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
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 modeling 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 resample 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 Chapleau, 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 (µg/cm²) 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 spectrally analysed 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 (µg/cm²) was measured using the method reported by (Moorthy et al., 2008). Effective LAI (Le) 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.
Table 1
Site characteristics and ground measurement data.

<table>
<thead>
<tr>
<th>Stand ID</th>
<th>Year established</th>
<th>Age (years)*</th>
<th>Height (m)</th>
<th>Crown radius (m)</th>
<th>Density (trees/ha)</th>
<th>LAI</th>
<th>Clumping index</th>
</tr>
</thead>
<tbody>
<tr>
<td>JP04</td>
<td>1975</td>
<td>37</td>
<td>14</td>
<td>1.78</td>
<td>800</td>
<td>3.59</td>
<td>0.86</td>
</tr>
<tr>
<td>JP07</td>
<td>1952</td>
<td>60</td>
<td>17</td>
<td>1.81</td>
<td>1400</td>
<td>3.19</td>
<td>0.93</td>
</tr>
<tr>
<td>JP10</td>
<td>1994</td>
<td>18</td>
<td>4</td>
<td>1.37</td>
<td>2370</td>
<td>1.37</td>
<td>0.88</td>
</tr>
<tr>
<td>JP12</td>
<td>1957</td>
<td>55</td>
<td>16</td>
<td>2.50</td>
<td>1870</td>
<td>2.84</td>
<td>0.86</td>
</tr>
<tr>
<td>JP14</td>
<td>1993</td>
<td>19</td>
<td>8</td>
<td>1.79</td>
<td>1500</td>
<td>2.66</td>
<td>0.89</td>
</tr>
<tr>
<td>JP15</td>
<td>1997</td>
<td>15</td>
<td>7</td>
<td>1.55</td>
<td>4730</td>
<td>4.13</td>
<td>0.89</td>
</tr>
<tr>
<td>JP22</td>
<td>1991</td>
<td>21</td>
<td>7</td>
<td>1.61</td>
<td>1930</td>
<td>2.59</td>
<td>0.94</td>
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<tr>
<td>JP23</td>
<td>1993</td>
<td>19</td>
<td>6</td>
<td>1.72</td>
<td>3030</td>
<td>4.32</td>
<td>0.90</td>
</tr>
<tr>
<td>JP41</td>
<td>1922</td>
<td>90</td>
<td>24</td>
<td>2.50</td>
<td>970</td>
<td>2.82</td>
<td>0.83</td>
</tr>
</tbody>
</table>

* Age is relative to ground measurement date in 2012.

Table 2
Landsat 5 TM image acquisition information.

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Path</td>
<td>21, 27</td>
<td>21, 27</td>
<td>21, 27</td>
<td>21, 27</td>
<td>21, 27</td>
<td>21, 27</td>
<td>21, 27</td>
<td>21, 27</td>
<td>21, 27</td>
<td>21, 27</td>
</tr>
<tr>
<td>SZA/VZA (°)</td>
<td>42, 0</td>
<td>43, 0</td>
<td>43, 0</td>
<td>38, 0</td>
<td>36, 0</td>
<td>47, 0</td>
<td>39, 0</td>
<td>31, 0</td>
<td>42, 0</td>
<td>38, 0</td>
</tr>
</tbody>
</table>

2.4. Spectral vegetation indices

This study uses empirical vegetation indices to derive leaf chlorophyll content and LAI from satellite-derived reflectance data. Within the visible part of the electromagnetic spectrum, chlorophyll is known to have strong absorption features in blue (∼490 nm) and red (∼680 nm) wavelengths, and maximum reflectance in green wavelengths (∼560 nm). Conversely, the NIR wavelengths are dominated by structural elements and canopy architecture. The Transformed Chlorophyll absorption ratio index (TCARI) was adapted from the Modified Chlorophyll Absorption Ratio Index due to a sensitivity to non-photosynthetic elements and effects, and revised (RTCARI) further by Wu et al. (2008) to increase the linearity of its relationship with chlorophyll content (Eq. (2)). In a recent study, Croft et al. (2014) found that RTCARI was the best performing vegetation index (out of 47 tested) for coniferous trees at the canopy level. RTCARI is calculated as follows:

\[
RTCARI = 3 \times \left[ (R_{750} - R_{705}) - 0.2 \times (R_{750} - R_{550}) \right] \times \frac{R_{750}}{R_{705}}
\]  

