{-2}$ s$^{-1}$. During the measurements relative humidity of the leaf chamber was kept between 50 and 80%. Light-saturated photosynthetic rate ($A_{sat}$) and stomatal conductance ($g_s$) at $CO_2$ concentration of 380 ppm and maximum assimilation rate ($A_{max}$) at 2000 ppm were derived from $A_n/C_i$ curves. Values for the photosynthetic parameters, maximum carboxylation rate ($V_{cmax}$) and maximum electron transport rate ($J_{max}$), were estimated from the $A_n/C_i$ curves by fitting the biochemical photosynthesis model of Farquhar et al. (1980) with the least squares method (cf. Appendix