



Stand age effects on Boreal forest physiology using a long time-series of satellite data



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ABSTRACT

Many ecosystem variables and processes show a relationship with stand age, including leaf area index (LAI), nutrient and water cycling, biomass production and photosynthesis. However, investigations into stand age dependency have typically focused on stand structure, and are limited by the availability of measurement sites. This study uses a measured chronosequence of 9 sites, ranging in age from 15 to 90 years, supported by a time-series of satellite-derived data to further validate temporal trends in LAI and leaf chlorophyll values. Managed *Pinus banksiana* stands in Northern Ontario, Canada were sampled for canopy structural parameters (LAI, stand density, crown radius, tree height) and leaf biochemistry (Chlorophyll a + b). Landsat 5 TM (30 m) data was obtained from 1989 to 2011 and chlorophyll- (Revised Transformed Chlorophyll absorption ratio index; RTCARI) and LAI- (Reduced Simple Ratio; RSR) sensitive spectral vegetation indices (VI) were calculated. Stand age showed strong relationships with tree height ($R^2 = 0.95$, $p < 0.001$), canopy radius ($R^2 = 0.68$; $p < 0.01$) and with stand density ($R^2 = 0.49$; $p < 0.01$). The measured LAI and leaf chlorophyll chronosequence showed an excellent correspondence with the VI-derived LAI and chlorophyll over time, modelled from the satellite archive. The temporal dependency of LAI and leaf chlorophyll with stand age was quantified through the fitting of a spherical model (chlorophyll = 44 years; LAI = 22 years), after which further increases in forest age did not increase leaf chlorophyll or LAI. Variation in the temporal lags indicates differences in the maturation period for leaf biochemistry and canopy physical structure, with LAI likely related to a reduction in stand density. The demonstrated stand age-dependency of leaf chlorophyll content is crucial for understanding stand age effects on photosynthetic processes and carbon assimilation, both for quantifying net primary production (NPP) within carbon budgets and for guiding forest management and harvesting strategies in light of a changing climate.

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1. Introduction

Forest age affects ecological attributes such as biodiversity, leaf area index (LAI), biomass production, NPP, and nutrient and water cycling, with aboveground NPP being found to reach a peak early in stand development and then gradually decline by mean reduction of 34% (Gower et al., 1996). Rapid tree growth in early development means that young forests have the potential to sequester a large amount of carbon (Houghton et al., 2009), relative to old growth forests, although individual tree carbon sequestration rates can increase with age (Stephenson et al., 2014). The dependency of ecological processes on tree age is particularly important in areas which are subject to frequent disturbance, for example through

fire, insects, extreme weather, land use change and harvesting (Schroeder et al., 2011; Wulder et al., 2010). Clearcut harvesting results in the removal of biomass, the loss of important habitat structures, such as coarse woody debris, and a decline in insect and animal communities (Niemelä, 1999). Monitoring the rate and successive development of forest re-establishment following harvest is therefore important for a number of ecological processes, including nutrient cycling, carbon storage potential and habitat structures (Schroeder et al., 2007). As forest disturbance often affects large land areas, it has been identified as a key driver of forest net carbon balance (Gough et al., 2007; Kurz et al., 2009; Schroeder et al., 2011). Although there has been considerable research into changes in forest structural composition (i.e. LAI, biomass, stand density), there has been little interest in leaf biochemistry, such as chlorophyll content. Leaf chlorophyll plays a central role in the conversion of solar radiation via photosynthesis into

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stored chemical energy (Gitelson et al., 2006). As chlorophyll concentration largely determines the amount of photosynthetically active solar radiation absorbed by the leaf, low concentrations of chlorophyll can limit photosynthetic potential and hence primary productivity (Ellsworth and Reich, 1993; Koike et al., 2004; Richardson et al., 2002). Forest NPP is closely related to forest age, with NPP increasing rapidly during early development stages, reaching a maximum towards middle age and gradually declining in later stages (Chen et al., 2002b; He et al., 2012; Wang et al., 2011). Franklin et al. (2002) define the first 20 years following disturbance as cohort establishment followed by canopy closure, with biomass accumulation occurring from around 30–90 years of age, depending on the species. A maturation stage begins as biomass accumulation levels off by reaching an asymptote around 70–100 years in Douglas-fir (Franklin et al., 2002).

Substituting space-for-time is widely used in ecological modelling to infer past or future trajectories from measured spatial patterns (Blois et al., 2013), based on assumptions that sites are not affected by underlying spatial controls and instead represent temporal dynamics of the parameter of interest. Here we use a space-for-time substitution approach to develop a chronosequence to investigate variations in stand structure and leaf chlorophyll content over a long-term time frame. To support the information derived from multiple spatial sites, satellite data was used to re-sample each site at regular time intervals to assess the changes at a per site level (Foster and Tilman, 2000). The longevity of Landsat missions offers an unparalleled resource of high quality satellite images, at fine spatial resolution (30 m) and regular revisit intervals (circa 16 days). Previous studies have used Landsat time series to derive a wide range of forest applications, including resource management (Wilson and Sader, 2002) and pest mortality (Goodwin et al., 2010). Schroeder et al. (2007) used a multi-temporal image series to create “re-growth trajectories” comprised of a series of mathematical or statistical models used to characterize vegetation response to disturbance. In this study we examined nine Jack Pine (*Pinus banksiana* Lamb.) stands of varying ages (from 15 to 90 years old) within a managed forestry environment to assess the effect that stand age has on physical and biochemical parameters, at the canopy and leaf level. The objectives of this work are to: (1) examine the differences in stand structure across a range of stand ages; (2) investigate if LAI and leaf chlorophyll content varies with stand age; (3) develop a chronosequence from satellite time-series data to monitor changes at a site level.