2.5. Quantifying temporal thresholds in stand age physiological relationships

Spherical models are often used in geostatistics to statistically describe the spatial scale of variation in a dataset (Croft et al., 2013a), where an asymptote denotes the maximum extent of spatially correlated variance. Here the spherical model (Eq. (3)) is fitted to the satellite time-series data in order to quantify the age at which an asymptote is reached (\(x = \text{range distance}\), therefore...
signifying that further increases in stand age do not result in subsequent changes in leaf chlorophyll or LAI. Eq. (5) gives details of the spherical model fitted to the time-series; where $y_{\text{mod}}$ is the modelled parameter (LAI or chlorophyll) for a given time lag ($h$), $c_T$ is the maximum $y$ parameter value and ($c_0$) the sum of $y$ intercept, with $c_1$ the being difference, if $h < a$. $c_T = c_0 + c_1$ where $\gamma_{\text{mod}}(h) = c_1$ if $h > a$ (Deutsch and Journel, 1998).

$$y_{\text{mod}}(h) = c_1 \left[ 1.5 \frac{h}{a} - 0.5 \left( \frac{h}{a} \right)^3 \right] + c_0$$ (5)

3. Results and discussion

3.1. Measured tree growth patterns across a chronosequence

Changes in tree and stand structure with increasing tree age have been noted by several authors (Long and Smith, 1992; Peichl and Arain, 2006; Schlerf et al., 2005), however the nature of these changes can depend on the specific ecological parameter measured, with not all tree variables changing linearly or in temporal uniformity with increasing age. The changes in tree height, crown radius and stand density across the measured chronosequence (15–90 years old) are shown in Fig. 3.

Fig. 3 shows a strong curvilinear log relationship ($R^2 = 0.95$) between tree height and stand age, whilst stand density appears to decrease rapidly up to approximately 40 years of age and then subsequently levels off. This result supports the conceptual model suggested by Franklin et al. (2002), where after the biomass accumulation growth stage reaches an asymptote, trees continue to increase in height, but stand density remains fairly stable. The crown radius measurements indicate a weaker linear relationship with stand age ($R^2 = 0.68$), which could be due a result of a lack of availability of older sites in the dataset reaching the maturation stage, which sees the trees attain maximum crown spread (Franklin et al., 2002).

3.2. Temporal changes in leaf chlorophyll content and LAI at each site from a Landsat time-series

Deriving leaf chlorophyll and LAI data from satellite-derived reflectance data has received considerable research focus, due to their key roles in plant photosynthesis and energy and water fluxes, and methods are well-developed (Chen et al., 2002a, 1997; Croft et al., 2013b; Zhang et al., 2008). Consequently, a long time series of Landsat data can be used to allow a temporal re-sampling at each site in the chronosequence to better validate any time-dependent dynamics in these variables (Foster and Tilman, 2000). The modelled changes in leaf chlorophyll and LAI from satellite data show increasing values for both parameters in the earlier stages of re-growth, followed by a levelling off period (Fig. 4). However, the leaf chlorophyll values increase more gradually with stand age, and begin to plateau at a later age (~40–50 years). In comparison, the LAI values reveal a sharp increase until an asymptote is reached at ~20 years, after which the values do not increase. This result is supported by the ground measurements of structural parameters in Fig. 3, which show a levelling off of canopy radius and stand density values after approximately 20 years. Crown closure of well-stocked JP stands usually occurs by about 20 years, which is likely is the main driver for the LAI...
peak value (Vose et al., 1994). Crown closure in jack pine has been shown to be the dominant factor influencing the spectral response in Landsat TM images (Franklin et al., 2002). Whilst the results in Fig. 4 show strong trends with age, there is some scatter in the modelled values within each site by year, which could be due to error as a result of atmospheric scattering or BRDF effects, or due to changes at site level. Chlorophyll content is known to vary according to plant stress (Carter and Knapp, 2001), for example and LAI variations may occur due to thinning and other management actions, or from extreme weather events.

3.3. Quantifying temporal differences in chlorophyll content and LAI

In order to quantify the temporal relationship between leaf chlorophyll and LAI, spherical models were fitted to the data to extract the stand age where an asymptote is reached for each variable (Fig. 5). Additionally, the measured leaf chlorophyll values from ground sampling in 2012 are shown for comparison alongside the modelled chlorophyll estimates from the Landsat time-series.

The measured chlorophyll values show a good fit within the modelled chlorophyll chronosequence, indicating that the use of the Landsat archive has produced reliable results. The additional data points derived from modelled Landsat data supports the trend shown by the measured data. The LAI measured data broadly support the modelled LAI values, particularly in the early- and mid-stand ages. There is some discrepancy in the older stands, particularly JP41 (90 years old), where the measured data are lower than the modelled satellite estimates. This could have been due to measurement error in ground sampling or overestimations arising due to incomplete crown cover and a well-developed understory, including smaller trees. The fitted spherical models quantitatively demonstrate the temporal differences in the development of stand physical and biochemical variables. Leaf chlorophyll has a range value of 44 years, compared to LAI which is 22 years. The levelling off of LAI values may be due to crown closure and the reduction in stand density, shown in Fig. 3c, which also occurs around 20 years. The stabilisation of chlorophyll values at mid growth stages (44 years) does not appear to be related to forest structural changes, and may be related to nitrogen availability, which has been found to decline with age as it becomes immobilized in woody biomass (Murty and McMurtrie, 2000). However, other studies have found no evidence of decreases in nitrogen availability, and this may be ecosystem or site specific, depending nitrogen uptake from soil nitrogen pools (Drake et al., 2010; Johnson, 2006; Smithwick et al., 2009).

3.4. Changes in leaf chlorophyll and LAI values from 1989 to 2010

The positive and negative changes in leaf chlorophyll and LAI between 2010 and 2001 are mapped in Fig. 6. The images of 1989 and 2010 were used because they represent earliest date after all plantations within this study have been established (1997; PJ15) and latest date with all sites cloud-free. The largest changes in both LAI and chlorophyll are for managed stands, that have either been harvested since 2001 (large negative change) or have undergone re-growth since 2001 (large positive change). For chlorophyll this typically represents changes of around 20–30 µg/cm², which corresponds to the results in Fig. 4. Any extreme values of chlorophyll and LAI outside the measured range of values contain a degree of uncertainty, as empirical relationships between the vegetation index and stand property are only inferred through the regression line, and not mathematically demonstrated.
Over the sampled time period, increases in LAI at re-growth sites are typically around LAI = 2–3, whereas for any harvested stands, the drop is around LAI = 4. In the managed stands, the spatial and temporal variations in leaf chlorophyll content and LAI values typically agree. In the less obviously managed areas of forest, leaf chlorophyll appears to stay neutral or slightly increase across large areas of land. LAI also remained relatively consistent, with slightly larger areas showing small declines in LAI. These differences may be attributable to the point in the forest's growth stage, which is demonstrated in Fig. 5; where changes in LAI and leaf chlorophyll appear to occur at different rates and over different temporal ranges.

These findings have potentially far reaching implications for the monitoring of carbon assimilation and biomass accumulation in the managed P. banksiana plantations. As chlorophyll is the 'photosynthetic apparatus' of the plant (Peng et al., 2013), only the PAR absorbed by chlorophyll is used for photosynthesis (Zhang et al., 2009). As a result, studies have demonstrated that leaf chlorophyll content is well correlated with temporal changes in light use efficiency (Peng et al., 2011; Wu et al., 2009) and between canopy chlorophyll content and GPP (Gitelson et al., 2003, 2006; Peng et al., 2011). The stabilisation of chlorophyll content at a stand age of 44 years correlates with the temporal dependency of NPP to stand age, where NPP increases rapidly at the early development stage, reaches a maximum in middle ages and gradually declines in later ages. He et al. (2012) found that the stand-age-NPP curve peaked at approximately 35 years for Jack Pine. These results may inform management decisions for optimising harvest ages, in order to maximise productivity increases within a given timescale and reduce atmospheric CO2 levels by managing the age-class structure of forested landscapes (He et al., 2012).

4. Conclusion

Our research has shown that, along with the well-known changes in stand structure with tree age, leaf biochemistry also shows a high level of age dependency. The difference in chlorophyll content between young and old needles is well known, but these findings indicate that for mature needles, tree age also affects stand chlorophyll concentration. This has important implications for better understanding and mapping the changes in photosynthetic processes and NPP. Leaf chlorophyll content showed a strong temporal correlation with stand age, which was quantified through the fitting of a spherical model. This temporal dependence for chlorophyll was 44 years, after which no further increase in forest age resulted in an increase in leaf chlorophyll. Conversely, the temporal lag for LAI was much shorter, at 22 year old, demonstrating differences in the maturation period for leaf biochemistry and canopy physical structure. These results represent the first important stages of investigating age dependency in needle leaf chlorophyll content. Further work is needed to better understand how leaf chlorophyll responds to nitrogen availability, and other factors thought to limit NPP, such as stomatal conductance and hydraulic limitation.

References