2. Methods

2.1. Study sites

Nine jack pine (*P. banksiana* Lamb.) (JP) stands located southeast of Chappleau, Ontario (47°36'17"N to 47°33'40"N, and 83°08'23"W to 82°43'04"W) were sampled. Stand ages ranged from approximately 15- to 90-years-old (Fig. 1) and all stands were greater than

100 ha in area. The sites are underlain by well-drained silt loam soils over deep gravelly sand, with mean annual temperatures of 4.6 °C and annual precipitation of 871 mm (Zhu et al., 2004). Understory species included dense moss, upland willow (*Salix humilis*), blueberries (*Vaccinium* spp.) and grasses.

2.2. Ground measurements

Leaf chlorophyll content ($\mu\text{g}/\text{cm}^2$) and a range of structural parameters were measured at each field sampling site from the 16th–19th July, 2012. Leaves and shoots were sampled from the upper sunlit canopy using a shotgun, sealed in plastic bags and kept at a temperature below 0 °C for further analysis (Zhang et al., 2007). This process was performed on five representative trees within each stand, approximately 50–100 m apart and three branches from each sampled tree canopy, giving 15 samples per stand. Mature needles (i.e. not current year) were systematically sampled from the top of canopy branches, with one needle leaf taken from each year's growth and homogenised into one sample for laboratory leaf chlorophyll analysis. Foliar chlorophyll was extracted using spectranalysed grade *N,N*-dimethylformamide, and absorbance measured at 663.8 nm, 646.8 nm, and 480 nm using a Cary-1 spectrophotometer (Wellburn, 1994). The measured leaf chlorophyll values reported in this study were calculated as mean values from all leaf samples collected within each site. Total leaf chlorophyll (Chl a + b) content ($\mu\text{g}/\text{cm}^2$) was measured using the method reported by (Moorthy et al., 2008). Effective LAI (L_e) was measured using the LAI-2000 plant canopy analyzer (Li-Cor, Lincoln, NE, USA) (Chen et al., 1997). The element clumping index and leaf area index were measured using TRAC (Tracing Radiation and Architecture of Canopies) (Chen and Cihlar, 1995). Both the LAI2000 and TRAC measurements were collected across a 100 m transect at 10 m intervals within each stand. Additional stand structural parameters including tree height, canopy radius and tree density were also measured (Table 1).

2.3. Landsat 5 TM data acquisition and processing

Ten Landsat 5 TM scenes were acquired from 1989 through to 2011 (Landsat TM 5 suffered a mechanical failure in 2012) at 30 m spatial resolution. The scenes were selected to match as closely as possible the time frame of ground data collection (16–19th July, 2012), and are representative of the middle of the growing season (Table 2). The coarse temporal resolution of Landsat acquisition (every 16 days) and cloudy skies makes exact correspondence very difficult to achieve. As a consequence there are gaps in the annual sequence due to a lack of availability of cloud-free images.

Landsat 5 TM images were radiometrically and geometrically corrected and georeferenced to UTM map projection. The geometric accuracy of the images is usually between 30 and 50 m. The Landsat scenes were atmospherically corrected using cosine estimation of atmospheric transmittance (Chavez Jr., 1996). Whilst radiative

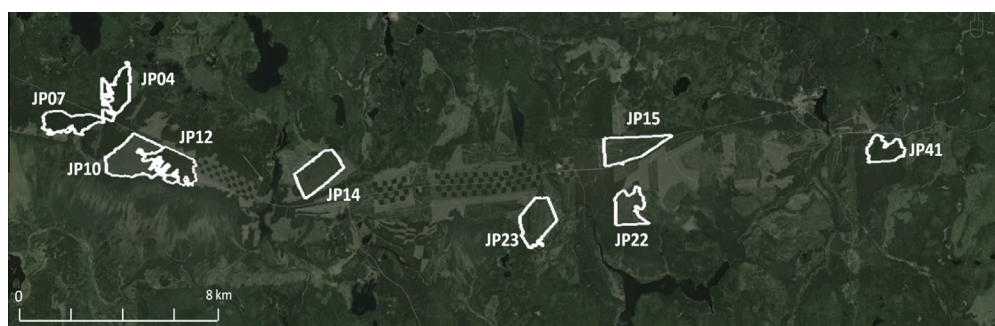


Fig. 1. Locations of the Jack Pine stands of varying ages. Source: Google earth.

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